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The most primitive *Elasmotherium* (Perissodactyla, Rhinocerotidae) from the Late Miocene of northern China

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ABSTRACT

The origin of *Elasmotherium* has been a puzzle for many years. Herein, we report the earliest representative of *Elasmotherium*, based on a Late Miocene skull from Dingbian County in Shaanxi, northwestern China. The skull bears a unique mosaic of primitive and derived features different from all hitherto known elasmotheres, henceforth demarcated as holotype of *Elasmotherium primigenium* sp. nov. Dental characters of *E. primigenium* are more primitive than any other known species of *Elasmotherium*, e.g. relatively incipient enamel folding, fairly weak lingual groove on the base of the protocone, relatively weaker crista, small and closed posterior valley and straight ectoloph. *E. primigenium* is evidently more primitive than all the known species of *Elasmotherium*, yet appreciably more derived than *Sinotherium*, thereby marking an important transitional species between *Sinotherium* and further species of the genus *Elasmotherium*.

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Introduction

Elasmotheres are extinct rhinocerotids closely related to, but phylogenetically distinct from all living rhinos (Antoine 2002). The one-horned genus *Elasmotherium* had a massive frontal horn on its forehead, and coexisted with the early diaspora of *Homo sapiens* in northern Eurasia. The genus *Elasmotherium* was named by Fischer (1808) based on the materials discovered from Siberia, hence the type species *E. sibiricum*. Borissiak (1914) established another species, *E. caucasicum*, from the southern bank of Azov, Russia. In China, Teilhard de Chardin and Piveteau (1930) and Teilhard de Chardin and Leroy (1942) reported, from the Nihewan Basin, a fragmentary tooth and several limb bones, as *Elasmotherium* sp., but did not describe or discuss these findings in detail. Chow (1958) described two new species, *E. inexpectanum* and *E. peii*, based on some teeth from Shanxi. Antoine (2002, 2003) proposed a merger of *Elasmotherium* sp. from Nihewan, as well as *E. inexpectanum* and *E. peii* from Shanxi into *E. caucasicum*. Shvyreva (2004) established the species *E. chaprovicum* from Liventsovka, Russia, and considered that it was the earliest and most primitive species of the genus *Elasmotherium*. Petrova (2011) considered *E. chaprovicum* and *E. peii* to be junior synonyms of *E. caucasicum*. Tong et al. (2014) argued more recently that *E. peii* is a valid species, and referred all the early Pleistocene elasmothere fossils from China into *E. peii*.

At present, three species of *Elasmotherium* are generally considered as valid, *E. sibiricum* (Fischer 1809), *E. caucasicum* (Borissiak 1914) and *E. peii* (Chow 1958). The geographical distribution of *Elasmotherium* includes Russia, Azerbaijan, Uzbekistan, Mongolia and China, and the stratigraphical distribution is from Early to Late Pleistocene (Fischer 1808, 1809; Borissiak 1914; Teilhard; de Chardin and Piveteau 1930; Chow 1958; Beljaeva 1958; Antoine 2002) (Figure 1). Tong et al. (2014) reviewed the stratigraphic distribution of the genus *Elasmotherium* (*E. peii*

2.2–1.1 Ma BP, *E. caucasicum* 1.1–0.8 Ma BP, *E. sibiricum* 0.8–0.4 Ma BP).

The earliest elasmothere rhinos is *Bugtirhinus praecursor*, which first appeared in South Asia in the Early Miocene (Antoine and Welcomme 2000). In the Middle Miocene faunas, elasmotheres diversified and apparently became a more significant component of the large herbivore guild (Zhai 1978; Yan 1979; Guan 1988, 1993; Cerdeño 1996; Antoine 2003; Deng 2003; Deng and Wang 2004). The Late Miocene elasmotheres are probably the least studied large terrestrial mammals that inhabited China. There are only three small regions in Northwest China that 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), the Linxia Basin in southeastern Gansu (Qiu and Xie 1998; Deng 2001, 2005, 2007), and Zhongning in central Ningxia (Chen 1977). After the Baodean Land Mammal Age (Late Miocene, broadly equivalent to the European Turolian: Qiu et al. 2013), elasmotheres became relatively rare in China, considering their scarcity in the well-sampled Chinese Pliocene vertebrate fossil record. However, elasmotheres apparently underwent a Chinese ‘renaissance’ in the Early Pleistocene, indicated by findings from the Nihewan Basin in Hebei (Teilhard de Chardin and Piveteau 1930; Deng and Zheng 2005).

The origin of *Elasmotherium* has been a puzzle for many years. Ringström (1924) established the prodigious Miocene elasmothere species, *Sinotherium lagrelii*, based on cranial and mandibular fragments and isolated teeth from Upper Miocene deposits in Baode County (Andersson Loc. 30), Shanxi Province, China. Bayshashov (1986) established another species, *Sinotherium zaisanensis*, based on specimens found in Kazakhstan. *Sinotherium* is the closest genus to *Elasmotherium* in terms of dental morphology, so the former has been considered to be ancestral to the latter (Prothero D R, Guérin

