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中国原大羚化石的再研究[1)]

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摘要：在研究新发现化石材料及对已有标本重新观察的基础上，讨论中国晚中新世至早上新世原大羚（？*Protoryx*）的系统分类位置。依据头骨、角心和牙齿等方面所具有的独特性状，建议把发现于中国北方曾归入？*Protoryx* 的种类从旧大陆同时代或时代稍早的 *Protoryx* Major，1891 中分出，另立2个新属：以？*Protoryx yushensis* Teilhard & Trassaert，1938 为属型种的华北羚（*Huabeitragus* gen. nov.）和以？*Protoryx shansiensis* Bohlin，1935 为属型种的粗壮羚（*Macrotragus* gen. nov.）。华北羚体型中等大小，头骨窄长，颅轴与面轴夹角近直角，弯曲发生在角前的额部，眶上孔小，分开远，脑颅部短窄，间顶骨长方形，基枕骨方形，没有中纵沟或中嵴，角心长而纤细，基部靠近，向上分散度大，基部横断面近三角形，具前棱。*Macrotragus* 头骨大而粗壮，其弯曲发生在角心基部之间的额面，弯曲度大于直角；角基之间的额中缝隆起呈脊；脸部宽；眶前窝浅；眶下孔后缘位于 P3 之上。眼眶向头骨两侧突出不明显，其前缘位于 M3 后缘之后；脑颅部短宽，呈筒状，背面稍凸；枕面高、呈半圆形；基枕部为长方形或梯形，具中纵沟和弱的中纵脊；卵圆孔大，面向侧方；角心大而粗壮，内外侧扁，无棱，基部紧靠，向上的分散度小，基部横切面为椭圆形。无角后窝。前臼齿列退化。这两个属之间的主要不同在于前者的个体较小；角心较细弱，向上分散度大（前面观），具前棱，基部横切面呈次三角形；头骨窄，其弯曲位置靠前，弯曲接近90°；脑颅部窄；枕面平，为低矮的长方形；基枕部呈方形，面平，无中纵沟和中纵脊，前、后节结不发育和卵圆孔相对小等。在系统位置上，它们可能属于山羊亚科（Caprinae）。

关键词：中国北部（山西和甘肃），晚中新世－早上新世，原大羚
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RESTUDY OF CHINESE FOSSIL BOVIDS REFERRED TO *PROTORYX* (BOVIDAE, ARTIODACTYLA)

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Abstract Based on newly discovered materials and old collections we review one important bovid group previously referred to ? *Protoryx*. Detailed comparison with other forms from western Eurasia suggests that all the *Protoryx* forms found in China can be separated into two groups, which are both different from other forms described as Late Miocene or earlier species of *Protoryx*. Hence, we propose two new

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genera, *Huabeitragus* gen. nov., and *Macrotragus* gen. nov. in this paper. *Huabeitragus* has a strongly bent cranial braincase, which makes the cranial axis interact with the facial axis at a right angle. The turning point occurs at the fontal anterior to the horn bases. The supraorbital foramina are small and widely set apart. There is a raised ridge along the frontal suture between the horn cores. The braincase is short and narrow. The occipital surface is low and wide, facing posteriorly. The basioccipital is rectangular with a flat or slightly concave surface, without a developed longitudinal groove or ridge, and the anterior and posterior tuberosities less developed. The horn cores have anterior keels and subtriangular shaped cross sections. The horn cores are very divergent upwards in anterior view. *Macrotrgus* has a large skull and horn cores. The facial, orbital, and cranial parts are wide. The upper orbital rims do not protrude laterally. The supraorbital foramina are small and widely set apart. The braincase is shorter and wide, with parallel lateral sides. The occipital surface is flat, facing posteriorly. The horn cores are laterally compressed and curved. Compared with the molar row the premolar row is shortened. *Huabeitragus* differs from *Macrotragus* in its smaller size, strongly bent braincase with the turning point more anterior, narrower braincase, lower and wider occipital surface, rectangular basioccipital without longitudinal groove and weak ridge, smaller foramina ovalia, and less robust, more divergent horn cores, with subtriangular cross section at the base and having keels. Characters shared by *Huabeitragus* and *Macrotragus*, are comparable with those of Caprinae. Therefore, we consider these two new genera as members of Caprinae.

Key words North China, Late Miocene-Early Pliocene, *Protoryx*

1 Introduction

A recent study showed that the Chinese Late Miocene witnessed the highest mammal diversity during the Neogene (Zhang et al., 2006). There developed a "favorable oasis" during the latest Miocene in North China. This scenario was supposed to be largely related to ecological environmental partitioning caused by the onset of the East Asia summer monsoon conditions and influx of immigrants from different directions (Fortelius and Zhang, 2006). However, the taxa used for analysis are in need of systematic revision; thus, uncertainties in the pattern of diversity still remain. In this paper, we try to review one important bovid group referred to ? *Protoryx* based on newly discovered materials and old collections.

