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A new species of *Shaanxispira* (Bovidae, Artiodactyla) from the upper Miocene of China

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Abstract

A new species of the bovid *Shaanxispira*, from the upper Miocene deposits of the Linxia Basin, Gansu Province, China, is described here. *Shaanxispira* is endemic to Northern China and was previously known only from the Lantian area, Shaanxi Province, by two species, *S. chowi* and *S. baheensis*. The new species, *S. linxiaensis* nov. sp., is of early Bahean in age, slightly older than the species from the Lantian area. The horn-cores of the new species are more derived, with large wing-shaped antero-medial keels, suggesting the occurrence of a different lineage of *Shaanxispira* in the Linxia Basin. Although *Shaanxispira* has homonymously twisted horn-cores, it is not closely related to other late Miocene bovids with homonymously twisted horn-cores, like *Oioceros* and *Samotragus*. Its phylogenetic status is still in debate, but might be more closely related to the late Miocene "ovibovines."

Key words: Linxia Basin, China, late Miocene, *Shaanxispira*, Ovibovini, Bovidae

Introduction

Since the beginning of last century, several late Miocene bovids with specialized horn-cores have been reported from China, including *Hezhengia* (Qiu *et al*. 2000), *Plesiaddax* (Bohlin 1935a; Xue *et al*. 1995; Deng *et al*. 2011), *Tsaidamotherium* (Bohlin 1935b; Shi 2014) and *Urmiatherium* (Bohlin 1925, 1935a) (their stratigraphic distributions are shown in figure 1). They were considered to be closely related to each other, characterized by having short and almost vertical braincase, strengthened cranium-atlas articulation, and especially the accessory articular surface between occipital condyle and paroccipital process (Bohlin 1935a; Qiu *et al.* 2000; Shi 2014). Some other bovids like *Lantiantragus* and *Shaanxispira* were also grouped with them, according to the similarities on teeth and skull (Liu *et al.* 1978; Zhang 2003; Chen & Zhang 2004, 2009).

Shaanxispira is a large late Miocene bovid with derived horn-cores: long and straight, moderately divergent, homonymously twisted, and with a distinct antero-medial keel. This genus was endemic to northern China, and its fossil record, especially the skulls, is quite sparse. Until now, only two *Shaanxispira* species have been described: the type species, *S. chowi*, and *S. baheensis*. Both of them were discovered from the upper part of the Bahe Formation (Unit 2), in Lantian area of Shaanxi Province, China. The age of the type species is about 8.21Ma (Loc.30, 59S6, 63702.L4), whereas the age of *S. baheensis* is 8.07Ma (Loc.6/33, 59S5, 63702.L1) (Liu *et al*. 1978; Zhang *et al*. 2002, 2013; Zhang 2003; Zhang & Liu 2005; Deng 2006).

The current literature includes a brief mention of the occurrence of *Shaanxispira* in the Linxia Basin, Gansu Province, but no detailed information has ever been provided (Deng *et al*. 2004a, b, 2013). Here we describe a new species of *Shaanxispira* from the Linxia Basin, represented by a well preserved skull with a pair of horn-cores. It is the first description of this genus outside of the Lantian area, and the preservation state of the new specimen is better than all previously known specimens of *Shaanxispira*. The discovery also provides important supplement to the morphological features of the skull, especially the upper dentitions and the bone sutures.

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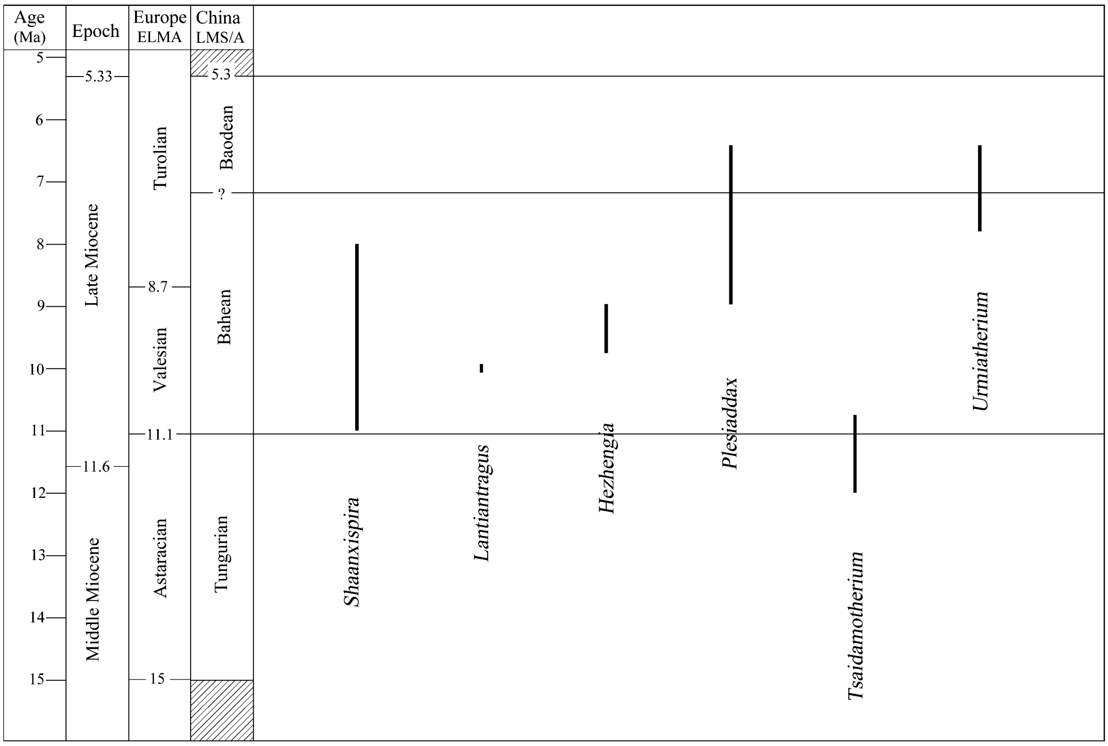

FIGURE 1. Geological distribution of the late Miocene fossil "ovibovines" in China (modified from Qiu *et al.* 2013: fig. 1.7c). The first appearance of *Urmiatherium* in China is modified to 7.8 Ma according to an unpublished skull from the Hezheng area.

The skull, HMV 1922, was found in the locality Panyang (LX 0037, in IVPP locality number system), which is in the south of the Hezheng County (Fig. 2). The specimen has been excavated from the light yellowish-brown calcareous muddy siltstones that belong to the lower part of the upper Miocene Liushu Formation. The fossil mammals from the locality Panyang belong to the Dashengou Fauna, of early Bahean Age, approximately 11 Ma in age (Deng *et al*. 2013). Thus, the new species from the Linxia Basin is older than *S. chowi* and *S. baheensis* from the Lantian area.

