第64卷 第1期
2026年1月

古 脊 椎 动 物 学 报
VERTEBRATA PALASIATICA

pp. 47–58
figs. 1–6

DOI: 10.19615/j.cnki.2096-9899.251030
CSTR: 32090.14.j.cnki.2096-9899.251030

First discovery of the spiral-horned antelope *Antilospira* (Bovidae, Artiodactyla) from the Linxia Basin, Gansu, China

XU Xing-Dong[1,2] SHI Qin-Qin[1*]

(1 *Key Laboratory of Vertebrate Evolution and Human Origins*, *Institute of Vertebrate Paleontology and Paleoanthropology*, *Chinese Academy of Sciences* Beijing 100044 * Corresponding author: shiqinqin@ivpp.ac.cn)
(2 *University of Chinese Academy of Sciences* Beijing 100049)

Abstract *Antilospira* is a small to medium-sized antelope with heteronymously spiraled horn cores. It was widely distributed in northern China from the Late Pliocene to the Early Pleistocene. It is a typical fossil bovid with important implications for biostratigraphy and antilopin evolution in China. *Antilospira robusta* is a species with highly fragmentary materials and has previously only been briefly discussed. Here we report on a new frontal with horn cores from the Early Pleistocene Wucheng Loess in Nalesi Township, Dongxiang Autonomous County, Linxia Basin, Gansu Province. This new material features heteronymously spiraled horn cores, deep longitudinal grooves, a sharp anterior carena on the horn core, and a large body size, which are characteristics similar to those of *A. robusta*. However, the horn base of the new material is more compressed than all the previously discovered spiral-horned antelopes, so we attributed it to *Antilospira* cf. *A. robusta*. This is the first time *Antilospira* has been found in northwestern China, and this discovery provides more morphological data for the classification of this group. CT scans of the horn core reveal the well-remodeled horn core trabeculae in *Antilospira*, which is different from what is observed in *Spirocerus*. The frontal sinuses are moderately developed in the Linxia specimen, extending backwards to the orbit but not to the horn base. The virtual reconstruction of the endocranial cast indicated that *Antilospira* has bending and narrow frontal lobes, wide temporal lobes, and relatively complex sulci on the cerebral hemisphere, which differ from extant Antilopini bovids in China.

Key words Linxia Basin, Early Pleistocene, spiral-horned antelope, bovid

Citation Xu X D, Shi Q Q, 2025. First discovery of the spiral-horned antelope *Antilospira* (Bovidae, Artiodactyla) from the Linxia Basin, Gansu, China. Vertebrata PalAsiatica, 64(1): 47–58

1 Introduction

In the Pliocene to Pleistocene strata of northern China, fossil bovids with heteronymously twisted horn cores (the left horn core twist counterclockwise from base to top) are common,

国家自然科学基金(批准号：42472042)和中国科学院古脊椎动物与古人类研究所自主部署项目资助。
收稿日期：2025-07-01

such as *Antilospira*, *Spirocerus*, *Sinoreas*, and *Lyrocerus* (Teilhard de Chardin and Trassaert, 1938; Bai et al., 2019; Tong et al., 2022; Zhang et al., 2024). These fossil bovids with heteronymously twisted horn cores mainly belong to two bovid groups. *Sinoreas* and *Lyrocerus* are considered to be large caprines, which are currently known only from the Pliocene strata of Yushe, Shanxi (Zhang et al., 2024). *Antilospira*, *Spirocerus* and the recently reported *Gazellospira* are medium to large sized antilopins, which are very common in Eurasia in the Pliocene and Pleistocene with many fossil materials and taxa (Boule et al., 1928; Teilhard de Chardin and Yang, 1931; Teilhard de Chardin and Trassaert, 1938; Sokolov, 1959; Kambaritdinov, 1966; Vangengeim et al., 1966; Alekseeva, 1977; Dmitrieva, 1977; Sharapov, 1986; Duvernois and Guérin, 1989; Athanassiou, 2005; Garrido, 2008; Dong et al., 2009; Rodrigo, 2011; Bellucci and Sardella, 2015; Bai et al., 2019; Hermier et al., 2020; Vislobokova et al., 2020; Tong et al., 2022; Wang et al., 2023). *Antilospira* and *Spirocerus* are mainly discovered in China, Russia, Mongolia, and Kazakhstan, and are important indicators for reconstructing paleoclimates and paleoenvironments (Zhang et al., 2024). In contrast, *Gazellospira* are mainly discovered in Europe and West Asia, but they are also reported from the Zanda region of the Tibetan Plateau (Wang et al., 2023). Despite the close relationships among *Antilospira*, *Spirocerus*, and *Gazellospira*, their phylogenetic status is highly debatable (Pilgrim, 1939; Bai et al., 2019; Hermier et al., 2020). Bai et al. (2019) claimed that these genera are closely related to extant *Tragelaphus*, whose horn cores are similarly heteronymously twisted, and assigned these genera to the subfamily Bovinae. However, Hermier et al. (2020) considered Rodrigo's (2011) cladistic analysis to be much more robust, which indicates *Gazellospira* as a stem antilopin. The classification at the species level is even more debatable. For example, *Antilospira zdanskyi* from the Yushe Basin was considered a synonym of *Spirocerus wongi* by Bai et al. (2019), but it has been referred to as *Gazellospira* in recent studies (Hermier et al., 2020; Wang et al., 2023). Fragmentary remains from the Yushe Basin, Shanxi Province, have also been reassigned to *Gazellospira* by the latter. Zhang et al. (2024) followed the traditional opinion. They retained *A. zdanskyi* in the genus *Antilospira*, noting that the primary difference between *Antilospira* and *Spirocerus* is that the horn cores of *Antilospira* are spirally arranged. In contrast, the horn cores of *Spirocerus* are torsioned.