Protoryx Major, 1891 is an extinct group of medium to large sized bovid species, recorded from the Middle to Late Miocene of Turkey, Iran, Greece, and Tunisia, and the Late Miocene to Early Pliocene of Eastern Asia. Its phylogenetic status has long been under discussion. Contrary to the traditional classification in Subfamily Hippotraginae, Gentry (1971) assigned this genus to subfamily Caprinae. Meanwhile, Solounias (1981) considered that *Protoryx* and other contemporaneous European genera, *Palaeoryx*, *Tragoreas*, *Sporadotragus*, and *Pseudotragus* constitute the so called *Palaeoryx-Protoryx* complex. Erdbrink (1988) insisted on the traditional Hippotraginae status.

Protoryx fossils from China were originally described by Bohlin (1935) and Teilhard and Trassaert (1938). They named five species in total: ? *Protoryx planifrons* Bohlin, 1935, ? *Protoryx shansiensis* Bohlin, 1935, ? *Protoryx yushensis* Teilhard & Trassaert, 1938, ? *Protoryx bohlini* Teilhard & Trassaert, 1938, and ? *Protoryx* sp. All five species were found from Late Miocene and Early Pliocene deposits of North China (Gansu and Shanxi). Both Bohlin (1935) and Teilhard and Trassaert (1938) considered that these species might belong to new taxa pending confirmation by more materials. Gentry (1971) mentioned the possible conspecific status of ? *P. planifrons* Bohlin, 1935, ? *P. shansiensis* Bohlin, 1935, and ? *Protoryx* sp., a form that would be representative of Eastern Asia.

During the last few years, we have collected three well-preserved skulls from Baode and Yushe, Shanxi Province. Judging by the morphology of their skull and horn cores, they can be attributed to Chinese *Protoryx*. Detailed comparison with other forms from western Eurasia suggests that all the *Protoryx* forms found in China can be separated into two groups, which are both different from other forms described as Late Miocene or earlier species of *Protoryx*. Hence,

we propose two new genera, *Huabeitragus* gen. nov., and *Macrotragus* gen. nov.

Abbreviation: IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. THP, Yushe collection in the Tianjin Natural History Museum.

2 Systematic paleontology

Artiodactyla Owen, 1848
Bovidae Gray, 1821
Caprinae Gill, 1872
***Huabeitragus* gen. nov.**

Type species ? *Protoryx yushensis* Teilhard & Trassaert, 1938.

Age Late Miocene to Early Pliocene.

Etymology Huabei, Chinese for North China.

Diagnosis Medium size. The skull is narrow and long. The facial axis makes an angle of approximately 90 degrees with the cranial axis. This turning point of curvature occurs at the frontal anterior to the horn base. The supraorbital foramina are small and widely separated. The braincase is short and narrow, with a rectangular interparietal. The occipital surface is inclined posteriorly and downwards. The mastoids are small and do not contact the parietal. The basioccipital is square and lacks longitudinal grooves and/or ridges. The anterior and posterior tuberosities are less developed. The horn cores are long and slender. Both horns are closely set at the base and diverge greatly upwards. The cross section of the horns at the base is subtriangular in shape, with a flat outer surface, slightly convex inner side. There is an anterior keel. The horn cores moderately incline in side view.

Species included Type species, *Huabeitragus yushensis* (Teilhard & Trassaert, 1938) is the only one in the genus.

***Huabeitragus yushensis* (Teilhard & Trassaert, 1938)**
(Fig. 1)

1938 ? *Protoryx yushensis* Teilhard & Trassaert, p. 41, Text-fig. 39, Pl. I, fig. 6

Holotype One partial skull with horn cores (THP 31116). Collected from Zhangcun, Early Pliocene, Yushe Basin, Shanxi Province.

Referred specimens Two partial skulls with horn cores (IVPP V 14753, V 14754), found from Beicun (Late Miocene or Early Pliocene) and Wangjiagou (Early Pliocene), respectively, both Yushe Basin.

Diagnosis Same as the generic diagnosis.

Distribution Late Miocene to Early Pliocene, Yushe Basin.

Measurements See Table 1.

Description Specimens V 14753 and V 14754 are very similar to the type specimen in skull and horn core morphology.