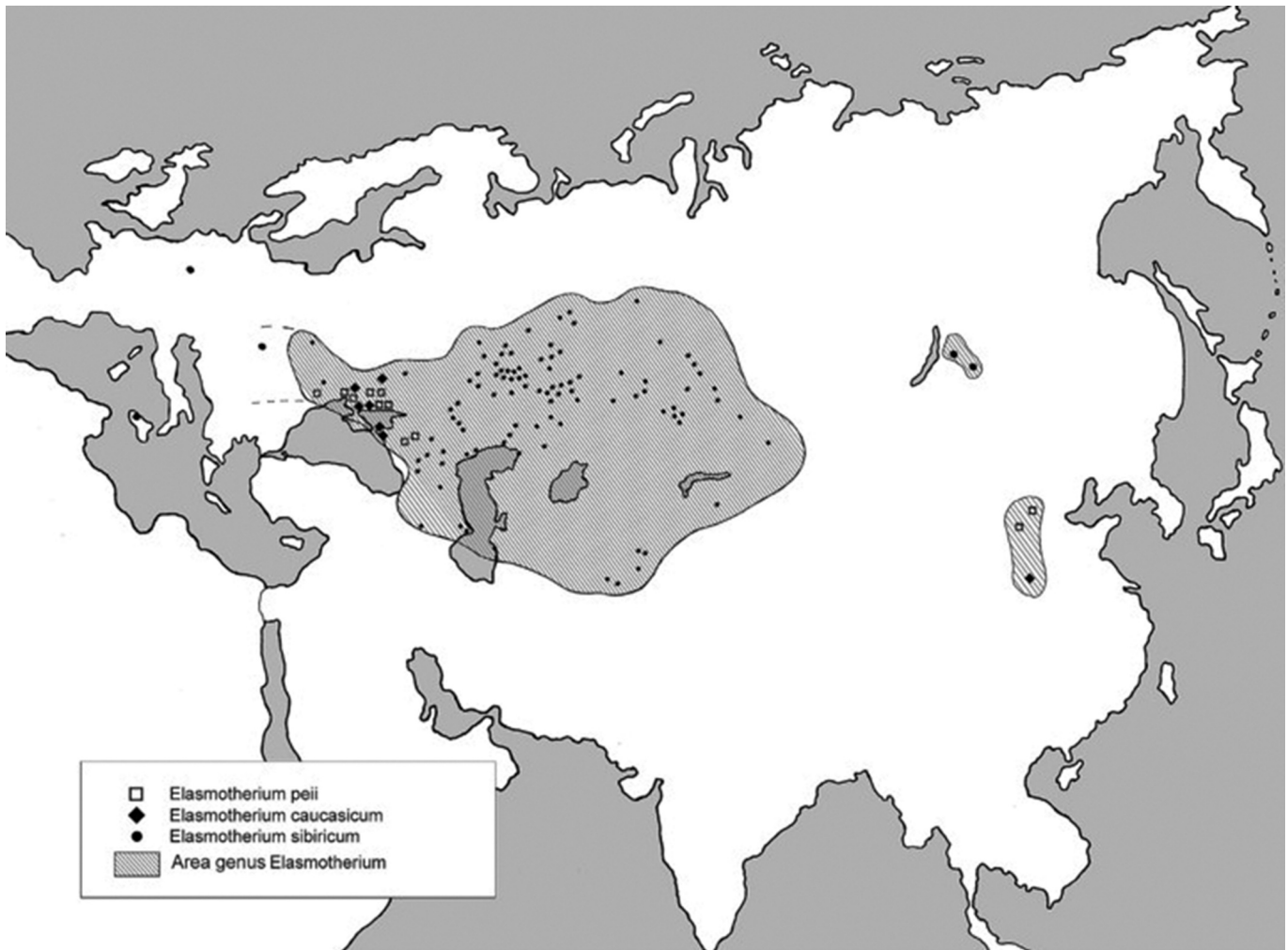


Figure 1. Paleozoogeography of giant elasmotheres, modified from Shvyreva (2015).

C, Manning E 1989; Antoine 2003). Deng et al. (2013) described a partial skull (IVPP V 18539) found in the Huaigou locality within the Linxia Basin, Gansu. Crucially, IVPP V 18539 demonstrates that *Sinotherium lagrelii* had a distinctive frontal structure that elucidates a morphologically intermediate stage in the nasal-to-frontal horn transition of elasmotheres. Therefore, *Sinotherium* merits consideration as an important transitional taxon between derived and primitive elasmotheres (Deng et al. 2013).

However, a recently discovered skull (IVPP V 24051) from Dingbian, Shaanxi complicates our understanding of how *Elasmotherium* originated. The morphology and geological context of IVPP V 24051 imposes new constraints upon our understanding of when and how *Elasmotherium* originated, thereby improving our overall knowledge of the tribe Elasmotheriini.

IVPP V 24051 is a skull belonging to an aged individual, housed in the Institute of Vertebrate Palaeontology and Palaeoanthropology (IVPP), Chinese Academy of Sciences, Beijing. General osteological terms here follow Sisson (1953), and odontological notations are adopted by Qiu and Wang (2007). The specimen was measured according to the procedures described in Guérin (1980). A phylogenetic analysis is carried out by adapting the craniodental character matrices of Antoine (2002) and Deng (2008) in order to assess the phylogenetic position of the new specimen among rhinocerotids.

Systematic palaeontology

Order Perissodactyla Owen, 1848 Family Rhinocerotidae Owen, 1845 Subfamily Rhinocerotinae Dollo, 1885 Tribe Elasmotheriini Dollo, 1885 Genus *Elasmotherium* (Fischer 1808)

Elasmotherium primigenium sp. nov.