Recently, a frontlet with spiral horn cores was collected for the first time in the Wucheng Loess of the Early Pleistocene in the Linxia Basin, Gansu. This discovery provides more fossil material and clues for the morphological and phylogenetic studies of this clade. The new material was excavated at the Shitougou fossil locality (LX0201) in Nalesi Township, Dongxiang County, Linxia, Gansu Province (Fig. 1). The new find belongs to the Early Pleistocene Longdan fauna. The fossil layer dates from 2.15 Ma to 2.58 Ma, and fossils of *Sivapanthera linxiaensis* have been reported here (Qiu et al., 2002, 2004).

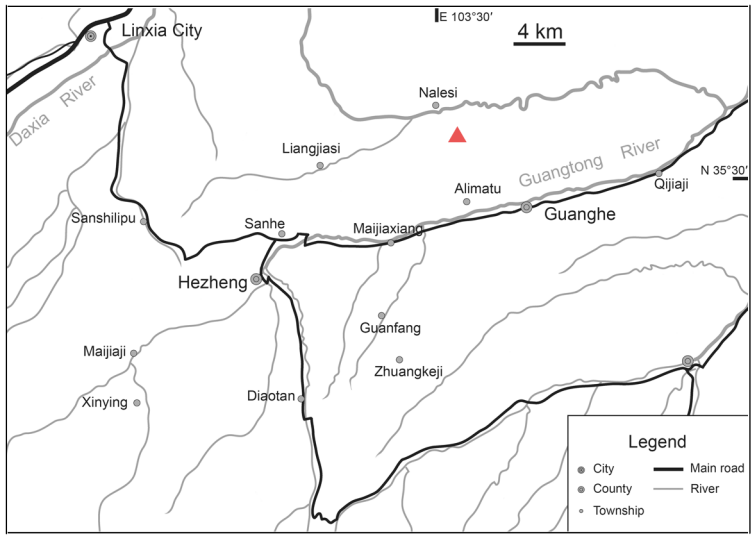

Fig. 1 Geographic map of China and Nalesi Village, Linxia Basin, Gansu Province
A red triangle labels the Shitougou locality (LX0201)

2 Materials and methods

The specimen described in this paper is housed at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP). The terminology and measurement of the skull and horn core follow Teilhard de Chardin and Trassaert (1938). For example, "carena" is the keel along the horn core, which is also called "carina" or "keel" (Sokolov, 1959; Bai et al., 2019). Ribbons are horn core surfaces divided by two carenas. Ribbon 1 is the zone above the anterior carena at the horn base in anterior view, and ribbon 2 is the zone below the anterior carena (Fig. 2). The terminology of the endocranial cast follows Evans and de Lahunta (2013) and Edinger (1948). All measurements were taken using a caliper with an accuracy of 0.1 mm. We use the 450 kV CT scanner at the IVPP to get the internal features of the frontal bone and horn core. The 3D reconstruction was performed using VGStudio 3.0 and Mimics 21.0.

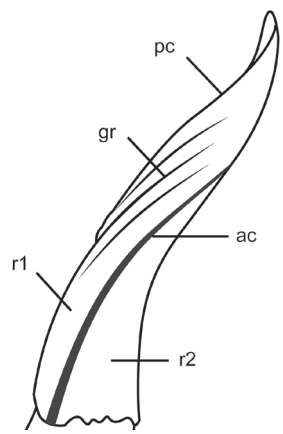

Fig. 2 Schematic diagram of the left horn core of *Antilospira* in anterior view
Abbreviations: ac. anterior carena; gr. groove; pc. posterior carena; r1. ribbon 1; r2. ribbon 2

3 Systematic paleontology

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821

***Antilospira* Teilhard de Chardin & Young, 1931**

Antilospira cf. *A. robusta* Teilhard de Chardin & Piveteau, 1938

Referred material IVPP V28541, a frontlet with two horn cores.

Description The frontal of V28541 is preserved from the supraorbital foramen to the fronto-parietal suture. The distal parts of the two horn cores are both missing. The deformation is weak (Fig. 3, Table 1).