Specimen V 14753 (Fig. 1A), a partial skull, preserving the cranial part, partial frontals and two broken horn cores, lacks the face and all teeth. From this fragmentary skull, we can tell that this animal had a long and narrow skull, which was strongly bent at the frontal anterior to the horn base, at an angle about 90 degrees. The supraorbital foramina are small and well separated on the frontals. Although the orbital rims are broken, it is possible to tell that they are less laterally protruding. The frontals between the horn cores are slightly raised up, forming a frontal suture ridge that is higher than the upper orbital rims. The cranial roof is short and narrow, rectangular in outline. The lateral sides are almost parallel to each other. The parietals are short, without prominent temporal ridges. The interparietal is large and trapezoidal. The

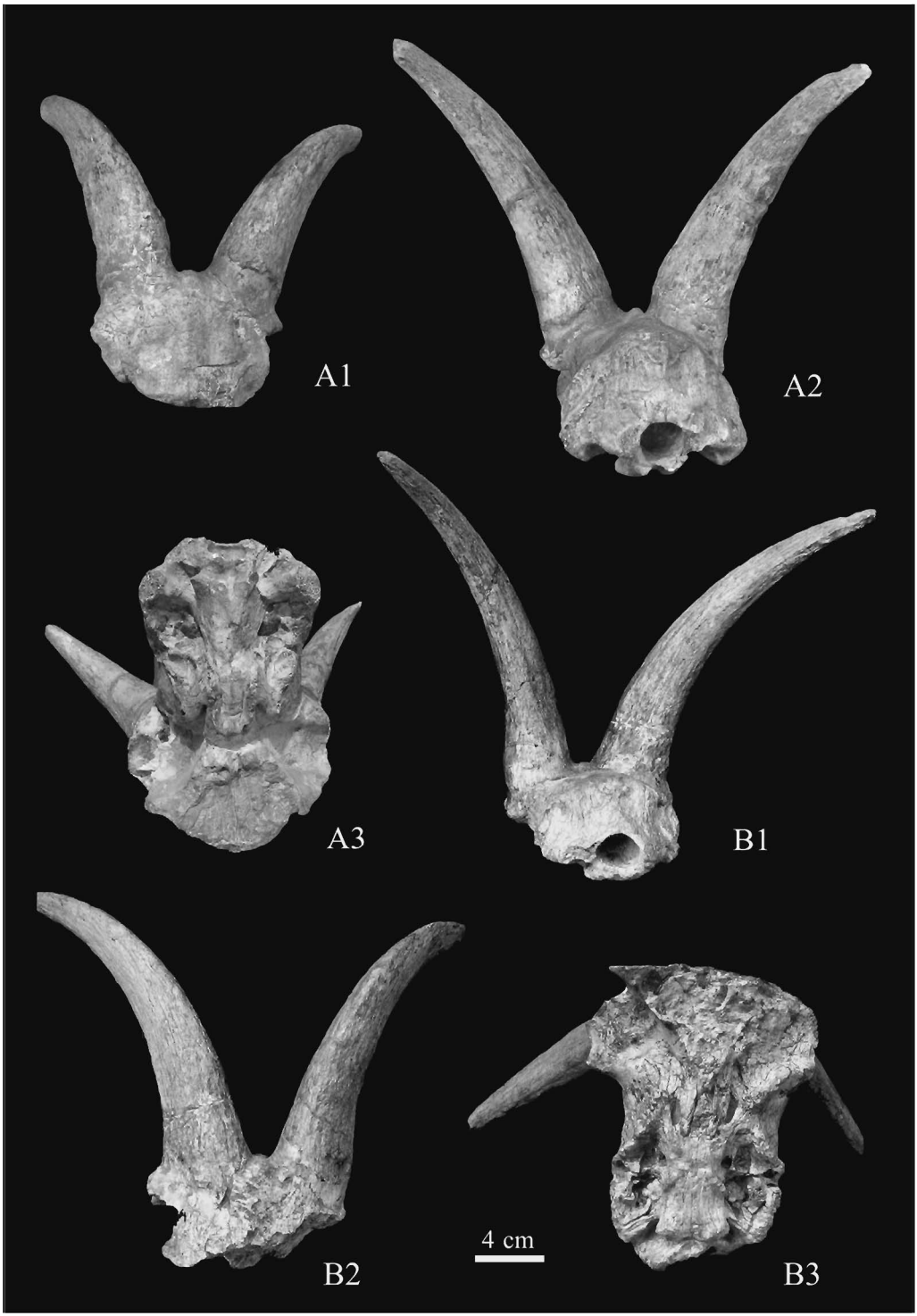

Fig. 1　*Huabeitragus yushensis* (Teilhard & Trassaert, 1938)
Two partial skulls, A. V 14753, B. V 14754; A1, B1. anterior view; A2, B2. posterior view; A3, B3. ventral view

rectangular occipital surface is slightly convex, facing posteriorly and downwards, with a strong occipital ridge in between the lateral parts. The occipital is wider than high. The mastoid is small and do not contact the parietal. Although broken, the paraoccipital processes are large and robust. The occipital processes are in the same plane as the occipital surface. The basioccipital is badly broken. No auditory bulla is preserved. Judging by its outline, the auditory bulla would have been small and laterally flattened. The horn cores are inserted above the orbitals. They are long and slender, with anterior keels. The outer surface is flat and the inner side slightly convex. The cross section at the base is subtriangular, with its longitudinal axis extended antero-interiorly, making the anterior edges of the horn cores converge antero-interiorly. In anterior view, the horn cores diverge strongly upwards. The distance between the horn cores at their base and at a height 10 cm above the bases is 30 mm and 116 mm, respectively. The pedicles are short. There is no postcornual fossa.