According to a preliminary fossil list, the mammalian fauna of the locality Panyang includes *Parazhizomys hipparionum*, *Parataxidea sinensis*, *Hyaenictitherium hyaenoides*, *Tetralophodon exoletus*, *Hipparion chiai*, *Hipparion weihoensis*, and *Chilotherium wimani* (Hezheng Paleozoological Museum fossil index). Although five bovid genera are found in the same fossiliferous horizon of the Linxia Basin, e.g., *Hezhengia*, *Miotragocerus*, *Gazella*, Bovidae gen. nov. (Deng *et al*. 2004b, 2013), *Shaanxispira* is the only bovid found in the Panyang locality.

Abbreviations: HMV, vertebrate fossil specimens of Hezheng Paleozoological Museum in Gansu, China; IG, Institute of Geology and Geophysics, Chinese Academy of Science, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China.

Systematic paleontology

Order ARTIODACTYLA Owen, 1848

Family Bovidae Gray, 1821

? Tribe Ovibovini Gill, 1872

Genus *Shaanxispira* Liu, Li, and Zhai, 1978

Type species. *Shaanxispira chowi* Liu, Li, and Zhai, 1978

Emended diagnosis of the genus. A bovid of large size; horn-core long and straight, moderately divergent, homonymously twisted, slightly inclined, inserted behind the orbit, and with an antero-medial keel ascending from the antero-medial base of the horn-core to the top. Frontal higher than upper rim of orbit.

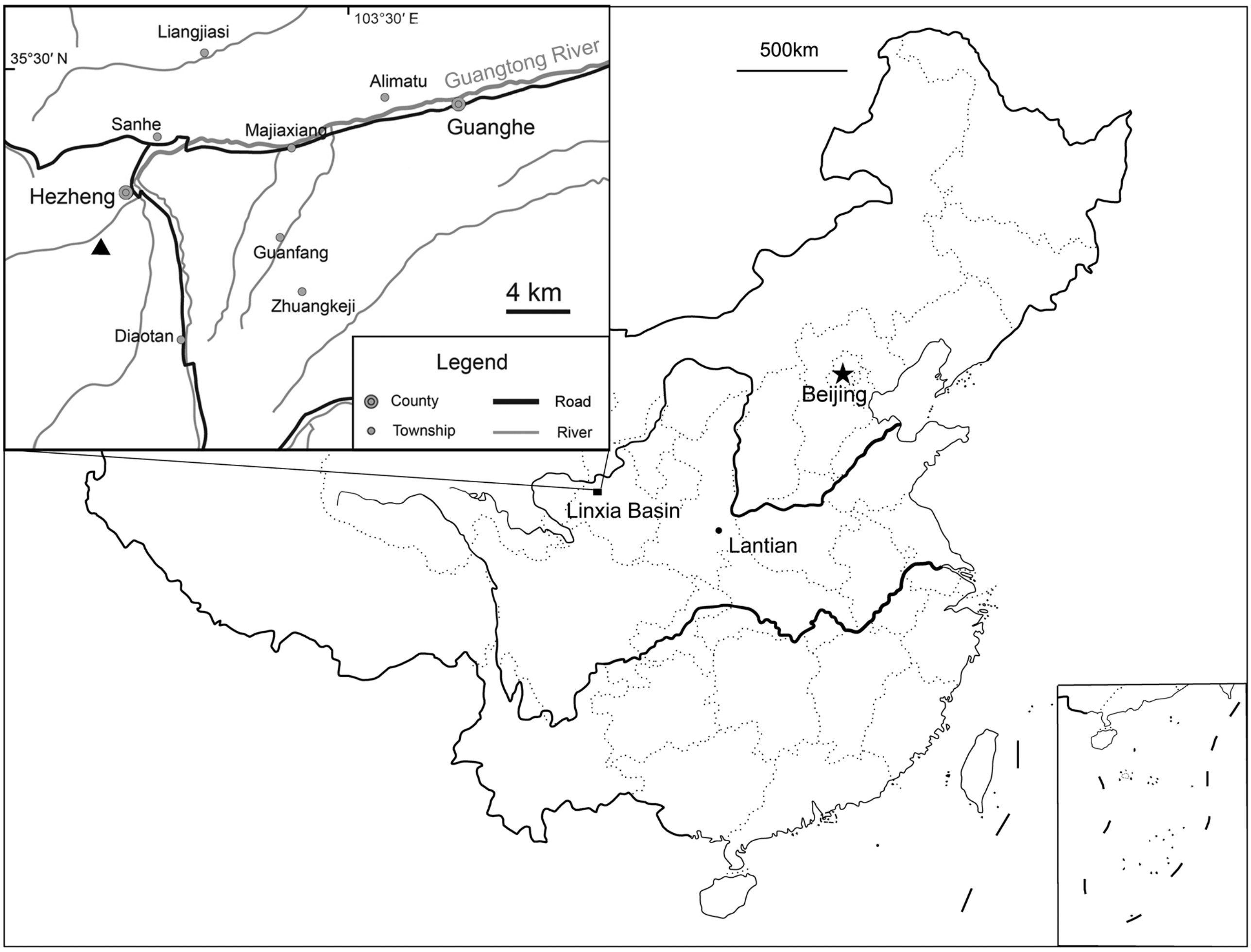

FIGURE 2. Map of the fossil locality Panyang (LX 0037) in the Linxia Basin (black triangle).

Shaanxispira linxiaensis nov. sp.

(Figs. 3–4; Tables 1–3)

Holotype. HMV 1922 (Figs. 3–4). An almost complete and undeformed skull.

Etymology. The species name comes from the locality of the holotype, Linxia Basin.

Geological distribution. Lower part of the upper Miocene, Liushu Formation, Linxia Basin, Gansu Province, China. The age of the associated fauna is equivalent to European MN9.

Diagnosis. Horn-core with only one keel. Antero-medial keel large and wing-shaped, extending anteriorly intensively at the base and protruding above the frontal. Cross section of the horn base sickle-shaped. Horn-core inserted uprightly and caudally. Parietal slightly inclined in side view. Braincase short and broad. Paroccipital process strong. Depression medial to paroccipital process shallow, but without accessory articular surface. Supraorbital foramen small, facing mostly forwards, with distinct supraorbital groove extending to lachrymal. Pre-orbital fossa wide and shallow. Infra-orbital foramen above P3. Nasals domed. Muzzle low and narrow. Teeth mesodont, without strong ribs or styles. Premolar row much shortened. Basal pillars absent or weak.