In the anterior view, horn cores are moderately divergent, and the divergence angle is approximately 75° (Fig. 3A). The horn cores are spiral and loosely torsioned. The remaining horn core exhibits approximately half a circle, so the complete horn core spiral is probably less than a circle. The surface of the horn core is rough. Originating from the anteromedial side of the horn base, the anterior carena is evident and sharp. In contrast, the posterior carena originates postero-laterally at the horn base, which is weak and round, and becomes weaker upwards. Ribbon 1 is convex, with a wide and deep groove parallel to the anterior carena. This groove is weak near the base of the horn core but becomes prominent in the distal part. Ribbon 2 is relatively flat, with only a shallow groove. The horn cores have strong anterolateral-posteromedial compression at the base, with a compression index of approximately 55%. In the lateral view, the horn cores are positioned directly above the orbits and incline noticeably backwards (Fig. 3C). The pedicle is short.

The internal structures of the right horn core were examined by using the CT scan machine. The cross-section is elongated, elliptical at the horn base, nearly circular at half length, and compressed and olive-shaped close to the top of the preserved section (Fig. 4A).

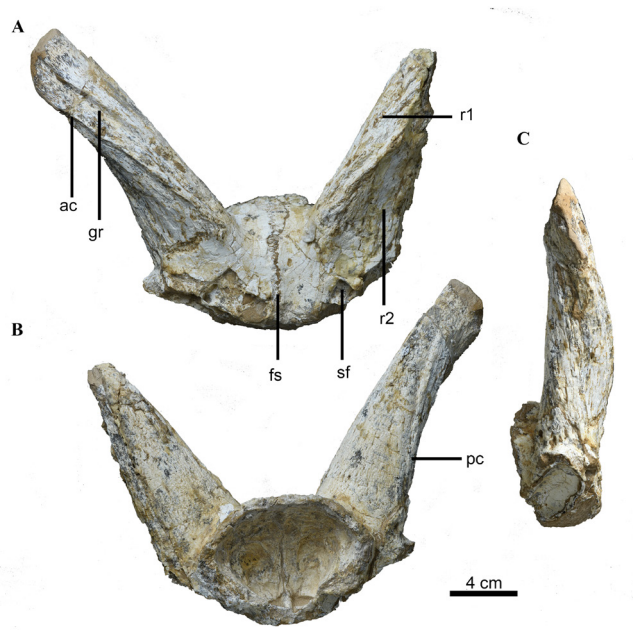

Fig. 3 Photograph of *Antilospira* cf. *A. robusta* (IVPP V28541) from Linxia Basin in anterior (A), posterior (B) and right side (C) views
Abbreviations: fs. frontal suture; sf. supraorbital foramen. Other abbreviations are defined in Fig. 2

Table 1 Measurements of the horn cores of *Antilospira* cf. *A. robusta* (IVPP V28541) (mm)

Items	Measurements
Anteromedial-posterolateral diameter of the horn base (APD)	56.3 (L), 57.8 (R)
Transverse diameter of the horn base (TD)	31.1 (L), 32.6 (R)
Maximal diameter at the half	37.3 (R)
Minimal diameter at the half	28.7 (R)
Distance between the horn bases	27.2
Distance between the supraorbital foramina	59.5
Horn length, preserved	141.0 (L), 163.0 (R)

The anterior carena of the right horn core twists evenly upwards, with ribbon 1 and ribbon 2 on its two sides. At the horn base, ribbon 1 is more convex and longer than ribbon 2 in the cross-section. In contrast, ribbon 2 becomes more convex and longer in the cross section in the upper half of the horn core (Fig. 4A). The spiraled horn core has undergone strong remodeling, with irregular trabeculae and unevenly thick compact bone. The bone wall of ribbon 1 is markedly thicker and denser than ribbon 2, especially in the lower half of the horn core. Along the longitudinal groove, the compact bone wall is almost absent, probably due to bone resorption after the horn core growth (Fig. 4). The center of the horn core is porous, with relatively larger sinuses, which extend longitudinally along the horn core. However, these sinuses are irregular in the cross sections and do not form a long straight canal as in *Spirocerus wongi* (Fig. 4B; Tong et al., 2022).