Specimen V 14754 (Fig. 1B) also preserves the cranial part, partial frontals, and horn cores. Judging by the smaller size of the skull and horn cores, this specimen is more similar to the holotype (THP 31116). The well-preserved basioccipital shows its rectangular shape and flat surface, with no longitudinal groove or ridge between the less well developed anterior and posterior tuberosities. The foramina ovalia are small, and facing laterally.

Macrotragus gen. nov.

Type species ? *Protoryx shansiensis* Bohlin, 1935.

Etymology Macro, Latin, meaning large and/or robust.

Diagnosis A large sized bovid. The skull and horn cores are massive. The face is wide, with shallow preorbital fossa. The braincase is wide and short. The cranial roof curved down posteriorly, forming an obtuse angle with the facial axis, and the turning point occurs at the frontal surface between the horn bases. The supraorbital foramina are small and widely set apart. The occipital surface is high and semi-circular in outline. The basioccipital is long and narrower at the anterior tuberosities than at the posterior ones, with a longitudinal groove and a ridge. The horn cores are laterally compressed, less divergent in anterior view, and slightly curved. They are inserted above the orbits and have an elliptical cross-section at the base, and without keel. The teeth are mesodonty. The styles are prominent on the upper molars. The premolar row is short in relation to the length of the molar row.

Differential diagnosis *Macrotragus* differs from *Huabeitragus* in its larger size, less bent braincase with the turning point more posterior, in between the horn cores, wide and robust braincase with slightly convex cranial roof, subtriangular interparietal, semicircular occipital surface facing posteriorly, trapezoidal basioccipital with longitudinal grooves and weak ridge at the anterior part, large foramina ovalia, and large, robust, less divergent horn cores, with oval cross section at the base and lacking a keel.

Distribution and age North China (Shanxi and Gansu provinces), Late Miocene.

Species included *Macrotragus shansiensis* (Bohlin, 1935), *M. planifrons* (Bohlin, 1935), and ? *M. bohlini* (Teilhard & Trassaert, 1938).

Macrotragus shansiensis (Bohlin, 1935)

(Fig. 2)

1935 ? *Protoryx shansiensis* Bohlin, p. 123, Text-fig. 92 – 94

Holotype A broken skull with horn cores (Bohlin, 1935: Text-figs. 92 – 94, 114, 131). This specimen was found from Zdansky's Loc. 31z, which is kept in the Evolution Museum of Uppsala University, Sweden.

Referred specimen A broken skull (IVPP V 14755). Collected from Baode, Shanxi Province. No detailed provenance. Matrix on the skull shows that this specimen might have

been collected from Baode Red Clay.

Diagnosis Smaller sized *Macrotragus*. Horn cores are moderately laterally compressed. Basal pillars on upper molars are very small.

Age Late Miocene.

Measurements See Table 1.

Description Specimen V 14755 (Fig. 2) is very close to the type specimen of ? *Protoryx shansiensis* described by Bohlin (1935) in size and morphology of the skull and horn cores. The skull is large and massive. The cranial roof is curved down posteriorly at an obtuse angle with the facial axis, and the turning point occurs at the frontal surface between the horn bases. The frontals between the horn cores are raised up slightly, forming a ridge along the frontal suture. The facial part is wide, with a shallow preorbital fossa. The infraorbital foramina are large, situated above P3s. The frontal surface anterior to the horn cores is flat. The supraorbital foramina are small, and widely set apart. The orbital fossa is large, without wide dorsal orbital rims. The anterior rim of the orbit is situated behind the vertical line of M3. The braincase is short, wide, and cylindrical. The lateral sides are almost parallel. There exist temporal ridges. The interparietal is subtriangular. The occipital is unfortunately broken. The basioccipital is trapezoidal in outline. Between the tuberosities is a central groove and, in the anterior part, in addition a short ridge. The anterior tuberosities are less developed, and the posterior tuberosities are large and laterally extended as ridges. The length of basioccipital is 48.2 mm long, and widths at anterior and posterior tuberosities are 28.6 mm and 43.6 mm, respectively. The auditory bulla would have been small, judging by the preserved remains. The foramina ovalia are small and laterally oriented. The palatal surface is wide, 62.7 mm between M3s. The palatine foramina are situated at the level of the posterior lobe of the M2s. The medial and lateral indentations of palate are almost aligned. The horn cores are broken. The remnant bases indicate they were large and robust with a short pedicle inserted above the posterior half of the orbits. The cross section is oval. The interior of the horn base is hollow. There is no postcornual fossa. The left P2 – M3 and right M2 – M3 are preserved and show medium wear. The premolar row is shortened, and the length ratio of premolar row to molar row is 0.62. Mesostyles on the molars are well developed. There are anterior ribs, and the labial surfaces of the metacones are flat or slightly concave. The tooth enamel surface is smooth. The basal pillars of the M1 – M2 are very small. P2 is relatively large and similar to P3 in tooth structure, having the hypocone and developed anterior rib. There is a spur in the central fossette of P4.