Description. The skull, HMV 1922, is nearly complete, with a well-preserved right horn-core. The tips of the horn-cores are broken, but skillfully restored with plaster. The tip of muzzle is missing. The right maxilla and left squamosal are slightly damaged. The tooth row is well preserved apart from the left P2 that is missing. The skull belongs to an adult specimen.

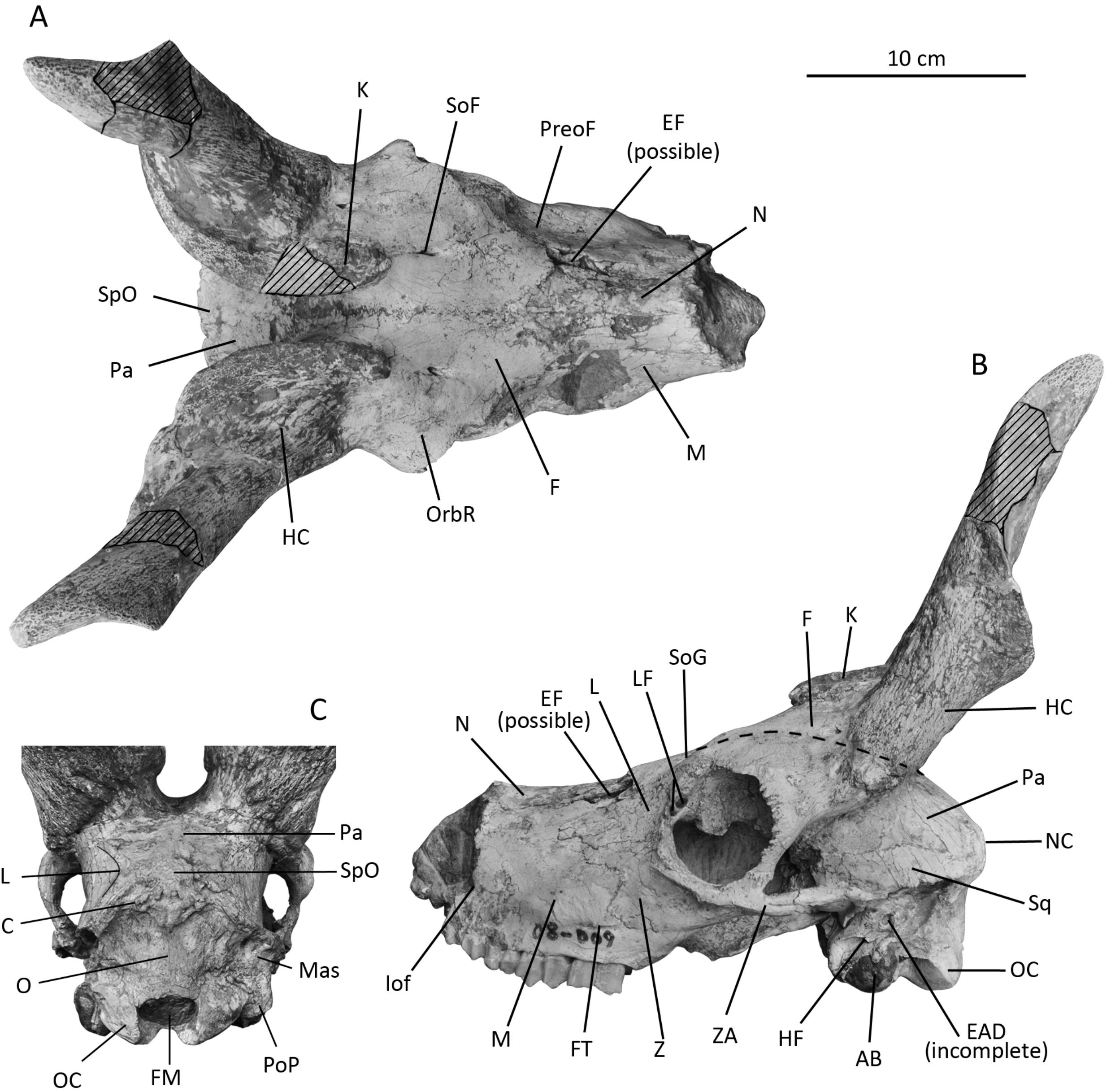

FIGURE 3. Holotype skull of *Shaanxispira linxiaensis* **sp. nov.** (HMV 1922): (A) dorsal view, (B) left lateral view, (C) posterior view; the dashed lines show the lateral profile of the frontals; the shadows indicate the parts mended with plaster. Abbreviations: AB, auditory bulla; EAD, external auditory duct; EF, ethmoidal fissure; F, frontal; FM, foramen magnum; FT, facial tuberosity; HC, horn-core; HF, hyoid fossa; K, antero-medial keel of the horn-core; L, lachrymal; LF, lachrymal foramina; IoF, infraorbital foramen; M, maxilla; Mas, mastoid exposure; N, nasal; NC, nuchal crest; O, occipital; OC, occipital condyle; OrbR, orbital rim; Pa, parietal; PoP, paroccipital process; Preof, preorbital fossa; SoF, supraorbital foramen; SoG, supraorbital groove; SpO, supraoccipital; Sq, squamosal; TL, temporal line; Z, zygomatic; ZA, zygomatic arch.

The muzzle is relatively low, with the nasal aperture being about as broad as high. The nasal is narrow and domed, and slightly widens caudally. The caudal end of the nasal is pointed, extending behind the level of the anterior rim of the orbit (Fig. 3A, N). The naso-incisival notch is anterior to the level of P3. The infra-orbital foramen opens near the tooth row, at the level of P3 (Fig. 3B, Iof). The facial tuberosity is caudally positioned, close to the maxillo-jugal suture (Fig. 3B, FT). There is no facial crest. The facial part of the jugal is large and bilobed (Fig. 3B, Z). The lachrymal is small, quadrangular, long and low (Fig. 3B, L). The pre-orbital fossa is wide and shallow, without clear margins (Fig. 3A, PreoF). The maxillae close to the ethmoidal fissure are broken on both sides. However, the ethmoidal fissure is probably present because the nasal and lachrymal bones remain wide apart, and their margins are smooth, but size and shape of the ethmoidal fissure are uncertain (Fig. 3B, EF).