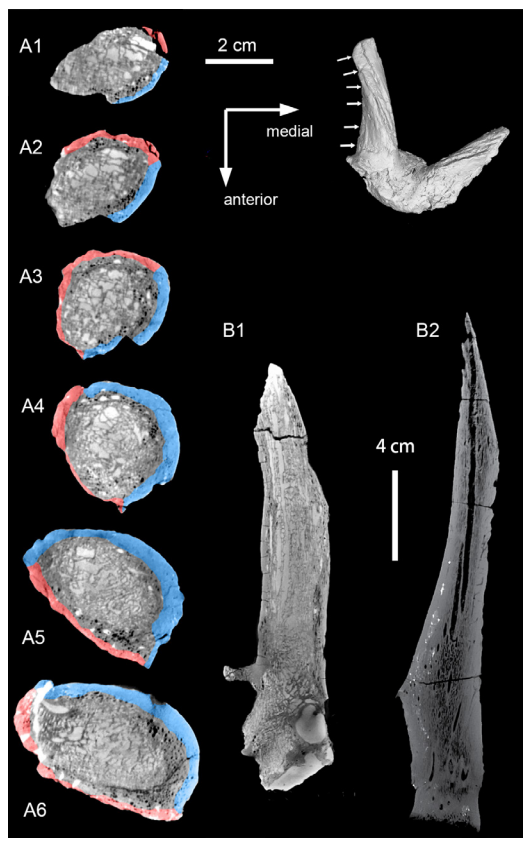

Fig. 4 Cross and sagittal sections of the right horn core of *Antilospira* cf. *A. robusta* (IVPP V28541) from Linxia Basin
A. cross section from tip to base (1–6);
B. comparison of the sagittal sections of the horn cores in *Antilospira* (B1) and *Spirocerus* (B2)
The bone wall of ribbon 1 in A is indicated in blue, and the bone wall of ribbon 2 is indicated in red
B2 is modified from Tong et al. (2022)

The frontal bone anterior to the horn core is broad and flattened, and the frontal curves slightly between the horn cores (Fig. 3). The interfrontal suture is clear, with slight elevation. The supraorbital foramen sunk deeply in a large and deep fossa, which is nearly triangular. The supraorbital foramina are wide apart, but are close to the horn base, with a distance of approximately 2–3 cm. The frontal bone is moderately thick with moderate frontal sinuses seen in

bovids (Farke, 2010). The frontal sinuses pervade into the frontal anteriorly, but do not extend backwards to the horn base (Fig. 5A).

Only the anterior half of the braincase was preserved. The cerebral hemisphere of *Antilospira* cf. *A. robusta* is wide. In dorsal view, the endocranial cast narrows strongly from the temporal lobe to the frontal lobe (Fig. 5C). The frontal lobe of *A.* cf. *A. robusta* are different from the extant antilopins in China, such as *Procapra gutturosa* and *Gazella subgutturosa*, whose brains are typically pear-shaped, and the frontal lobe has straight or convex lateral profiles in dorsal view. In lateral view, the dorsal profile bends down between the frontal lobe and the parietal lobe (Fig. 5D). The sulci on the endocranial cast are relatively clear. The sulci above the Sylvian sulcus are complicated by the presence of ectosylvian sulcus beneath suprasylvian sulcus (Fig. 5D).

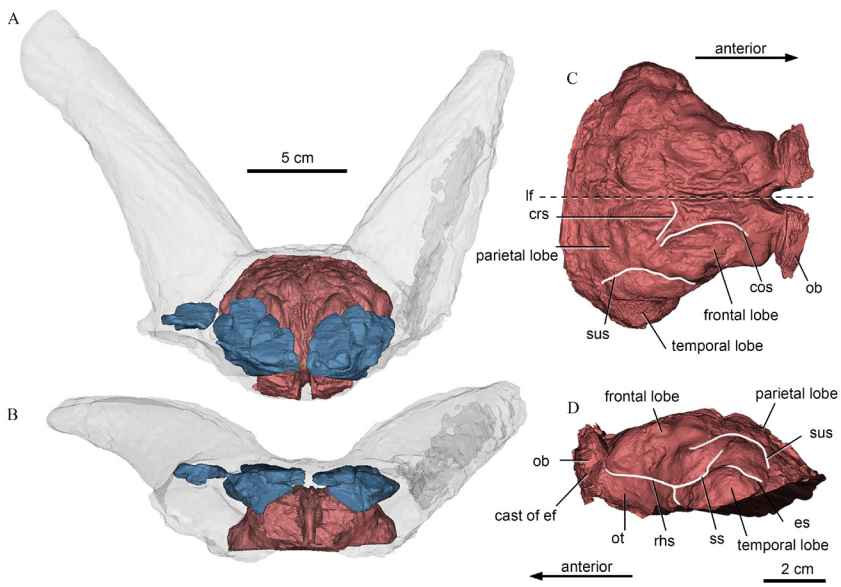

Fig. 5 3D reconstruction and endocranial cast of *Antilospira* cf. *A. robusta* (IVPP V28541) from Linxia Basin
A, B. 3D reconstruction of the frontal sinuses (blue), endocranial cast (red), and the skull (transparent) in frontal (A) and anterior (B) views; C, D. virtual reconstruction of the endocranial cavity in dorsal (C) and left lateral (D) views. The main sulci are indicated with white lines
Abbreviations: cos. coronal sulcus; crs. cruciate sulcus; ef. ethmoidal foramen; es. ectosylvian sulcus; lf. longitudinal fissure; ob. olfactory bulb; ot. olfactory tract; rhs. rhinal sulcus; ss. Sylvian sulcus; sus. suprasylvian sulcus

4 Comparison and discussion

With heteronymously spiraled horn cores, relatively weak torsion, evident anterior carena and deep longitudinal grooves on the horn core, compressed horn base, large pits around the supraorbital foramen, flat frontal anterior to the horn bases, and a large body size, the new specimen is most similar to *Antilospira robusta* from the Yushe Basin. However, the horn

base of the new specimen is much more compressed than all other spiral-horned antelopes. Considering that there is only one specimen from the Linxia Basin, we are not sure whether it is a stable difference or within the intraspecific variation. Thus, we refer the new material from the Longdan fauna to a conformis species of *A. robusta* (Fig. 6).