Macrotragus planifrons (Bohlin, 1935)

1935 ? *Protoryx planifrons* Bohlin, p. 119, Text-figs. 89 – 91

Holotype A broken skull with horn cores from Zdansky's Loc. 116, Qingyang, Gansu Province. Bohlin, 1935; Text-figs. 88 – 91, Pl. 15, fig. 1.

Diagnosis Size of skull and horn cores larger than *Macrotragus shansiensis*. Horn cores are less laterally compressed. There are developed basal pillars on upper molars.

Distribution North China (Gansu Province), Late Miocene.

Description See Bohlin, 1935:119 – 123.

Discussion ? *Protoryx planifrons* is here assigned as *Macrotragus planifrons* because it shares the same horn core characters with *Macrotragus shansiensis*. *M. planifrons* differs from the type species *M. shansiensis* by its larger horn cores and developed basal pillars on the upper molars.

? *Macrotragus bohlini* (Teilhard & Trassaert, 1938)

1938 ? *Protoryx bohlini* Teilhard & Trassaert, p. 45, Text-fig. 41; Pl. II, fig. 2

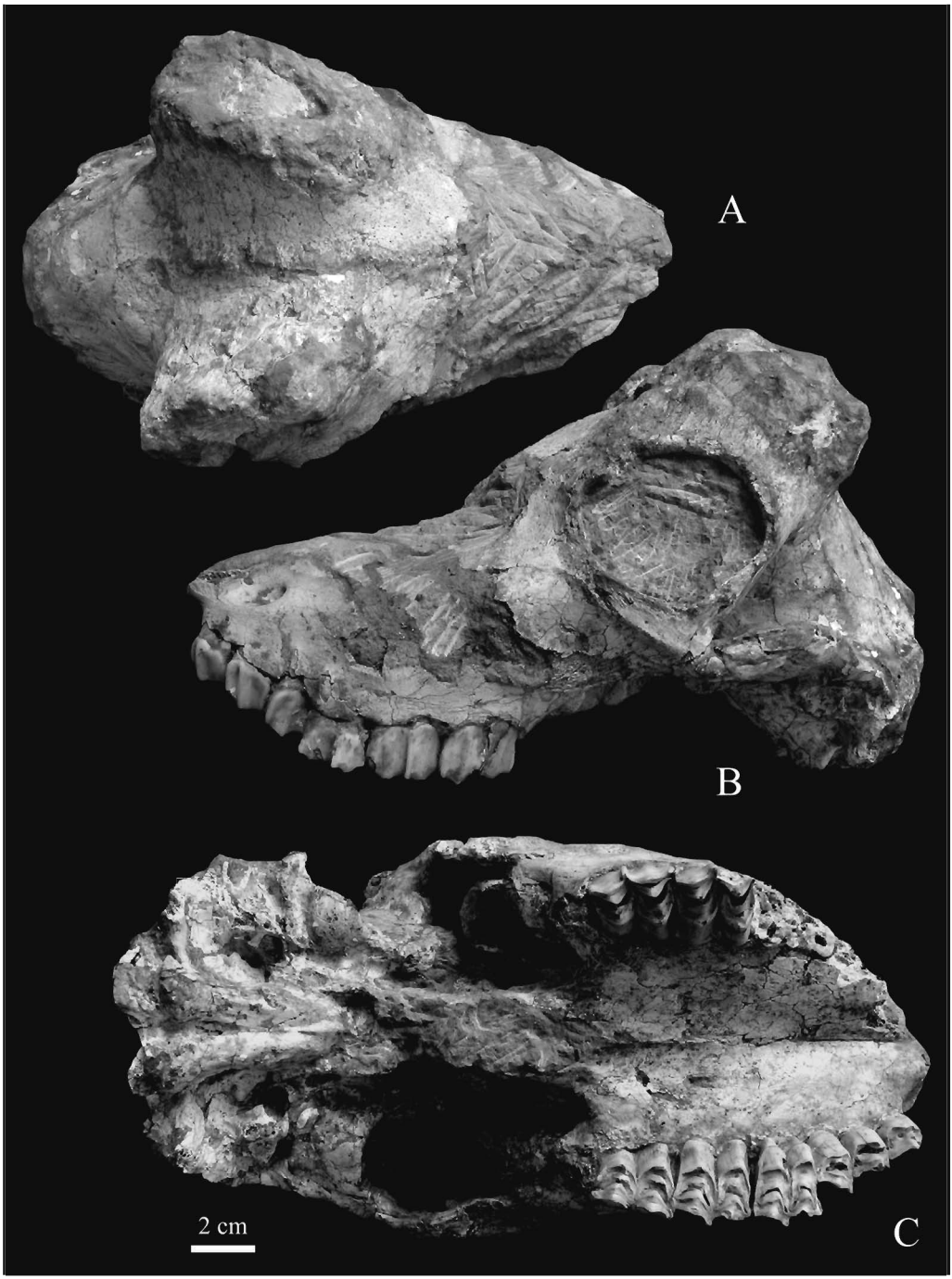

Fig. 2 *Macrotragus shansiensis* (Bohlin, 1935), a broken skull (V 14755)
A. dorsal view; B. lateral view; C. ventral view