Etymology

The specific name derives from ‘primigenius’, first in Latin. This new species is considered the most primitive species of *Elasmotherium*.

Holotype

IVPP V 24051, a well-preserved skull (senior individual) except for the anterior portion, lacking the premaxilla and the nasal bone, as well as part of the maxilla (Figure 2). Only the right M2 is well-preserved. The M3 and left M2 are badly broken.

Diagnosis

Large elasmothere, with huge frontal horn; prominent orbital rim, anterior margin situated at level of M3; parietal crests broadly separate; occipital surface vertical; teeth hypsodont, covered and

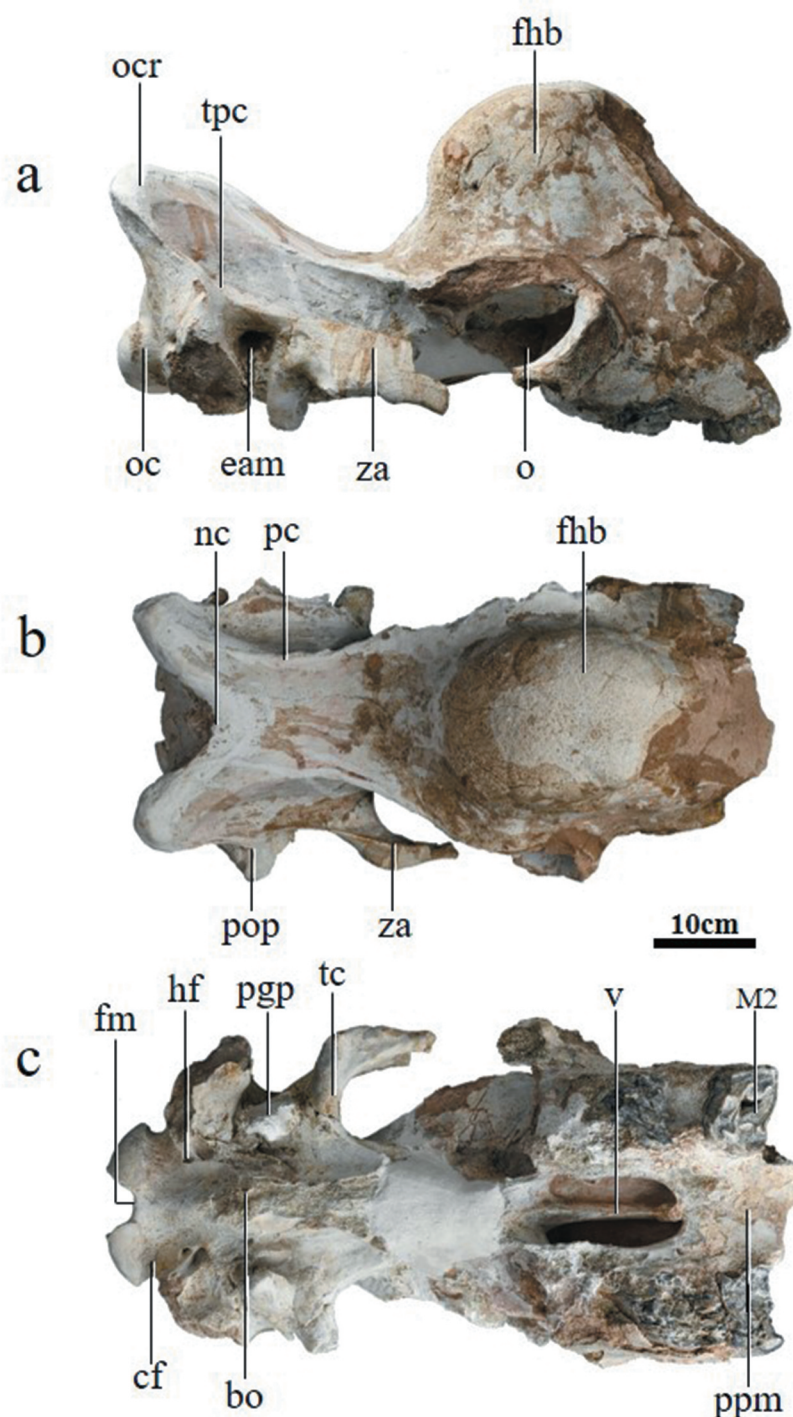


Figure 2. Skull (IVPP V 24051) of *Elasmotherium primigenium* sp. nov. from Dingbian. a lateral view; b dorsal view; c ventral view. cf, condyloid fossa; eam, external auditory meatus; fhb, frontal horn boss; fm, foramen magnum; hf, hypoglossal foramen; nc, nuchal crest; oc, occipital condyle; ocr, occipital crest; pc, parietal crest; ppg, postglenoid process; pop, paroccipital process; ppm, palatine process of maxilla; tc, temporal condyle; tpc, temporal crest; v, vomer; za, zygomatic arch.

filled by cement; enamel wrinkled; expanded protocone; strongly constricted protocone and hypocone; posterior valley closed; crista developed and bifurcate; crochet absent; paracone and metacone folds absent; ectoloph straight; labial and lingual cingula absent.

Locality and horizon

Yangjing Township, Dingbian County, Shaanxi Province, China; Late Miocene.