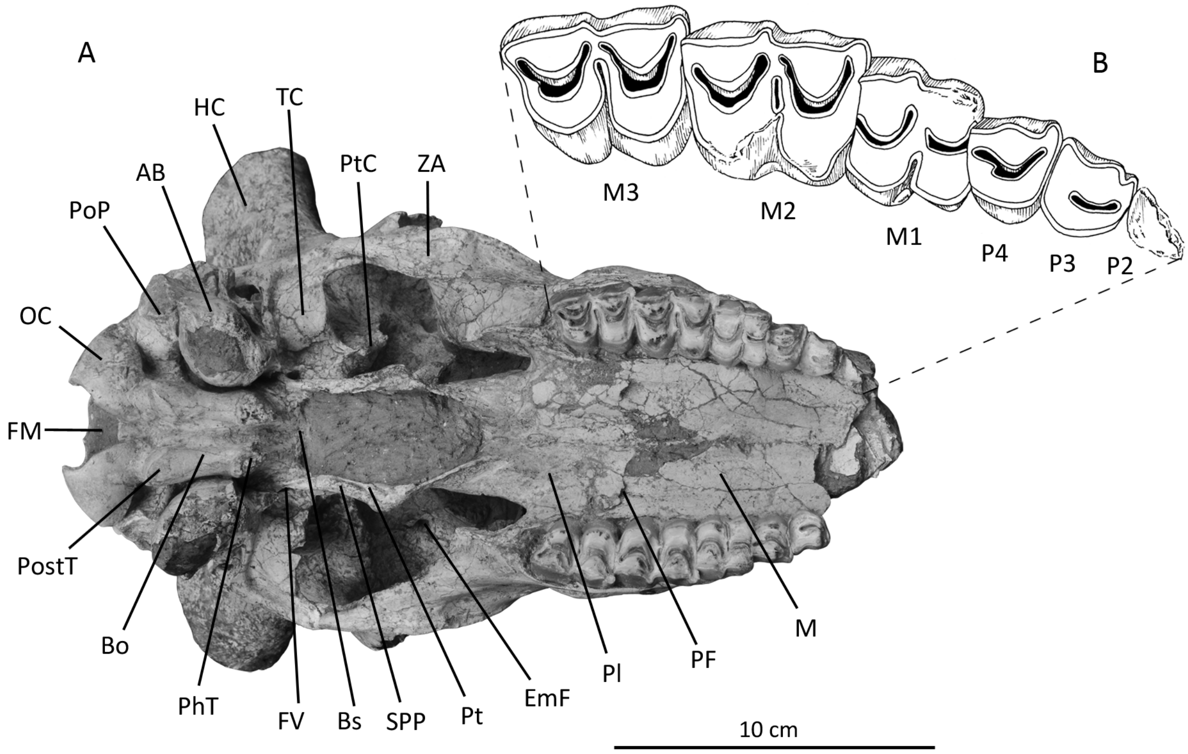

FIGURE 4. The skull and dentition of *Shaanxispira linxiaensis* **sp. nov.** (HMV 1922): (A) ventral view of the skull, (B) sketch of the right dentition; the scale bar is for A.
Abbreviations: Bo, basioccipital; Bs, Basisphenoid; EmF, ethmoidal foramen; FV, foramen ovale; PF, palatine foramen; PhT, pharyngeal tuberosity; Pl, palatine; PostT, posterior tuberosity; Pt, pterygoid; PtC, pterygoid crest; SPP, pterygoid process of sphenoid; TC, temporal condyle. Other abbreviations are defined in figure 3.

The frontal is wide and flat in front of the horn-core, rising slightly above the orbit, and declining at the horn-core. The bending of the frontal is weak (Fig. 3B, dashed lines). The mid-frontal suture is somewhat complex and elevated as a sagittal ridge before the horn bases, whereas between the horn-cores, the suture is flat, but more complex (Fig. 3A, F). The fronto-parietal suture points forwards in the centre, with the midpoint positioned between the horn-cores. The supra-orbital foramen is small, deeply sunken into the frontal, and facing mostly forwards, making the opening nearly round in anterior view, but tear-shaped in dorsal view (Fig. 3A, SoF). The internal opening of the supra-orbital foramen faces mostly downwards, and is more caudal than its external opening. The supra-orbital groove is long and distinct (Fig. 3B, SoG). There is no post-cornual fossa. The orbit is large with wide orbital rims; its dorsal border is lower than the frontal surface; its anterior border is posterior to the back of M3 (Fig. 3B). The lachrymal foramen is large, and is partitioned into two foramina by a thin bone layer (Fig. 3B, LF). The zygomatic arch is weak.

The horn-core is straight, homonymously twisted, making a little more than one whorl, and diverging at an angle of about 35˚ (Fig. 3C). In lateral view, the horn-core is inserted far behind the orbit and is almost perpendicular to the dorsal border of the cranium, and only slightly inclined backwards (Fig. 3B, HC). The antero-medial keel is large and wide, protruding like a wing (Fig. 3A, K). The keel twists homonymously, following the twist of the horn-core. At its base, the keel occupies an antero-medial position on the horn-core, extending anteriorly to the level of the posterior rim of the orbit, and being strongly prominent above the frontal (Fig. 3B, K). As the keel ascends from the base to the tip, the size decreases gradually. In the basal part, the keel has a thickened margin (approximately 2 cm wide at the base, and becomes thinner upwards) with porous surface, whereas the surface of the horn-core is covered by many small longitudinal grooves. The cross section of the horn base is sickle-shaped because of the prominent keel. There is no posterior keel.

The braincase is short and wide, with parallel lateral sides (Fig. 3C). The lateral part of the parietal is long, separating the frontal from the squamosal. The temporal lines are wide apart (Fig. 3C, TL). The occipital is low and broad. The angle between the parietal and occipital planes is about 120˚ (Fig. 3B). The nuchal crest is thick, with a coarse and large external occipital protuberance below (Fig. 3C, NC). The mastoid exposure is long and broad; its dorsal part faces caudally and the ventral part faces laterally. The mastoid exposure is separated from the parietal by the squamosal and the occipital.