Four species of *Antilospira* have been described to date. The type species, *A. licenti* (Teilhard de Chardin and Yang, 1931), was first discovered in the Late Pliocene strata of Jingle, Shanxi. This small-sized antelope also represents the most abundantly documented species in the genus, with fossil specimens subsequently reported from Hebei, Shanxi, and Gansu (Tang, 1980; Chen, 1994; Zhang et al., 1999). The new material differs from *A. licenti* in its considerably larger body size, more compressed horn cores, and weaker posterior carenas. *A. yuxianensis*, named by Tang (1980) based on specimens from Yuxian, Hebei, is currently recognized as a junior synonym of *A. licenti* (Zhang et al., 2009; Bai et al., 2019).

?*Antilospira gracilis*, *A. zdanskyi*, and *A. robusta* were first discovered in Yushe, Shanxi. ?*Antilospira gracilis* and *A. zdanskyi* were found in Late Pliocene strata, whereas *A. robusta* was found in Early Pleistocene strata (Teilhard de Chardin and Trassaert, 1938; Zhang et al., 2024). ?*Antilospira gracilis* is relatively small-sized; in contrast, the new material exhibits a larger body size and horn cores with more anteroposterior compression. However, both

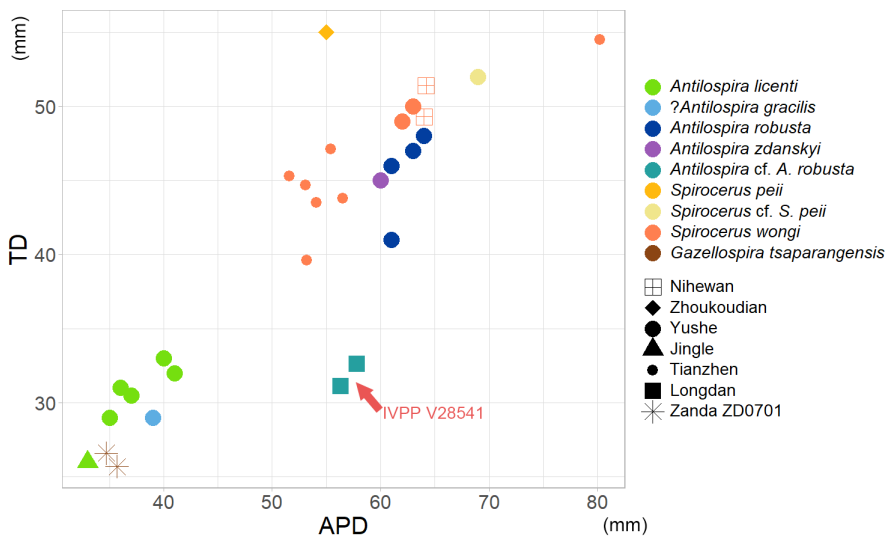

Fig. 6 Comparison of the horn base diameters of *Antilospira*, *Spirocerus*, and *Gazellospira* species found in China

Data for *A. licenti*, ?*A. gracilis*, *A. robusta* are from Teilhard de Chardin and Trassaert (1938), data for *A. zdanskyi* are from Teilhard de Chardin and Trassaert (1938), and Bai et al. (2019), data for *S. wongi* are from Teilhard de Chardin and Trassaert (1938), and Tong et al. (2022), data for *S. peii* is from Yang (1932), data for *S.* cf. *S. peii* is from Teilhard de Chardin and Trassaert (1938), data for *G. tsaparangensis* are from Wang et al. (2023)

Abbreviations: APD. anteromedial-posterolateral diameter of the horn base; TD. transverse diameter of the horn base

share a similar concentration of grooves on ribbon 1. Notably, no fossil specimens beyond the holotype have been attributed to ?*A. gracilis*.