Description

IVPP V 24051 is well preserved except for the anterior portion, lacking the premaxilla and the nasal bone, as well as part of the maxilla (Figure 2). The frontoparietal part of the skull is strongly concave, forming a dorsal profile with a deep saddle. The skull roof has the widest dimension (335.08 mm) at the level of the lacrimal tubercle. The middle part of the frontal at the entire width is strongly swollen and highly elevated to form a very large, rough

Table 1. Measurements of the skull of *Elasmotherium primigenium* sp. nov. compared with other elasmotheres. (mm).

Measures	<i>E. primigenium</i> IVPP V 24,051	<i>E. sibiricum</i> NHM 12,429	<i>S. lagrelii</i> IVPP V 18,539	<i>I. morgani</i> HMV 0979, 1098	<i>P. linxiaense</i> HMV 1411	<i>N. euryrhinus</i> HMV 1449	<i>N. longirhinus</i> V 5163
5 Minimal width of braincase	142.02	~194	186	123–140	166	190	146
6 Distance between occipital crest and postorbital process	366.87			310–348	365	390	349.5
7 Distance between occipital crest and supraorbital process	435.72			355–380	420	425	381
8 Distance between occipital crest and lacrimal tubercle	483.12			390–453	~450	475	456
13 Distance between occipital condyle and M3	523.38			330–395	438	450	445
15 Width of occipital crest	271.43			190–212.4	183	224	205
16 Width of paramastoid process	351.27	432	410	251–309	306	379	268
17 Minimal width between parietal crests	132.7	181	161.5	80–91	113.6	121	108.4
18 Width between postorbital processes	293.01	408	390	211–244	228	270	222
19 Width between supraorbital processes	303.98	381	405	253–260	231.5	282	~248
20 Width between lacrimal tubercles	335.08	409	375	282–295	~207	400	~284
21 Maximal width between zygomatic arches	372.5			340–420		460	360
23 Height of occipital surface	162.24			137–138	193.5	154.5	212
26 Cranial height in front of M1	387.83			180–251	237.3	154	279
29 Width of palate in front of M1	121.02			68–93	104	140	79
31 Width of foramen magnum	67.15		78	44–57	88	71	71.7
32 Width between exterior edges of occipital condyle	178.85	203	239	133–183	186	215	181.4

Numbers in front of measuring method correspond to those of Guérin (1980:47, Table 1).

Table 2. Measurements of the M2 of *Elasmotherium primigenium* sp. nov. compared with other species of *Elasmotherium* and *Sinootherium* (mm).

M2	<i>E. primigenium</i>	<i>E. peii</i>	<i>E. sibiricum</i>	<i>E. caucasicum</i>	<i>S. lagrelii</i>
Length/Width	64.79/78.39	84/63	68/61	69–86/70–76	~70/71

surface characterised by significant convexity both transversely and sagittally, demarcating the horn boss. The lateral walls of the frontal bones descend strongly and are nearly vertical. The diameters of the frontal horn boss are 182.14 mm wide and 237.97 mm long, and the height is 156.62 mm. The anterior rim of orbit projects strongly so an anteriorly oriented broad surface forms in front of the orbit. The position of the orbit dorsal margin is low, and the anterior orbital margin is located at the level of the mid-M3. The whole upper rim of the orbit is thick, straight and rough. The anterior margin of the orbit is projected. The maxillary surface before the orbit is high, vertical, smooth and flat. The postorbital processes are visibly projected from the frontal. The zygoma is defective on both sides, with only the anterior and posterior parts of the left zygomatic arch well preserved. The anterior part of the zygomatic arch is located at the level of M3 and the posterior part of the zygomatic arch of the left side is low and the dorsal margin is flat (Figure 2(a)).

In dorsal view, the widest part of the cranium is at the level of lacrimal tubercle. The parietal crests are broadly separated, with a minimum width of 132.7 mm, and the surface between the postorbital crests is wide, flat, and smooth. The braincase is wide and high, with nearly vertical sidewalls. The occiput is so highly elevated that the parietal forms a very steep surface. The occipital or nuchal crest is forked. The temporal condyle is anteroposteriorly wide, smooth and low. The postglenoid processes are robust and lightly twisted, with a prismatic cross-section. The well-developed and laterally expanded posttymppanic process and the paroccipital process are fused to each other at their bases, which are not fused with the postglenoid process, and there is an open external pseudoauditory meatus between them. There is a distance of 94.56 mm between the anterior margin of the posttymppanic process and the

posterior margin of the paroccipital process. Part of both paroccipital processes is lost, but their remains still indicate a large transverse width (Figure 2(b)).

In ventral view, the hypoglossal foramen is large, situated in the lateral side of the middle of the condyloid fossa that is broad and shallow. The basal tuberosity is broad and rough, without a distinct sagittal ridge, situated in the front of the lacerate foramen. The occipital and ventral surface of the condyles is rounded, without a median ridge. The posterior half of the muscular process is very wide and high, the anterior half is slender. The tympanic bulla is small and low. The articular tubercle of the squamosal is smooth and low, with a straight transverse profile. The posterior margin of the pterygoid is nearly vertical. The vomer is thick and rounded. The flat palate has a very wide and U-shaped posterior margin, levelled with the posterior part of M2, and is fused with the vomer. The ethmoidal, optic and orbital foramina are deeply hidden (Figure 2(c)).