TABLE 1. Measurements (mm) and comparison of the skulls of *Shaanxispira.*

	S. linxiaensis **sp. n.**	*S. chowi*	*S. baheensis*[a]	
	HMV 1922	IVPP V 3124	IVPP V 13626	IVPP V 13635
Width across the horn bases (lateral edges)	141.6	131	139.5	
Minimum distance between the horn bases	26	37		
Skull length from P2 to posterior edge of condyle	249.5			
Skull length from P3 to posterior edge of condyle	240.8		250	
Skull width across the orbit (posterior edges)	155		154	
Skull width across the zygomatic	132		128	129
Width of braincase	91		80	81.5
Distance from the posterior edge of the horn base to the occipital surface	59.5		53	54
Maximum width of occipital surface	106[b]		99	104
Maximum height of occipital surface	73		75.5	88.5
Distance between the supraorbital foramina (lateral edges)	57.5		53	54
Width of basioccipital across the posterior tuberosities	34		35.5	31
Width of basioccipital across the pharyngeal tuberosities	28.7		23.7	25.5
Distance between the posterior tuberosities and pharyngeal tuberosities	32		21.5	24.8

[a] Measurements taken from Zhang (2003); [b] Estimated measurement

TABLE 2. Measurements (mm) and comparison of the horn-cores of *Shaanxispira.*

	S. linxiaensis **sp. n.** HMV 1922		*S. chowi* IVPP V 3124		*S. baheensis*[a] average	
	L	R	L	R	L	R
Antero-posterior diameter[b]	77.5	72.5	57	59	47.7	46.5
Transverse diameter[c]	55.5	49.5	42	39.5	52	54
Length of horn-core (straight line in lateral view)	214	218				
Distance between horn-core tips (restored)	212					

[a] Measurements taken from Zhang (2003)

[b] The longest distance from antero-medial point to posterior-lateral point

[c] The diameter perpendicular to the antero-posterior diameter

TABLE 3. Dental measurements (mm) of *Shaanxispira linxiaensis* **sp. n.** (HMV 1922)

		P2	P3	P4	M1	M2	M3	Premolar	Molar	P2?M3	P/M (%)
Length	L	-	12.5	13.5	17.1	24.7	25.5	-	65	-	-
	R	11.5	12.6	13.5	16.8	24.8	26.1	35.2	65.2	96	54%
Width	L	-	13	14	19.5	21.2	20				
	R	-	12.8	14.2	19.9	21.5	20.7				

The foramen magnum is large (Fig. 3C, FM). The occipital condyle is not as strong as in other "ovibovines" like *Hezhengia* or *Plesiaddax*; it is divided into dorsal and ventral articular surfaces by a clear ridge, and the dorsal articular surface forms a notable angle with the occipital surface above (Fig. 3B, OC). The depression between the condyle and paroccipital process is shallow and small, but no accessory articular surface is visible (Fig. 4A). The paroccipital processes are broken on both sides, with their bases considerably robust and converging anteriorly (Fig. 4A, PoP).

The basioccipital is rectangular and thick. A deep and broad longitudinal groove runs along its midline (Fig. 4A, Bo). Both the posterior tuberosity and the pharyngeal tuberosity are well developed and of similar size (Fig. 4A, PhT, PostT). The basioccipital makes an angle with the palate of about 20°. The auditory bulla is large and round. The posterior tip of the auditory bulla is laminar, positioned laterally to the paroccipital process. A triangular muscular process is visible anterior to the auditory bulla (Fig. 4A, AB). The hyoid fossa is deep and small, and hardly observable in ventral view (Fig. 3B, HF). The external auditory duct is small and short, pointing postero-laterally (Fig. 3B, EAD). The oval foramen is moderate in size, facing mainly laterally (Fig. 4A, FV). The pterygoid crest is robust (Fig. 4A, PtC). The ventral border of the pterygoid process of the sphenoid is thick. A small groove is observed along the spheno-pterygoid suture in ventral view (Fig. 4A, SPP, Pt). The palatine is long, and the anterior edge of the choanae is much more caudal than the tooth row (Fig 4A, Pl).

The cheek teeth are mesodont. The premolar row is short, and the length ratio of premolar to molar row is 54% (Fig. 4B, Table 3). P2 is broken, but was certainly small. Its lingual border is straight. P3 is larger than P2, with a round lingual border. The width of P3 is similar to its length. The protocone is more distal than the paracone. The fossette of P3 is simple but deep. P4 is similar to P3 in morphology but is a little larger. The protocone is more mesial, making P4 almost symmetrical. The fossette is long and narrow, with its anterior and posterior ends close to the border of the tooth. A spur is observed in the posterior part of the fossette, pointing forwards.

M1 is almost square, being only slightly wider than long. The first lobe is shorter than the second lobe. The fossettes are U-shaped, and lack spurs. The lingual valley is narrow but deep, reaching almost 1/3 of the width of M1. The enamel island is thin and long. There is a tiny basal pillar on the posterior lobe of M1. M2 is much larger and longer than M1. The parastyle and mesostyle are moderately strong in M2, whereas the metastyle is not developed, and the buccal ribs are weak. The fossettes are simple, with the anterior and posterior ends close to the buccal wall. There are small folds along the border of the fossettes, but no distinct spur. The enamel island is also thin and long in M2. M3 is similar to M2 in size and morphology, but is a little longer and narrower. The ribs and styles are even weaker in M3 than in M2, with only a moderately developed parastyle. There is no enamel island in M3, and the lingual valley penetrates deeply towards the buccal wall.

Comparisons and discussion

(1) Comparison with other species of *Shaanxispira*

The new species has long straight horn-cores, with a protruding and homonymously twisted anterio-medial keel, which is a diagnostic feature of the genus *Shaanxispira*, differentiating it from other late Miocene bovids in China. The skull, horn-cores, and teeth of all three species of *Shaanxispira* are broadly similar to each other.

The type species *S. chowi* was established on a pair of incomplete horn-cores with partial frontal and parietal (Liu *et al*. 1978: IVPP V 3124). The most marked difference between *S. linxiaensis* and *S. chowi* is that *S. chowi* has a well-developed postero-lateral keel on the horn-core, which is absent in *S. linxiaensis*. In *S. chowi*, the antero-medial keel is blunter, the diameter of the horn base is smaller (Table 2), the torsion of the keel is weaker, the cross section of the horn base is rounder with a slightly concave anterior outline and a convex posterior outline (Fig. 5A, B), the horn-core is less upright (the angle is approximately 80° between the horn-core and the parietal, whereas in *S. linxiaensis*, the angle is approximately 100°), the distance between the horn bases is wider, the skull is slightly narrower.

In addition to IVPP V 3124, Liu *et al*. (1978) reported more specimens of unknown large antelopes from the same locality (most of them represented by teeth and mandibles), which were assigned originally to "Antelope spp. indet.". Some of these specimens are from the same fossiliferous layer as IVPP V 3124 (IVPP V 3127, IG 59 S6-2, IG 59 S6-3), and were later assigned to *S. chowi*, based mainly on their size and stratigraphic position (Zhang 2003). These teeth of *S. chowi* are longer than those of *S. linxiaensis*, which is in contradiction with the fact that *S.*

linxiaensis has larger skull and horn-core, and the premolar to molar ratio is larger (Table 1, 3). Besides, the features of the teeth are usually indistinguishable among closely related bovids. Therefore, the assignment of these teeth and mandibles to *S. chowi* is still uncertain.