Antilospira zdanskyi is a relatively large species within the genus *Antilospira.* The new material approaches it in body size and similarly possesses deep and enlarged supraorbital foramina. However, the horn cores of the new material are more compressed, with weakly developed posterior carenas and a greater number of grooves on the surface. The taxonomic classification of *A. zdanskyi* remains a subject of controversy. Based on their study of fossils from Tianzhen, Shanxi Province, Bai et al. (2019) assigned this taxon to *Spirocerus wongi*, proposing *A. zdanskyi* as a junior synonym of *S. wongi*. However, a comparative examination of their horn cores reveals evident morphological distinctions between spiral and twist. Moreover, the posterior carena of the *S. wongi* horn core is markedly less developed than that of *A. zdanskyi*. Additionally, *Antilospira* exhibits a gradual increase in size over time, while *Spirocerus* demonstrates a progressive decrease in size (Tong et al., 2022). Therefore, body size cannot serve as a diagnostic criterion for taxonomic assignment of these sympatric taxa during the Late Pliocene, thus precluding their synonymization (Fig. 5). Hermier et al. (2020) proposed synonymizing *A. zdanskyi* with *Gazellospira gromovae* under the new combination *Gazellospira zdanskyi* comb. nov. and assigned a fragmentary left horn core from Yushe to this taxon (Hermier et al., 2020; Kostopoulos, 2022). The horn core morphology of *Antilospira* and *Gazellospira* is extremely similar, with both exhibiting a heterotrophically spiral morphology. Their most significant distinction lies in the horn core surface: *Antilospira* possesses numerous longitudinal grooves and typically displays a more evident anterior carena, while *Gazellospira* exhibits a relatively smooth surface lacking distinct grooves, but features a more pronounced posterior carena (Hermier et al., 2020; Wang et al., 2023). The designation *G. zdanskyi* is justified by its relatively smooth horn core surface. However, in light of its evident anterior carena and its closer geographic and temporal proximity to the type species of *Antilospira*, we leave this debate open for future research to resolve.

Antilospira robusta likewise represents a larger morphotype within the genus. The holotype is a partial cranium with horn cores (THP (Accession number of Tianjin Natural History Museum) 14308), collected from Qingyangping (Loc. 46) in the Yushe Basin, with an age of Early Pleistocene (Teilhard de Chardin and Trassaert, 1938). Comparisons with the new material reveal shared morphological features in several aspects: these specimens exhibit comparable size, with horn cores extending posterolaterally and displaying a weak heteronymously spiral; ribbon 1 is convex, with an extremely sharp anterior carena, followed posteriorly by a deep longitudinal groove and several shallower grooves; ribbon 2 lacks well-developed longitudinal grooves; the supraorbital foramen is deeply sunken within a fossa–the external margin of which is subtriangular. However, the new material also differs in having more compressed horn cores and a smoother surface on ribbon 2. Considering these differences, we attribute the new spiral-horned antelope specimens from the Linxia Basin

to *Antilospira* cf. *A. robusta*. *Antilospira robusta* was initially considered a doubtful species of the genus *Antilospira* in its first report by Teilhard de Chardin and Trassaert (1938), and its uncertain phylogenetic position was not discussed by subsequent researchers due to the scarcity of their fossil materials (Zhang et al., 2024). Bai et al. (2019) referred to *Antilospira* without providing further discussion, and we follow them in this study. Until now, only four incomplete skulls have been described in the Early Pleistocene of Yushe, Shanxi. These specimens have massive skulls, slowly torsional horn cores, and sharp anterior carena, which distinguish them from other species within the *Antilospira* genus. However, they also share the characteristics of heteronymously twisted horn cores and longitudinal grooves with the type species *A. licenti*. There are also records of *A. robusta* in the Early Pleistocene Xinyaozi fauna, without further reports (Zhou et al., 1991).

The new material also differs from other heteronymous-horned antelopes in several ways. In contrast to *Spirocerus*, its horn core exhibits a heteronymous spiral rather than a twist, with a lower degree of torsion, higher compression, and an indistinct posterior carena. The distinction between twisted and spiraled horn cores is also manifested in their internal structure. The specimen IVPP V28650 of *Spirocerus wongi* represents the only specimen among the two genera that has undergone CT scanning to reconstruct its internal anatomy (Tong et al., 2022). Compared to V28650, the new material exhibits a larger and irregularly shaped medullary cavity within the horn core, with a shorter longitudinal extension, indicating different bone resorption and remodeling processes. Compared to *Gazellospira*, its horn core exhibits a lower degree of torsion, bears longitudinal grooves, and develops an evident anterior carena but an unevident posterior carena (Garrido, 2008).

5 Conclusions

The new specimen from the Linxia Basin is a large antelope with slowly and heteronymously spiraled horn core, sharp anterior carena, and a strongly compressed horn base, and we assign it to *Antilospira* cf. *A. robusta* temporally. The new discovery enlarges the distribution of *Antilospira* to northwest China, and increases our knowledge of this bovid clade, including *Antilospira*, *Spirocerus*, and *Gazellospira*. For the first time, we reconstructed the frontal sinuses and partial virtual endocranial cast of *Antilospira*, revealing moderate frontal sinuses and clear, complex cerebral sulci. The CT images show well developed remodeling of the horn core trabeculae in the *Antilospira*, characterized by irregular cavities in the inner medullary region and unevenly thick compact bone in the outer region.