Holotype A partial skull with horn cores (THP 22823). This specimen was collected from Loc. 45, Taipingcun, Yushe, Shanxi Province, Mahui Formation or Taoyang member of Gaozhuang Formation equivalent. The geologic age would be Late Miocene to Early Pliocene

(Tedford et al., 1991).

Measurements See Table 1.

Diagnosis Large sized. The horn cores are short and robust, tapering off upwards quickly, and having a slight distal clockwise twist on the right side. The degree of divergence is moderate. The cross section at the base is triangular. The cranial roof is strongly bent downward. The cranial axis forms a 90 degree angle with the facial axis. The cranial part is short and wide.

Distribution Yushe, Shanxi Province. Late Miocene to Early Pliocene.

Description Teilhard and Trassaert (1938) briefly described the holotype. Beyond the features they offered, more characters are listed in the following. The skull is large and massive. The cranial roof curved down posteriorly at a right angle with the facial axis with the turning point occurring at the frontal between the horn bases. The frontals between the horn cores are raised up slightly, forming a ridge along the frontal suture. The supraorbital foramina are small and widely set apart. The cranial roof is short, wide, and cylindrical. The lateral sides are almost parallel. The occipital part is broken, but still shows a low, wide surface, facing posteriorly. The horn cores are short, straight, and inserted above the orbits, tapering off upwards quickly, less divergent distally. There is a weak anterior keel with a slight distal clockwise twist on the right side. The distance between the horn bases and at 10 cm above the bases is 22 mm, and 51 mm, respectively. The pedicles are short. There is no postcornual fossa.

Discussion *Protoryx bohlini* is here tentatively attributed as ? *Macrotragus bohlini* because it shares the main characters of *Macrotragus*, such as the large, robust skull and horn cores, not greatly divergent upwards, and short and wide braincase. However, the strongly bent braincase and keeled horn cores with a triangular cross section at the horn base resemble *Huabeitragus*. The slight distal twist of horn cores is its unique character. Considering the fragmentary nature of the material (a single broken skull with two partial horn cores), we tentatively assign it to *Macrotragus*. The loss of the fossil originally described as ? *Protoryx* sp. prevents any further comments on this taxon.

Table 1 Measurements of the skulls, horn cores, and teeth of *Huabeitragus* and *Macrotragus* and comparison with other related bovids (mm)

	A	B	C	D	E	F	G	H	I
Antero-posterior diameter at base of horn core	62.0	63.9	72.0	72.8	86.0	81.0	63.0	54.1	62.3
Medio-lateral diameter at base of horn core	43.0	49.1	54.0	53.9	71.0	59.2	51.0	38.7	51.6
Minimum width across lateral edges of the horn bases	113.0	126.0	132.0	150.0	140.0	138.5		97.7	133.5
Width across lateral edges of supraorbital foramina	60.0	61.1	59.6	67.0		68.0		45.6	68.1
Braincase length from frontal-parietal suture to occipital crest	62.5	62.5		65.0		66.5	82.0	66.8	69.5
Skull width across mastoids behind auditory meatus	83.0	89.8		121.6		126.0	106.0	93.5	114.3
Height of the occipital	60.4	59.0		73.0			77.0		
Width of the occipital	92.5	92.8		110.7					
Length M1 – M3				69.2	72.9		(67.0)	56.8	67.6
Length P2 – P4				43.0	45.4		(47.0)	37.2	50.1

Note: A. *Huabeitragus yushensis*, type (THP 31116); B. *Huabeitragus yushensis*, V 14753; C. *Macrotragus shansiensis*, type (after Bohlin, 1935); D. *Macrotragus shansiensis*, V 14755; E. *Macrotragus planifrons*, type (after Bohlin, 1935); F. ? *Macrotragus bohlini*, type (THP 22823); G. *Protoryx carolinae*, Br. Mus., M 10389 and M 11415 (after Pilgrim and Hopwood, 1928); H. *Pachytragus crassicornis* (after Gentry, 1971); I. *Palaeoryx pallasi* (after Gentry, 1971).