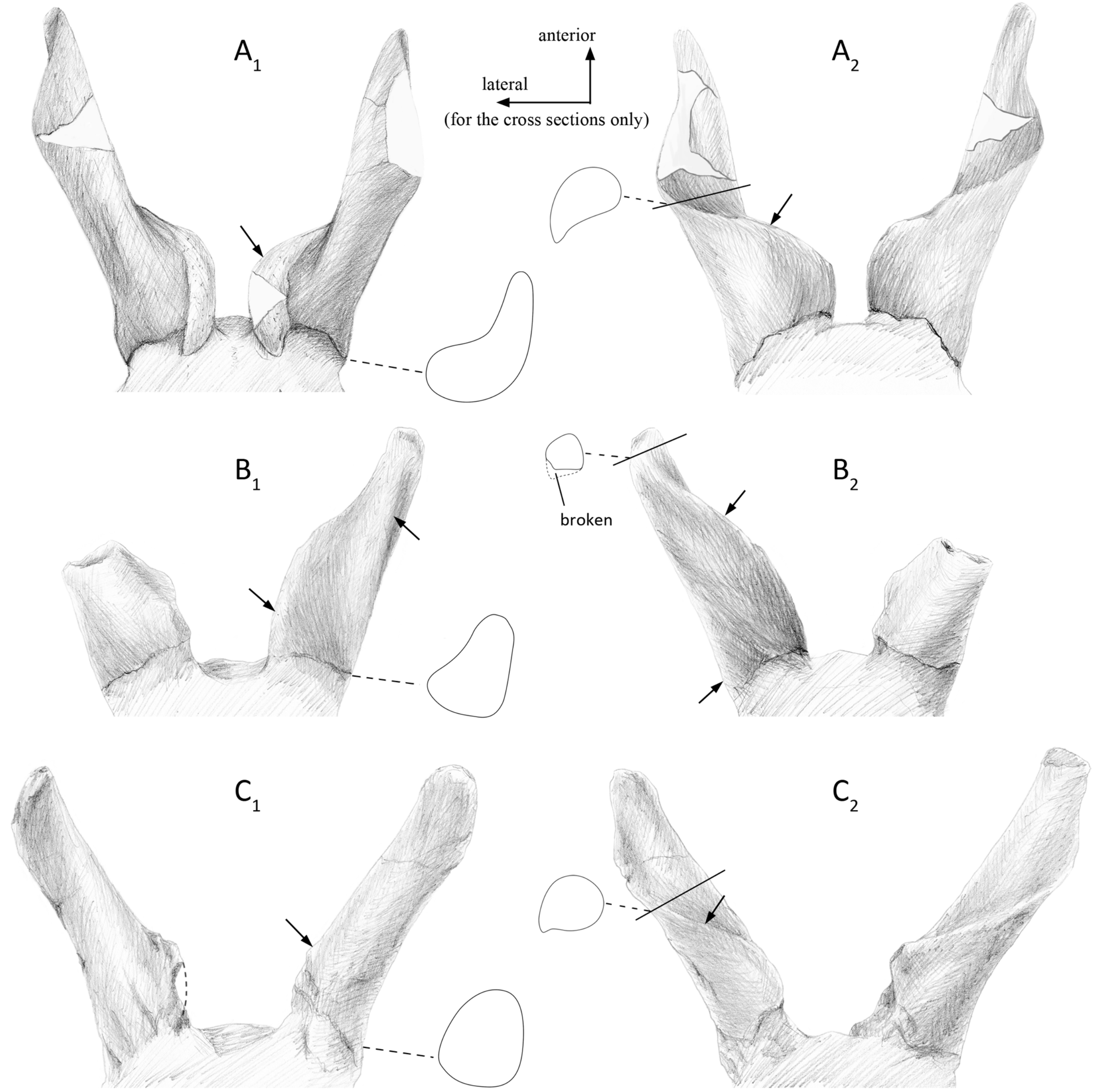

FIGURE 5. Comparison of the horn-cores in different species of *Shaanxispira.* (A) *S. linxiaensis*: (A_1), anterior view, (A_2), posterior view; (B) *S. chowi*: (B_1), anterior view; (B_2), posterior view; (C) *S. baheensis*: (C_1), anterior view, (C_2), posterior view. The cross sections of the left horn-core are drawn, one at the base and one at the basal half whorl; the arrows show the keels of the horn-cores; the blanks in $A_{1,2}$ illustrate the plaster patches.

Shaanxispira baheensis was originally described based on three partial skulls (one with articulated mandible), six pairs of horn-cores and some dentitions, from Loc. 6 and Loc. 33 in the Lantian area (Zhang 2003). The horn-cores of *S. linxiaensis* differ from that of *S. baheensis* in that the latter is sometimes slightly curved, with a much weaker antero-medial keel, and a round cross section of the horn base (Fig. 5C). The base of the keel is not anteriorly extended on the frontal bone. The horn-core is also more inclined in *S. baheensis*, with an angle of approximately 70°. The horn bases are widely apart.

The skull of *S. baheensis* is comparable in size to that of *S. linxiaensis*, and the former is only slightly longer and narrower (Table 1). The braincase of *S. linxiaensis* is wider and longer, but slightly lower (Table 1). Differences also occur in the morphology of the basicranium. The paroccipital process in *S. linxiaensis* is stronger, with a larger transverse diameter of its basal cross section. The basioccipital is thicker and longer, with a deeper sagittal groove, and more protruding pharyngeal tuberosity. Accessory articular surface for the atlas is absent in both species, but the depression between paroccipital and basioccipital is shallower in *S. linxiaensis* than in *S. baheensis*.

A partial skull from locality 59S5 of the Lantian area (IVPP V 3125), which was first assigned to "Antelope spp. indet.", was thought to be a possible female individual of *S. baheensis* (Liu *et al*. 1978; Zhang 2003). However, IVPP V 3125 is not a hornless old skull with very short parietal, as Liu *et al*. (1978) described. It is represented by a posterior part of skull, with partially preserved parietal. The parietal is not very short, and there is no evidence that the skull is hornless, because the frontal is not preserved. The morphology of IVPP V 3125 is however similar to that of *Shaanxispira*, with wide mastoid exposure, thickened basioccipital, and shallow depression between condyle and paroccipital process. So the specimen might belong to *S. baheensis* considering its stratigraphic position.