In posterior view, the outline of the occiput is trapezoid. The lateral part of the occipital surface is very rough. The occipital face is vertical. The lateral margin of the occipital crest is strongly inclined anteriorly and slightly divergent inferiorly, and it extends anteriorly to form the straight temporal crest. The foramen magnum is circular and very large. The upper margin of this foramen is at the same level as the upper border of the occipital condyle. The occipital condyles are anteroposteriorly short, with a length of about 48 mm, and very wide transversely, with a great distance between their lateral margins (Table 1). The occipital condyles are very large, indicating strongly reinforced attachment with the neck, in order to support the sheer weight of a dolichocephalic head with one huge horn (Figure 3).

Only the right M2 is well preserved (Figure 4) (Table 2). Both the M3 and left M2 are badly broken. These teeth are hypsodont, have wrinkled enamel, and are covered and filled with cement. The buccal and lingual cingula are absent. The protocone is strongly constricted and its lingual margin is rounded and convex. The crista

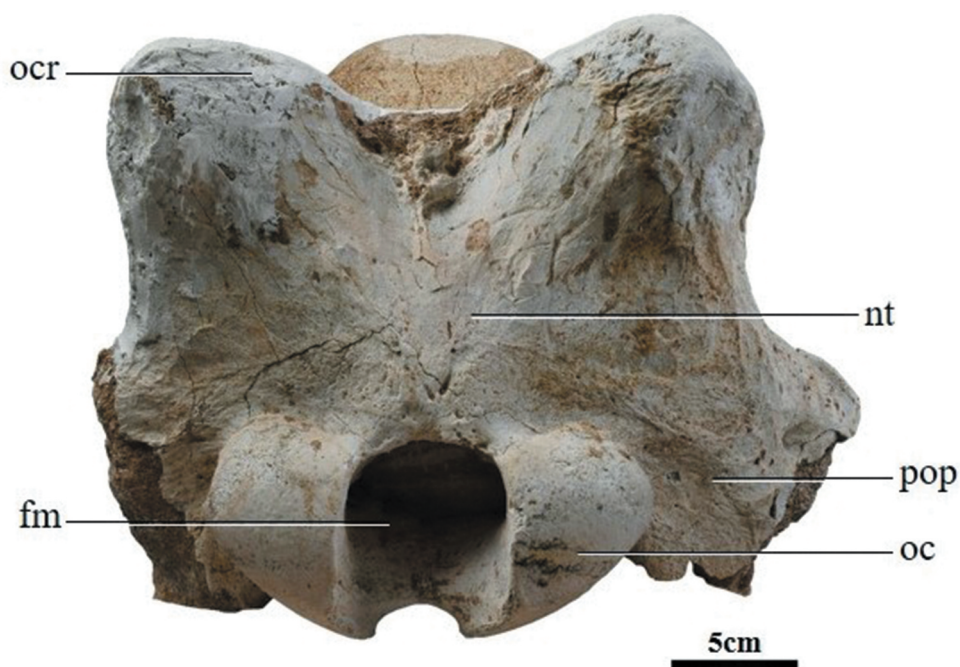


Figure 3. Occipital view of the skull (IVPP V 24051) of *Elasmotherium primigenium* sp. nov. from Dingbian. fm, foramen magnum; nt, nuchal tuberosity; oc, occipital condyle; ocr, occipital crest; pop, paroccipital process.

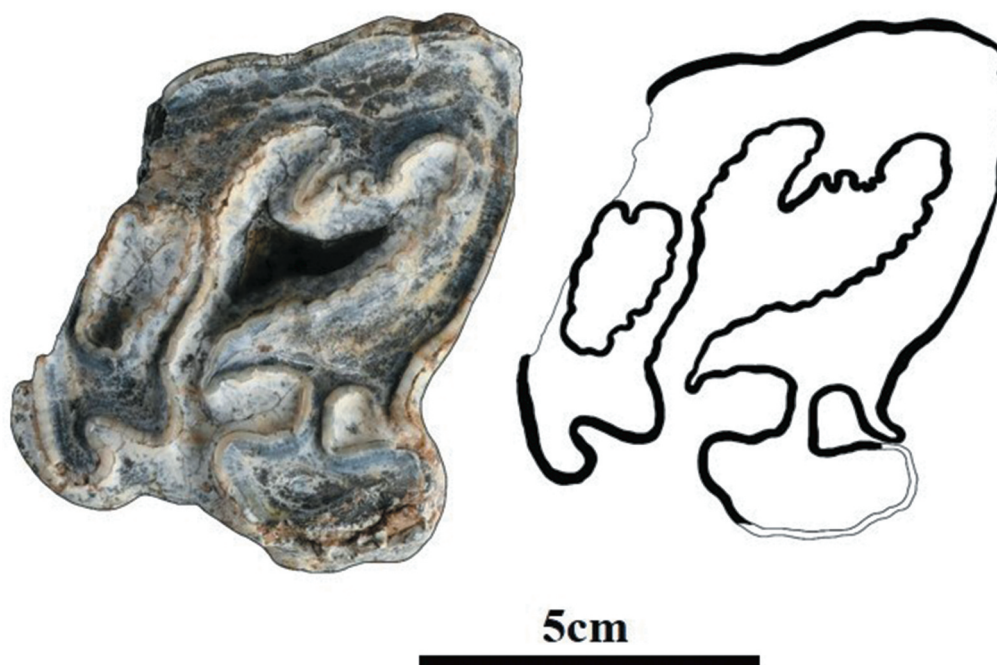


Figure 4. M2 (IVPP V 24051) of *Elasmotherium primigenium* sp. nov.