3 Comparison with related taxa

Protoryx was named by Major (1891) for a group of antelopes from Pikermi, Samos, and Maragha. However, its phylogenetic status has long been under discussion. To sum up, there are at least three viewpoints:

1) Gentry (1971) considered that *Protoryx* and *Pachytragus* were two distinct and valid genera. The type species of *Protoryx*, *P. carolinae* represented fossils from Pikermi, Greece, whereas those from Samos were attributed to *Pachytragus*. The main difference between the genera lie in the derived genus *Pachytragus* having higher tooth crowns, less developed basal pillars on the upper molars, and a short premolar row. Kostopolous (2005) confirmed that there was no *Protoryx* from Samos Island and agreed with Gentry to align species from Samos and Maragha with *Pachytragus*.

2) Solounias (1981) restudied the fossil materials from Samos, and suggested that *Pachytragus* was congeneric with *Protoryx*. He recognized three species of *Protoryx* from Samos, namely *Protoryx carolinae*, *P. laticeps*, and *P. crassicornis*. Köhler (1987) adopted Solounias' classification in his work on Middle Miocene bovids from Turkey.

3) Erdbrink (1988) argued that *Pseudotragus*, *Pachytragus*, and *Microtragus* (= *Sporadotragus* Kretzoi, 1968) were all synonymies of *Protoryx*. His suggestion was later supported by Bouvrain (1994).

Without systematic study of the large collections from Pikermi and Samos, we hesitate to comment on the phylogenetic relationship of *Protoryx* and *Pachytragus*. Judging by the descriptions and figures in various publications, we tend to accept the Solounias' (1981) viewpoint (no. 2 above). The genera share the following characters: medium to large sized, a cranial roof that is bent downward at an angle about 105 – 130 degrees to the facial axis and the turning point occurring between the horn cores, a short braincase, horn cores that are inserted above the posterior part of the orbits without torsion and strongly lateral compression, with an oval cross section and less divergent upwards, developed mesostyles on the upper molars, and the labial wall flat or slightly concave. However, derived tooth characters of *Pachytragus* prevent definitive decision. For the time being, we use the classification of Gentry (1971).

Consistent with Gentry (1971), five species can be attributed to *Protoryx*: the type species *Protoryx carolinae* from Pikermi (MN12), *P. enanus* Köhler (1987) from Turkey (MN7/8), *P. solignaci* (Robinson, 1972) from Sinap, Turkey, and Tunisia (MN8-9), *P. tadzhikistanica* Dmitrieva, 1977, and *P. paralaticeps* Dmitrieva, 1977, both from Mongolia (possibly Early Pliocene). The main characters of the genus that distinguish it from *Palaeoryx* Gaudryi, 1961 include: a narrower, longer, and higher skull, dorsal orbit rims moderately protruding, the anterior rim situated behind the level of the M3, horn cores inserted above the orbits, and laterally compressed, less divergent in anterior view. By these characters, it is still difficult to determine if the latter two species from Mongolia should be attributed in the genus *Protoryx*. The two new genera from China, *Huabeitragus* and *Macrotragus*, show some similarities with *Protoryx* in medium to large size, cranial flexing, short cranial portion and compressed horn cores. In addition, *Macrotragus* shares more characters with *Protoryx*: the anterior orbital rim lying behind the level of the M3, large and shallow preorbital fossa, infraorbital foramina situated above the posterior part of the P3s, the central and lateral indent of the palate situated at the same level, moderate crown height. However, the characters listed above also occur in *Pachytragus* and *Pseudotragus* from Europe, as well as in *Olonbulukia* and *Qurlignoria* from China.

In fact, both *Huabeitragus* and *Macrotragus* possess their own distinct characters. *Huabeitragus* has a strongly bent cranial braincase, which makes the cranial axis interact with the facial axis at a right angle. The turning point occurs at the frontal anterior to the horn bases. The supraorbital foramina are small and widely set apart. There is a raised ridge along the frontal su-

ture between the horn cores. The braincase is short and narrow. The occipital surface is low and wide, facing posteriorly. The basioccipital is rectangular with a flat or slightly concave surface, without a developed longitudinal groove or ridge, and the anterior and posterior tuberosities less developed. The horn cores have anterior keels and subtriangular shaped cross sections. The horn cores are very divergent upwards in anterior view. *Macrotrgus* has a larger skull and horn cores than *Protoryx*. The facial, orbital, and cranial parts are wide, similar to the condition in *Palaeoryx*. The upper orbital rims do not protrude laterally. The supraorbital foramina are small and widely set apart. The braincase is shorter and wide, with parallel lateral sides. The occipital surface is flat, facing posteriorly. The horn cores are more laterally compressed and curved. Compared with the molar row the premolar row is shortened. All these characters differ from those of *Protoryx*.

Except for *Protoryx*, the following genera from the Late Miocene of Eurasia are also closely related to the two new forms discussed herein, e. g., *Pachytragus*, *Pseudotragus*, *Palaeoryx*, *Paraprotoryx*, *Qurlignoria*, and *Olonbulukia*.