All the three species of *Shaanxispira* are late Miocene bovids, and *S. chowi* and *S. baheensis* from the Lantian area are roughly contemporaneous. They have similar size and morphology of skull and teeth, and the most remarkable distinction is the various specializations of the horn-cores, but it is unlikely that the morphological differences represent individual variation, because horn-core morphology of nine individuals of *S. baheensis* do not display much intra-specific variation. The possibility of sexual dimorphism is also low. The skull of *S. linxiaensis* has the largest and most specialized horn-cores, which are likely to be male features. *S. chowi* has a slightly smaller skull, but an extra postero-lateral keel is developed on the horn-core, an unlikely feature for a female of *S. linxiaensis* or *S. baheensis*. *Shaanxispira baheensis* has less specialized horn-cores; however, they are sometimes slightly curved and more inclined, and the braincase is shorter, thus, it is more specialized than *S. linxiaensis* in this regard. We tend to interpret these species as representatives of different lineages of *Shaanxispira*: an earlier one in the Linxia Basin, and two later ones in the Lantian area.

(2) Comparison with other late Miocene bovids with homonymously twisted horn-cores

Several bovids with homonymously twisted horn-cores were discovered from the upper Miocene deposits in Eurasia, such as *Oioceros* and *Samotragus* (Mecquenem 1925; Sickenberg 1936). These two genera and *Shaanxispira* share the character of having homonymously twisted horn-cores, but they are quite different in other features of the skull and horn-cores, indicating a relatively distant relationship.

Oioceros is a widespread late Miocene bovid, distributed from Spain to Mongolia (Mecquenem 1925; Roussiakis 2003; Dmitrieva 2007; Kostopoulos & Bernor 2011; Geraads 2013; Kostopoulos 2014). The horn-core of *Oioceros* is lyrate, but the horn-core of *Shaanxispira* is straight or only slightly curved in a few individuals (Fig. 6A, B). In *Oioceros*, the cross section of the horn base is elliptic or round with a small depression at the lateral side, whereas in *Shaanxispira*, the cross section of the horn base is elliptic or round with a protruding part in the front, sometimes the protruding part is so enlarged that the cross section becomes sickle-shaped (Fig. 6C). There is a distinct lateral groove running along most of the horn-cores in *Oioceros*, and the edge of the groove forms a strong postero-lateral keel along the groove, whereas in *S. baheensis* and *S. linxiaensis*, there is neither lateral groove, nor postero-lateral keel besides the groove. Although *S. chowi* does have a lateral keel, the keel is more blunt, and is not accompanied with lateral groove. Besides, the horn-core of *Oioceros* is inserted more anteriorly than in *Shaanxispira*.

The skull morphology is also different between *Shaanxispira* and *Oioceros*. The basicranium of *Shaanxispira* is short, and is nearly hemicircular, whereas in *Oioceros*, the basicranium is relatively longer and narrower (Fig. 6D). The braincase is also relatively longer in *Oioceros*, whereas the muzzle is relatively smaller (Fig. 6E). In *Oioceros*, the orbit is much larger, relative to the skull size, and is more caudally located, with its anterior rim located at the level of M3, whereas in *Shaanxispira*, the orbit is smaller, with the anterior rim of the orbit far posterior to the back of M3. Furthermore, the premolar to molar ratio of *Oioceros* is larger.

The horn-cores of *Samotragus* are similar to that of *Oioceros*, but are larger and stronger (Sickenberg 1936; Bouvrain & Bonis 1985). They also differ from the horn-cores of *Shaanxispira* in that the horn-cores are lyrate, the lateral groove is present, and the horn-cores are inserted above the orbits.

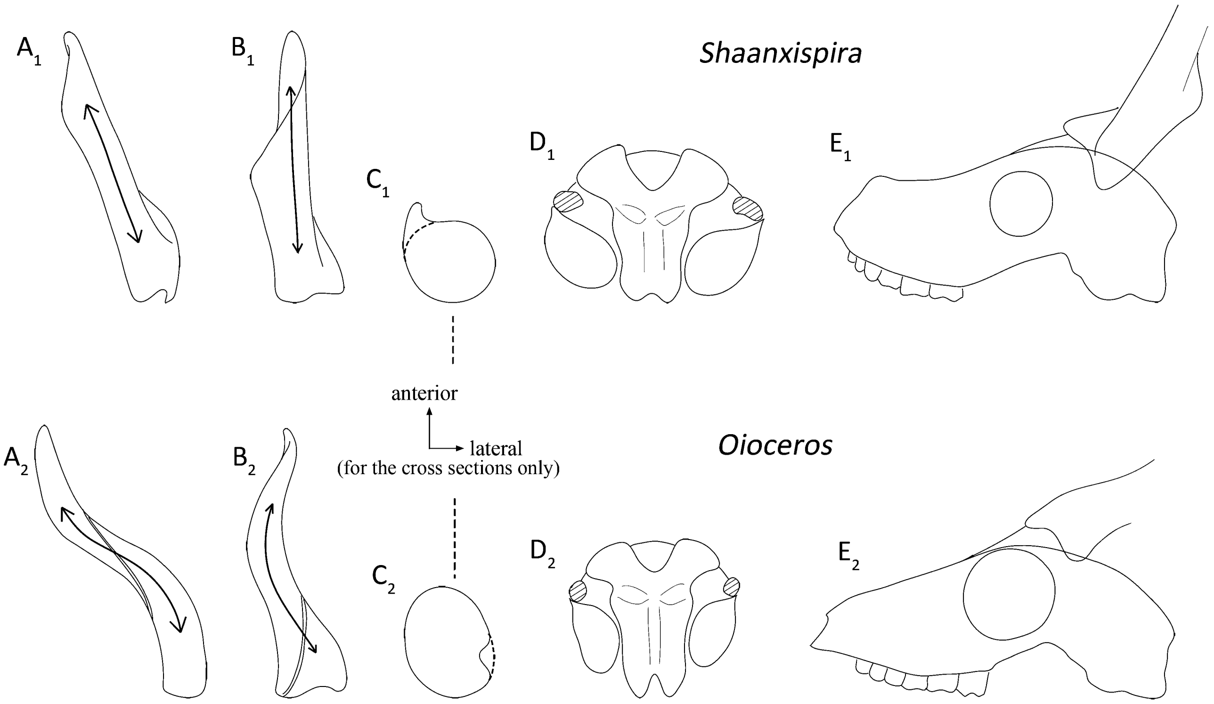

FIGURE 6. Comparison of the horn-cores and skulls in *Shaanxispira* and *Oioceros*. (A) anterior view of the right horn-core, (B) right lateral view of the right horn-core, (C) cross-section of the right horn-core at the base, (D) outline of the basicranium, (E) lateral profile of the skull (the pterygoid and the adjoining bones are not shown); the figures are adjusted to similar size, and only the shapes are compared.