is present. The M2, badly worn, shows the protocone expanded, with strongly anterior and posterior constrictions, and a strong antecrochet is extended backward. It has a weak lingual groove on the base of the protocone. The hypocone has a strongly anterior constriction. The crista is well developed and bifurcated. The crochets are absent. The paracone rib is absent. Both the paracone and metacone folds are absent. The posterior part of the ectoloph is straight and the metaloph is continuous. The posterior valley is closed and small. The median valley is open. The posterior

cingulum is low and reduced. The M3 is triangular in occlusal view, resulting from fusion of the ectoloph and metaloph.

Comparison

Sinootherium has been previously considered to be ancestral to the genus *Elasmotherium* (Prothero D R, Guérin C, Manning E 1989; Antoine 2003). Considering Deng et al.'s (2013) thoroughly revised diagnosis of *Sinootherium lagrelii*, based on the partial skull IVPP

V 18539 from the Linxia Basin, IVPP V 24051 can be regarded as a critical transitional species between a *Sinotherium*-like archetype and the derived species of the genus *Elasmotherium*. IVPP V 24051 has a huge frontal horn and no nasofrontal horn, different from *Sinotherium lagrelii* that has an enormous nasofrontal horn and a very small frontal horn. The enamel folds of IVPP V 24051 are stronger compared with those of *Sinotherium lagrelii*. The crochet is absent in IVPP V 24051; yet this dental structure is visibly developed in *Sinotherium lagrelii*. The expanded protocone and strongly constricted hypocone of IVPP V 24051 present further salient dental differences from *Sinotherium lagrelii*. The M2 crista of IVPP V 24051 is pronounced and bifurcate, distinct from the slender crista of *Sinotherium lagrelii*. The ectoloph of IVPP V 24051 is straight, while the parastyle of *Sinotherium lagrelii* is prominent. The external pseudoauditory meatus of IVPP V 24051 is open, similar to other elasmotheres, but differs from the closed pseudoauditory meatus of *Sinotherium lagrelii*.

Seen from the top, the upper rims of the orbits of the new specimen are relatively projected, which are different from those of the nasal-horned elasmotheres, but similar to those of the frontal-horned elasmotheres. The strongly elevated and rough frontal area of the skull is in sharp contrast to the flat and smooth area in large nasal-horned elasmotheres, such as *Iranotherium* (Deng 2005), *Parelasmotherium* (Deng 2007) and *Ningxiatherium* (Chen 1977; Deng 2008), and also different from the nasofrontal area of *Sinotherium lagrelii* (Deng et al. 2013).

Indeed, many characters of IVPP V 24051 are shared with *Elasmotherium*. These features include 1) the massive, single frontal horn; 2) orbital margins prominent, anterior rim vertically aligned to the M3; 3) postorbital crests widely separate; 4) teeth greatly hypsodont covered and filled with cement, enamel wear figures bearing prominent folds. Compared with the hitherto established species of *Elasmotherium* (*E. sibiricum*, *E. caucasicum* and *E. peii*), IVPP V 24051 is logically referable to a new, primitive species.

The M2 of IVPP V 24051 shares many similarities with that of *E. sibiricum*, *E. caucasicum* and *E. peii*: hypsodont crown, prominent enamel folding, extensive development of cement, absence of buccal and lingual cingula, expanded protocone, strongly constricted protocone and hypocone, absence of crochet, developed and bifurcate crista, and open median valley. However, IVPP V 24051 bears some distinctly primitive characters compared to Pleistocene *Elasmotherium*. For instance, the enamel folds are quite incipient compared with those of *E. sibiricum*, *E. caucasicum* and *E. peii*, indicating a more primitive condition. The M2 of IVPP V 24051 has a fairly nascent lingual groove at the base of the protocone, compared with the markedly more pronounced lingual groove in M2 of *E. sibiricum*; the M2 crista is relatively weaker than that of *E. sibiricum*, *E. caucasicum* and *E. peii*, elucidating a more plesiomorphic evolutionary state; the ectoloph is straight, lacking the paracone rib, which is different from the waved ectoloph of *E. sibiricum*; the posterior valley is closed and smaller than that of *E. caucasicum* and *E. peii*.

All evidence considered, IVPP V 24051 is proposed as a new species (*Elasmotherium primigenium* sp. nov.) (Figure 5), with a unique mosaic of primitive and derived features different from all hitherto known elasmotheres. Dental characters of *Elasmotherium primigenium* are more primitive than any other known species of *Elasmotherium*. These features include relatively incipient enamel folding, fairly weak lingual groove on the base of the protocone, a relatively weaker crista, a straight ectoloph and a small, closed posterior valley.