Acknowledgements This paper is dedicated to Prof. Qiu Zhanxiang, who made significant contributions to the study of Chinese Cenozoic fossil mammals, stratigraphy, and biochronology. We thank Su Dan for preparing the fossil, Gao Wei for taking the photographs,

Chen Jin for her assistance in comparing fossil specimens housed at the IVPP, Li Dongsheng for his help in comparing extant specimens housed at the IVPP, and Hou Yemao for his assistance with CT scanning. We thank Liu Wenhui for his useful discussions. We thank the two reviewers for their helpful suggestions. This study is supported by the National Natural Science Foundation of China (42472042), and the Key Research Program of the Chinese Academy of Sciences.

甘肃临夏盆地早更新世旋角羚羊化石的首次发现

许兴栋[1,2]　史勤勤[1]

(1 中国科学院古脊椎动物与古人类研究所，脊椎动物演化与人类起源重点实验室 北京 100044)

(2 中国科学院大学 北京 100049)

摘要：旋角羚羊(*Antilospira*)是一类长有异向旋转角心的中小型牛科动物，在晚上新世至早更新世广泛分布于中国北方，是中国上新世至更新世的代表性牛科动物之一，对生物年代的判断和羚羊族动物的演化研究都具有重要意义。其中粗壮旋角羚羊(*A. robusta*)由于化石较破碎，一直缺乏相关的研究。报道了产自甘肃省临夏盆地东乡族自治县那勒寺乡早更新世午城黄土中的一件带角心的额骨新材料，其个体较大，角心异向旋转且盘旋，角基侧扁，角心表面具长而深的沟槽，前棱尖锐等特征，与榆社盆地的粗壮旋角羚羊形态最为接近；但由于临夏盆地的新材料角基部侧扁强烈，暂将其定为粗壮旋角羚羊相似种(*Antilospira* cf. *A. robusta*)。新材料的发现将旋角羚羊的分布范围扩大到中国西北地区，并为同时期具有异向旋转角心的羚羊族动物间的分类关系讨论提供了更多的形态学证据。新材料角心的CT扫描结果表明旋角羚羊的角心内部存在复杂的骨小梁重建过程。额窦的三维重建显示旋角羚羊的额窦中等程度发育，向后延伸至眼眶上缘，但没有延伸至角心基部。旋角羚羊的颅内模额叶部分明显向下弯折，颞叶宽、脑沟回较复杂，与中国现生的羚羊族动物差别较大。

关键词：临夏盆地，早更新世，旋角羚羊，牛科动物

中图法分类号：Q915.876　　**文献标识码**：A　　**文章编号**：2096–9899(2026)01–0047–12

References

Alekseeva L I, 1977. Terrestrial fauna of the Early Anthropogene of Eastern Europe. Proc All-Union Paleont Soc, 300: 214

Athanassiou A, 2005. *Gazellospira torticornis* (Aymard, 1854) from the late Pliocene locality of Sésklo (Thessaly, Greece). In: Crégut-Bonnoure E ed. Les ongulés holarctiques du Pliocène et du Pléistocène. Actes colloque international Avignon, 10–22 septembre 2000. Quaternaire, hors-sér, 2: 137–144

Bai W P, Dong W, Zhang L M et al., 2019. New material of the Early Pleistocene spiral-horned antelope *Spirocerus*. (Artiodactyla, Mammalia) from North China and a discussion on its evolution. Quat Int, 522: 94–102

Bellucci L, Sardella R, 2015. The last Antilopini bovids from the Early Pleistocene of Italy. Quat Int, 357: 245–252

Boule M, Breuil H, Licent E et al., 1928. Le Paléolithique de la Chine. Arch Inst Paléontol Hum Mém, 4: 1–138

Chen X F, 1994. Stratigraphy and large mammals of the "Jinglean" stage, Shanxi, China. Quat Sci, 4: 339–353

Dmitrieva E L, 1977. Neogene antelopes of Mongolia and adjacent territories. Joint Soviet-Mongol Paleont Exp Trans Paleontol Inst Acad Sci USSR, 6: 1–115

Dong W, Fu R Y, Feng X W et al., 2009. Late Pleistocene mammalian fauna from the Mashandong, Chaoyang, Liaoning Province. Acta Anthrop Sin, 28(1): 95–109

Duvernois M P, Guérin C, 1989. Les Bovidae (Mammalia, Artiodactyla) du Villafranchien supérieur d'Europe occidentale. Geobios, 22(3): 339–379

Edinger T, 1948. Evolution of the horse brain. Mem Geol Soc Am, 25: 1–177

Evans H E, de Lahunta A, 2013. Miller's Anatomy of the Dog. 4th ed. St. Louis: Elsevier Saunders. 1–850

Farke A A, 2010. Evolution and functional morphology of the frontal sinuses in Bovidae (Mammalia: Artiodactyla), and implications for the evolution of cranial pneumaticity. Zool J Linn Soc, 159(4): 988–1014