The horn-cores of *Samodorcas*, *Hispanodorcas, Sinotragus*, *Prosinotragus*, *Hezhengia*, and *Parurmiatherium* are also homonymously twisted (Sickenberg 1933; Bohlin 1935a; Solounias 1981; Thomas *et al.* 1982; Bouvrain & Bonis 1985; Qiu *et al.* 2000; Alcala & Morales 2006), but the twist is very weak, which distinctively differs from that of *Shaanxispira*.

(3) Comparison with other late Miocene "ovibovines"

The concept of the tribe Ovibovini is controversial, and is accepted by many researchers today as a non-monophyletic group (Bouvrain & Bonis 1984; Groves & Schields 1996; Gatesy *et al.* 1997; Lalueza-Fox *et al.* 2005; Ropiquet & Hassanin 2005; Bibi *et al.* 2009, 2012). The phylogenetic relationships of the late Miocene "ovibovines" are disputed. They are classified as Ovibovini traditionally (Solounias 1981; Qiu *et al.* 2000), or as members of a tribe of their own, Urmiatheriini (Köhler 1987; Chen & Zhang 2004, 2009). Besides, their affinities with each other were questioned and *Urmiatherium* was classified as Oiocerina or Oiocerinae by some researchers (Gentry 2010; Kostopoulos 2014). The strengthening of the atlanto-cranial joint, which is an important character of *Ovibos* and late Miocene "ovibovines," is probably linked to agonistic behavior and might therefore occur of convergence (Geraads & Spassov 2008). Regardless, the specialized features of the cranium, especially the shortened condyles and the developed accessory articular surfaces, are not observed in other bovids, and it is possible that they evolved from a common ancestor. Therefore, in this paper, we follow the traditional opinion and still treat them as Chinese late Miocene "ovibovines."

Lantiantragus is a late Miocene "ovibovine" only found in the Lantian area (Chen & Zhang 2004). It was described based on muzzle and dentition features. Chen and Zhang (2004) separated *Lantiantragus* from *Shaanxispira* for two reasons: 1) although the dentitions of the two genera are similar to each other, the features are not distinct and could hardly be distinguished from other late Miocene "ovibovines"; 2) *Shaanxispira* has lower and wider muzzle, wider nasals, shallower pre-orbital fossae, more prominent maxillary tuberosities, larger premolar to molar ratio, sharper metastyle on P4, more developed mesostyles on the upper molars, and more lingually positioned enamel islands. However, these reasons are not very convincing. The material of

Lantiantragus is laterally compressed, so the muzzle and the nasals seem narrower. The pre-orbital fossae and the maxillary tuberosities are not much different, and the teeth are similar. The premolar to molar ratio of *Lantiantragus* is 58.9%, whereas in *Shaanxispira*, the ratio is 54%. Unfortunately, the tip of muzzle is missing in *Shaanxispira*, and the most distinctive structure of *Lantiantragus* is the long slender tip of muzzle. Anyway, these two genera are very similar to each other, and more materials are needed in order to clarify their relationships.

Based on the characteristics of the teeth and skull, *Shaanxispira* is also closely comparable with *Plesiaddax* and *Hezhengia*. All of them have similar length of dentition, shortened premolar row, mesodont and square upper molars, simple outlines of fossettes, round labial walls of protoconid and hypoconid, short and wide braincase, relatively large muzzle, large mastoid portion, strong paroccipital process, thickened basioccipital, enlarged posterior tuberosities, prominent pterygoid crest, elongated palatine, and anteriorly positioned upper dentition. The muzzle is low and narrow.

The insertion of the horn-cores of *Shaanxispira* is upright or slightly inclined, which is quite different from that of *Plesiaddax* and *Hezhengia*, whose horn-cores are laterally directed. The long and straight shape of horn-cores in *Shaanxispira* is also less specialized than that in *Plesiaddax* and *Hezhengia*, whose horn-cores are shortened and thickened to various degrees (Bohlin 1935a; Köhler 1987; Qiu *et al*. 2000). The short and strong occipital condyles and presence of accessory articular surfaces are thought to be important to the classification of Ovibovini (Bohlin 1935a), but both features are absent in *Shaanxispira*. However, the thickened paroccipital process and the shallow depression between paroccipital process and basioccipital in *Shaanxispira* are also different from the common state in other bovids with large horn-cores like sheeps and goats, which have thinner paroccipital processes and deeper depressions. The reinforcement of the posterior part of the basicranium might prelude to the development of the accessory articular surfaces that occurs in *Hezhengia* and *Plesiaddax*. Conversely, the homonymous twist of the horn-cores and the well-developed antero-medial keel are apomorphic characters and are not found in other ovibovines, which might imply an evolutionary divergence from other late Miocene "ovibovines."

Other late Miocene "ovibovines"—*Urmiatherium* and *Tsaidamotherium*—are also similar (Bohlin 1935a; Geraads & Spassov 2008; Jafarzadeh *et al*. 2012; Shi 2014). Both of them have mesodont or hypsodont upper molars, with simple outlines of fossettes, short braincase, and posteriorly positioned orbits, just as in *Shaanxispira* (Fig. 6). However, these genera have distinctly specialized horn-cores and muzzle, indicating probable different evolutionary directions. The horn-cores of *Urmiatherium* are short and close to each other, partially or almost totally fused, and bear exostoses that extend anteriorly and posteriorly onto the frontals and the parietal (Mecquenem 1925; Bohlin 1935a; Jafarzadeh *et al*. 2012). The horn-cores of *Tsaidamotherium* are unique, with the horn-core proper retracted, and a plate-like horn apparatus formed upon the cranium (Bohlin 1935b; Shi 2014). In addition, the facial features are different as well. The muzzle is deepened in *Urmiatherium*, whereas it is much shortened in *Tsaidamotherium*. The accessory articular surfaces are well developed in both genera.

Conclusions

The new species of *Shaanxispira* described in this paper is the first confirmed discovery of this genus outside the Lantian area. The preservation of the specimen is better than that of any other previously found specimens of *Shaanxispira*, providing new information and allowing more detailed analysis of the genus. Although the new species is earlier than the Lantian species, it has more specialized horn-cores, indicating a different lineage than the Lantian species.

Bovids with homonymously twisted horn-cores were reported from Eurasia in late Miocene deposits, however, *Shaanxispira* is the only bovid having straight horn-cores, protruding antero-medial keel, but without lateral groove. With shorter braincase, larger muzzle, more posteriorly positioned orbits, shorter basicranium, and smaller premolar to molar ratio, *Shaanxispira* is probably not closely related to other bovids with homonymously twisted horn-cores like *Oioceros*, but might be a member of the late Miocene "ovibovine" group. Although the phylogenetic relationships of the late Miocene "ovibovines" are still in debate, and most of them have specialized horn-cores and skulls, they do have similarities in skull and dentition features, indicating possible affinities among these genera.

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