Phylogenetic analysis

In order to assess the phylogenetic position of *E. primigenium* among rhinocerotids, we performed a phylogenetic analysis using

a modification of the matrices from Antoine (2002: Appendix 2) and Deng (2008), with addition of the new species (Appendix 1). The matrix analysed in the present study contains 282 characters with all characters unordered. The phylogenetic analysis was performed using traditional search under TNT (Version 1.1) (Goloboff et al. 2008), with all characters equally weighted. In order to guarantee the availability of data, we deleted some taxa in the data matrix of Antoine (2002: Appendix 2) and Deng (2008), such as *Ningxiatherium eurynrhinus* and *Hispanotherium tungurensis*. The current matrix consists of 31 taxa coded at the species level with four outgroups (*Tapirus terrestris*, *Ronzotherium filholi*, *Hyrachyus eximius*, and *Trigonias osborni*) and 27 in group taxa. The analysis gives two most parsimonious trees (Appendix 2). The tree length is 1071 steps, with its consistency index of 0.356 and a retention index of 0.546.

E. primigenium shares many synapomorphies with *E. sibiricum* and *E. caucasicum*, including the huge frontal horn, the prominent orbit, broadly separated parietal crests, hypsodont teeth covered and filled by cement, wrinkled enamel, expanded protocone, strongly constricted protocone and hypocone, developed and bifurcate crista, absent crochet, and absent labial and lingual cingula. All these features support the placement of *E. primigenium* as a member of the genus *Elasmotherium*, being the sister taxon to the most recent common ancestor of *E. sibiricum* and *E. caucasicum*. Meanwhile, *E. primigenium* is characterised by the slightly wrinkled enamel (in comparison with other *Elasmotherium* species), fairly weak lingual groove on the base of the protocone, the relatively weaker crista, the straight ectoloph, the closed and small posterior valley, which are different from other *Elasmotherium* species.

Our cladistic analysis supports the viewpoint of Antoine (2002) and Deng (2008) (Figure 6). The phylogenetic analysis shows that *Sinotherium lagrelii* is phylogenetically near the root of the frontal-horned elasmothere radiation (Deng et al. 2013), and that *Parelasmotherium* is the sister group of the *Sinotherium-Elasmotherium* clade (Deng 2008).

Discussion

Sinotherium and more primitive elasmotheres with large nasal horn shared enormous occipital condyles, with wide spacing between their lateral margins (Chen 1977; Deng 2005, 2008; Deng et al. 2013). Among fossil rhinocerotoids, this feature can also be found among the gigantic paraceratheres (Chiu 1973), among the largest land mammals ever to have evolved (Qiu and Wang 2007), a conceivable adaptation for supporting a heavy, dolichocephalic skull. In contrast, *E. primigenium* exhibits fairly small occipital condyles, which may be interpreted as evidence for a relatively brachycephalic skull. In order to retain a huge horn, elasmothere evolution pursued two solutions: first, the nasal horn shifts posteriorly to become frontal horn; second, the dolichocephalic skull becomes brachycephalic (Antoine 2002). Both changes occurred in the skull of *Elasmotherium*, so its occipital condyles became reduced in size, compared with *Sinotherium* (Antoine 2002).

Elasmotherium is rare in the Chinese record, only occurring at the Nihewan Basin (Teilhard de Chardin and Piveteau 1930) and Shanxi (Chow 1958). The holotype skull of *E. primigenium* is discovered in Dingbian County, Shaanxi. Other associated fossil findings from the area include *Amphimachairodus* sp. and *Hyaenictitherium* cf. *hyaenoides*, which are typical members of the Late Miocene fauna. Thereby, we provisionally place the Late Miocene constrain on the timing of *Elasmotherium*'s separation from a close common ancestor with *Sinotherium*.



Figure 5. The reconstruction of *Elasmotherium primigenium* sp. nov.

E. primigenium had a head held at low position, cheek teeth with extensive cement filling, well-developed secondary folds, and wrinkled enamel, well adapted to resist the abrasion of high-fibre plant matter. We thereby infer that *E. primigenium* was adapted for feeding on tough grasses. Deng et al. (2013) interpreted that *S. lagrelii* lived in an open environment in northern China, where aridity was commonplace. Deng and Zheng (2005) argued that *E. caucasicum* has hypsodont cheek teeth with thick cement and complicated folds, as well as slender limbs, indicating this species to be well adapted for grazing and cursorial locomotion in a steppic habitat. Phylogenetically, *S. lagrelii* is positioned near the root of the *Elasmotherium* radiation characterised by retention and

enlargement of the frontal horn. Under a phylogenetic bracketing principle, we hypothesise *E. primigenium* to be a grazer in the open savannah-grassland biome of Late Miocene northern China, dominated by *Hipparion* fauna.

In extant rhinos, male individuals are commonly more robust in their physique than females (Heller 1913; Laurie 1982; Hillman-Smith et al. 1986; Owen-Smith 1988; Rachlow and Berger 1997; Rachlow et al. 1998). Male specimens of the extant Asian rhinos typically have longer horns with a larger basal girth than females. The greater girth is correlated as a rule to the greater width of the horn area of the frontal bones and with its coarser tuberculation or granulation in the male. The frontal horn base of *E. primigenium*