Garrido G, 2008. The most recent and complete set of *Gazellospira torticornis* (Bovidae, Artiodactyla, Mammalia) fossils known for the late Upper Pliocene of Western Europe (Fonelas P-1, Guadix Basin, Granada). In: Arribas A ed. Vertebrados del Plioceno terminal en el suroeste de Europa: Fonelas P-1 y el proyecto Fonelas. Publicaciones del Instituto Geologico y Minero de Espana, Cuadernos del Museo Geominero, 10: 413–460

Hermier R, Merceron G, Kostopoulos D S, 2020. The emblematic Eurasian Villafranchian antelope *Gazellospira* (Mammalia: Bovidae): new insights from the Lower Pleistocene Dafnero fossil sites (northern Greece). Geobios, 61: 11–29

Kambaritdinov R K, 1966. *Antilospira gracilis* and *Paracamelus* cf. *gigas* from the Pavlodar Pre-Irtysh Region. Dokl Akad Nauk USSR, 9: 50–52

Kostopoulos D S, 2022. The Fossil Record of Bovids (Mammalia: Artiodactyla: Ruminantia: Pecora: Bovidae) in Greece. Fossil Vertebrates of Greece, Vol. 2: Laurasiatherians, Artiodactyles, Perissodactyles, Carnivorans, and Island Endemics. Cham: Springer International Publishing. 113–203

Pilgrim G E, Schaub S, 1939. The spiral-horned antelope of the European Upper Pliocene and its systematic position. Abh Schweiz Paläontol Ges, 62: 1–30

Qiu Z X, Wang B Y, Deng T et al., 2002. Notes on the mammal fauna from the bottom of loess deposits at Longdan, Dongxiang County, Gansu Province. Quat Sci, 22(1): 33–38

Qiu Z X, Deng T, Wang B Y, 2004. Early Pleistocene Mammalian Fauna from Longdan, Dongxiang, Gansu, China. Beijing: Science Press. 1–198

Rodrigo M A, 2011. The Villafranchian bovids of La Puebla de Valverde and Villarroya: systematics, phylogeny and paleobiology. Ph. D Thesis. Zaragoza: Faculty of Geological Sciences, Department of Earth Sciences, Paleontology Area, University of Zaragoza, Spain. 1–317

Sharapov S, 1986. The Kuruksay complex of Upper Pliocene mammals of the Afghan-Tadzhik Depression. In: Proceedings of the Academy of Sciences of the Tajik SSR, Vol. 300. Dushanbe: Donish. 1–232

Sokolov I I, 1959. On the postcranial skeleton and the outward appearance of *Spirocerus kiakhtensis* M. Pavlova. Vert PalAsiat, 3(1): 23–33

Tang Y J, 1980. Note on a small collection of Early Pleistocene mammalian fossils from northern Hebei. Vert PalAsiat, 18(4): 314–323

Teilhard de Chardin P, Young C C, 1931. Fossil mammals from Northern China. Palaeontol Sin, Ser C, 9: 1–67

Teilhard de Chardin P, Trassaert M, 1938. Cavicornia of south-eastern Shansi. Palaeontol Sin, New Ser C, 6: 1–98

Tong H W, Zhang B, Chen X et al., 2022. New fossils of small and medium-sized bovids from the Early Pleistocene Site of Shanshenmiaozui in Nihewan Basin, North China. Vert PalAsiat, 60(2): 134–168

Vangengeim E A, Beliajeva E I, Garutt V E et al., 1966. Mammals of the Eopleistocene Key Sections of the Western Transbaikalia. Moscow: Nauka Press. 1–163

Vislobokova I A, Titov V V, Lavrov A V et al., 2020. Early Pleistocene spiral-horned Antelopes (Artiodactyla, Bovidae) from the Taurida Cave (Crimea, Russia). Paleontol J, 54: 81–90

Wang X M, Li Q, Tseng Z J, 2023. A new spiral-horned antelope, *Gazellospira tsaparangensis* sp. nov., from Pliocene Zanda Basin in Himalaya Mountain. J Mamm Evol, 30(4): 1067–1088

Young C C, 1932. On the Artiodactyla from the *Sinanthropus* Site at Choukoutien. Palaeontol Sin, Ser C, 8: 1–100

Zhang Y X, Sun D H, An Z S, 1999. Mammalian fossils from late Pliocene (Lwer MN 16) of Lingtai, Gansu Province. Vert PalAsiat, 37(3): 190–199

Zhang Z Q, Chen G F, 2009. Taxonomy and evolutionary process of Neogene Bovidae from China. Vert PalAsiat, 47(4): 265–281

Zhang Z Q, Wang L H, Chen G F et al., 2024. Palaeovertebrata Sinica, Vol. III, Fasc 9(2). Beijing: Science Press. 1–354

Zhou T R, Li H Z, Liu Q S et al., 1991. Cenozoic Paleogeography of the Nihewan Basin. Beijing: Science Press. 1–162