Pachytragus Schlosser, 1904 is a Eurasian Late Miocene caprine. No fossil has been reported from China. As previously discussed, *Pachytragus* is very close to *Protoryx* in its skull and horn core morphology. The present two new genera can be distinguished by the same characters as *Protoryx* from *Pachytragus*.

Pseudotragus was recovered mostly from Europe. Gentry (2000) attributed *Tragoreas* Schlosser, 1904 and *Sporadotragus* Kretzoi, 1968 from Greece to this genus. This *Protoryx*-related form can be distinguished by its smaller size, narrower braincase and large preorbital fossa. *Huabeitragus* and *Macrotragus* differ from this form by their larger size, robust horn cores and wide braincase etc.

Palaeoryx Gaudry, 1861 is a quite unique caprine of the Eurasian Late Miocene. There are two previously described species, *Palaeoryx sinensis* and *Palaeoryx* sp. from Baode, Shanxi Province, and Qingyang, Gansu Province, respectively. The most characteristic features are the round cross sections at horn bases, and horn cores in almost the same line with the facial axis.

Paraprotoryx Bohlin, 1935 is known from Baode and Yushe, and includes two species, *Paraprotoryx minor* and *Paraprotoryx killgusi*. They are characterized by horn cores with round cross section at the base, large distances between the horn cores, strong curvature, and moderate divergence upward.

Qurlignoria and *Olonbulukia* were named by Bohlin (1937). Fossils are known from Late Miocene sediments of the Qaidam (Tsaidam) Basin, Qinghai Province. Gentry (2000) suggested that *Qurlignoria* might be an ancestral form of *Pantholops hodgsoni*. Bohlin (1937), Gentry (2000), and Chen (2005) all agreed that *Olonbulukia* has similar characters to *Protoryx*. However, the following characters distinguish it from *Protoryx* and the new genera here described: the braincase is less bent downwards, the frontals between the horn cores are flat, in the same plane with the cranial roof, the horn core pedicles are long, the horn cores are widely set apart, and almost parallel, strongly laterally compressed, curved in lateral view, and have a large and shallow postcornual fossa.

4 Phylogenetic discussions

Until the 1970s, Chinese paleontologists referred ? *Protoryx* to Hippotraginae or Pseudotraginae following Bohlin (1935), Simpson (1945), and Teilhard and Trassaert (1938). Gentry (1971, 1978, 1992, 2000, 2003) suggested that *Protoryx* and its related taxa should be assigned to Caprinae rather than Hippotraginae, leaving the name Hippotraginae for taxa from Africa, Arabia, and South Asia.

The strongly bent braincase of *Macrotragus* and *Huabeitragus* differs from the horizontal

ones of Boselaphini (Bovinae) and Antilopinae. The living genera of Hippotragini, such as *Hippotragus*, *Oryx*, and *Addax* all possess more primitive characters than the new genera here described: less bent braincase, long cranial portion etc. Compared to *Macrotragus*, these extant genera have more anteriorly set orbits, with the anterior rim situated above or anterior to the M3, long premolar row, developed basal pillars and wrinkled enamel surface. In contrast with *Huabeitragus*, they have rectangular or trapezoidal basioccipitals with longitudinal grooves. Hence, it seems to be impossible for these new Chinese forms to be ancestral to the living forms of Hippotragini from Africa and Arabia.

The taxonomic name Urmiatheriinae was recently resurrected to encompass the specialized Chinese Late Neogene genera, including *Urmiatherium*, *Plesiaddax*, *Shaanxispira*, *Lantiantragus*, *Hezhengia* and others (Chen and Zhang, 2004). In addition, *Sinotragus* and *Parasinotragus* are also possibly members of this group (Zhang, 2003; Chen and Zhang, 2004). Characters of this subfamily, e. g., horn cores with twisted keels inserted posterior to orbits, less bent braincase, narrow face, large and shallow preorbital fossa, and extremely short premolar row exclude the new genera from membership in this subfamily. Characters shared by *Huabeitragus* and *Macrotragus*, such as strongly flexed braincase, small and wide set supraorbital foramina, short parietal, posteriorly facing occipital surface, small auditory bulla, absence of postcornual fossa, horn cores with hollow base, short premolar row, less developed longitudinal grooves or ridge on basioccipital, are comparable with those of Caprinae, such as *Capra* and *Ovis*. Therefore, we consider these two new genera as members of Caprinae.

According to a recent biochronologic study (Zhang and Liu, 2005), the localities producing *Huabeitragus* and *Macrotragus* from Qingyang, Gansu Province, Baode and Yushe, Shanxi Province, should be referred either to Baodean or Yushean stage. There are no related taxa in China recorded up to now from the Middle Miocene and the early Late Miocene (Bahean) localities. Their close relationships with *Protoryx* suggest that these two new genera were most likely descendants of *Protoryx* immigrated from western Eurasia and evolved into endemic taxa in the "favorable oasis" of North China during and after the latest Miocene.

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