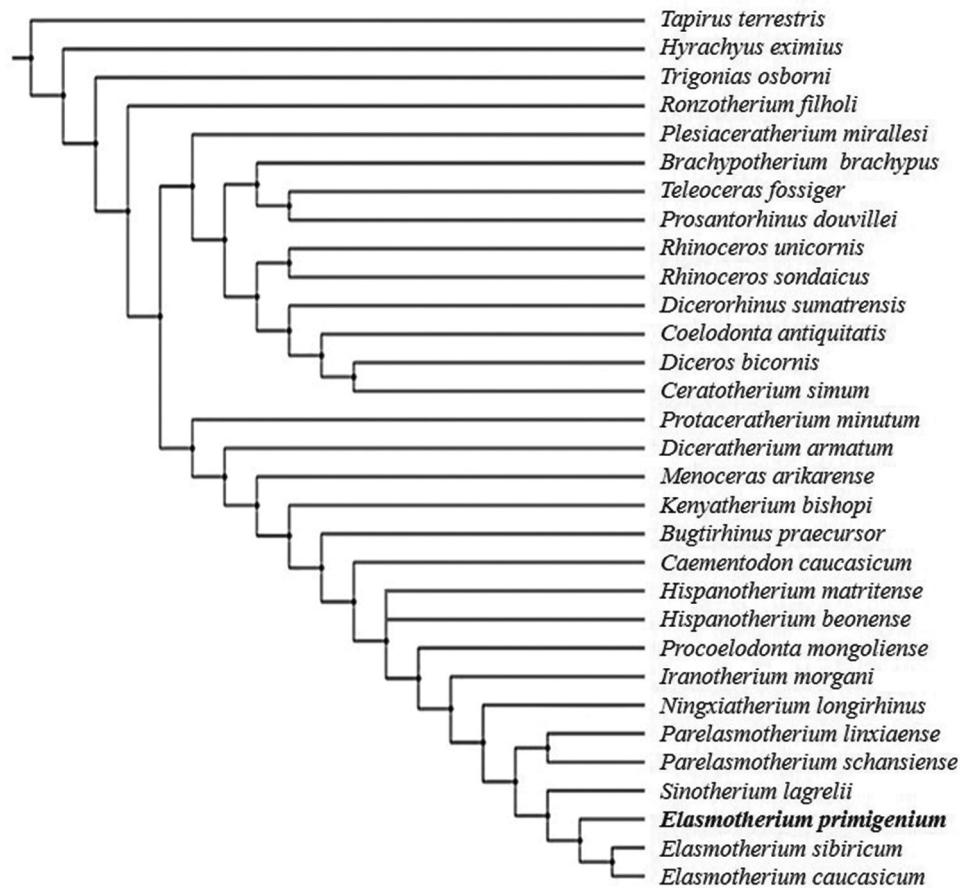


Figure 6. Strict consensus tree of two most parsimonious trees of elasmothere relationship.

dose not have much coarser tuberculation or granulation, indicating that IVPP V 24051 was likely an aged female individual.

Conclusions

A newly discovered elasmothere skull from Yangjing Town (Dingbian County, Shaanxi Province) described here does not confer in morphology to any hitherto described species within the tribe Elasmotheriini. The skull bears salient characters of *Elasmotherium*, such as its large size, retention of a single, massive frontal horn boss, prominent orbital rim, with anterior margin situated at level of M3, and the postorbital crests broadly separate. The teeth are hypsodont, extensively covered and filled with cement; the enamel is wrinkled; the protocone is expanded, strongly constricted alongside the hypocone; the posterior valley is closed; the crista is developed and bifurcate; the crochet is absent, as are the labial and lingual cingula.

Based on the aforementioned combination of features, we herein establish the new taxon *Elasmotherium primigenium* sp. nov. *E. primigenium* exhibits dental characters that are notably more primitive than any hitherto known species of *Elasmotherium*, such as the relatively incipient wrinkling of enamel, fairly weak lingual groove on the base of the protocone, the relatively weaker crista, the straight ectoloph, and the small, closed posterior valley. Yet on comparison with *Sinootherium lagrelii*, the apomorphies of *E. primigenium* are clear: the naso-frontal horn is absent, retaining only a single enormous frontal horn; the occlusal enamel figure is more wrinkled than that of

S. lagrelii; the crochet is absent; the protocone is expanded whilst the hypocone is strongly constricted; the crista in M2 is strongly developed and bifurcated; the ectoloph is straight; and the posterior valley is closed. The new specimen shows the mosaic evolution of craniodental morphology in the early evolution of *Elasmotherium*, with much of the generic cranial apomorphies pre-dating further specialisations of the dentition. We thereby conclude that *E. primigenium* sp. nov. is the earliest and most primitive species of *Elasmotherium*, a critical transitional species between a *Sinootherium*-like archetype and the derived Pleistocene species of *Elasmotherium*.

Contextually, we hypothesise *E. primigenium* to have been a committed grazer, inhabiting in the open savannah-grassland biome of northwestern China during the Late Miocene. Therefore, we postulate *Elasmotherium* to have originated in northwestern China during the Late Miocene, and separated from a common ancestor shared with *Sinootherium* since the Late Miocene.

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Appendix 1 Character codes of *Elasmotherium primigenium* sp. nov. (IVPP V 20451)

????? ?????? ?????? ?0012 100?? ?????? 111?? 21,100 02110 1210? ?????? ?????? ???21
 1213? ?????? ?????? ?????? ?????? ?????? ?????? ?????? ???33 03033 11-11 0010? ??110 -
 0102 1????? ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????? ?????? ??????
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Note: characters are after Antoine (2002).

Appendix 2 Two most parsimonious trees of elasmothere relationship

