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A new spiral-horned antelope, *Gazellospira tsaparangensis* sp. nov., from Pliocene Zanda Basin in Himalaya Mountain

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Abstract

Explorations in the past 20 years in the Plio-Pleistocene Zanda Basin (3,800–4,500 m above sea level) along the northern slopes of the Himalaya Mountains have substantially enriched our understanding of the paleoenvironments of the Tibetan Plateau and associated biologic evolution. Many elements of the mammalian fauna recovered are either new to science or shed new light about their special adaptations in this high elevation basin. Here we describe a new species of twisted-horned antelope, *Gazellospira tsaparangensis*, with a heteronymous spiral. Its small size and primitive morphology, such as relatively short horncore with less twisting, thin frontal bones, a lack of frontal and horncore sinuses, small size of supraorbital foramina, and lack of an anterior keel, helps to place it at the base of genus *Gazellospira*, substantially more stem-ward than the type species *G. torticornis* from the Plio-Pleistocene of Europe and western Asia. With an estimated age of 3.62 Ma, this also places *G. tsaparangensis* as one of the early occurrences in Eurasia, although some fragmentary records in Turkey may be slightly earlier. Considering this early appearance and primitive morphology, *G. tsaparangensis* once again may be a case of the ‘out-of-Tibet’ model of megafauna origin, with earlier progenitors adapted to cold environments in high Tibet before expanding their range to the rest of Eurasia.

Keywords Bovidae · *Gazellospira* · Tibetan Plateau · Zanda Basin · Zoogeography

Introduction

Gazellospira Pilgrim and Schaub is a spiral-horned antelope widely known in the Plio-Pleistocene of Europe and western Asia, especially in countries surrounding the Mediterranean and ancient Paratethys seas (Fig. 1). Commonly recognized by a single species, *G. torticornis*, it occurs in more than

30 European and western Asian localities and is known by nearly complete cranial and postcranial skeletons (Pilgrim and Schaub 1939; Garrido 2008; Hermier et al. 2020). Although initially thought as related to the living blackbuck, *Antelope cervicapra*, from India (Pilgrim and Schaub 1939), and recent authors generally include it in the tribe Antilopini (Garrido 2008; Hermier et al. 2020), *Gazellospira* may not be closely related to any living taxa. Because of the abundant fossil records in Europe and western Asia, *Gazellospira* was adopted as a taxon with zoogeographic and biochronologic significance (Duvernois and Guérin 1989; Masini and Torre 1989; Van Couvering 1997; Gliozzi et al. 1998; Geraads 2010; Rook and Martínez-Navarro 2010; Raffi et al. 2020), e.g., Agustí et al. (2001) and Cregut-Bonnoure (2007: fig. 1) listing *G. torticornis* as a first appearance datum for the Neogene European Mammal Zonation MN16 (3.2–2.5 Ma).

The genus *Gazellospira* was recently recognized by Hermier et al. (2020) in the Pliocene of Asia, as indicated by the species *G. zdanskyi* (Teilhard de Chardin and Trassaert 1938) from the Yushe Basin in Shanxi Province, China and also from Kuruksay Suite of Tajikistan (previously under the name *G. gromovae* Dmitrieva, 1975). However, the

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Fig. 1 Known fossil records of *Gazellospira* in Eurasia. Distribution of *G. torticornis* follows that of Hermier et al. (2020: fig. 1). Map is based on Google Earth image [Google Earth Pro (Version 7.3.6.9345) 2023]

Yushe form, based on horncores and skull fragments, is substantially different from the type species *G. torticornis*, and its new generic assignment by Hermier et al. remains to be confirmed by future discoveries.

Recent discovery of horncore materials from the Pliocene Zanda Basin in Himalayan Mountain (Figs. 2, 3) can be assigned to *Gazellospira*. Although represented by two horncores only, sufficient morphologic features are preserved to be recognized as a distinct species. This paper provides a detailed description and analysis of the Tibetan materials, and suggests another potential case of the out-of-Tibet model of megafaunal evolution (Deng et al. 2011).

Materials and methods

Definitions of terms

Horn torsion: A torsioned horncore is relatively straight with “screw” type twisting of keels (Kostopoulos 2014), i.e., it lacks a spiral (see below).

Horn spiral: A spiraled horncore is helicoidally twisted around a straight axis in the center (Kostopoulos 2014),

which may also be referred to as openly spiraled (Hermier et al. 2020). Bai et al. (2019: p. 95) defined spiral as “ideal axis of torsion becomes tangent or external to the surface of the horn.”

Horn twists: Twisting of horns refers to either torsion or spiral, often both.

Homonymous/heteronymous twists: We follow Kostopoulos (2014: p. 9) in defining homonymously twisted horncores as those with the left horncore twisted clockwise from the base up (viewed from the top down), and heteronymous horncores with the left horncore twisted anticlockwise from the base up [which is oppositely defined by Rowan et al. (2015) and Bibi et al. (2017) but arriving at the same characterizations of twist because these authors presumably viewed the horns from base up]. Homonymously torsioned horns have also been termed “inverse torsioned” (Kostopoulos 1997) or “inwardly torsioned” (apparently also viewed from top down) (Chen and Zhang 2009). Gentry and Heizmann (1996) and Gentry (2003) did not use the terms homonymous and heteronymous, but they appear to define the torsion by viewing from the bottom up, i.e., they characterized *Prostrepsiceros* with “anticlockwise

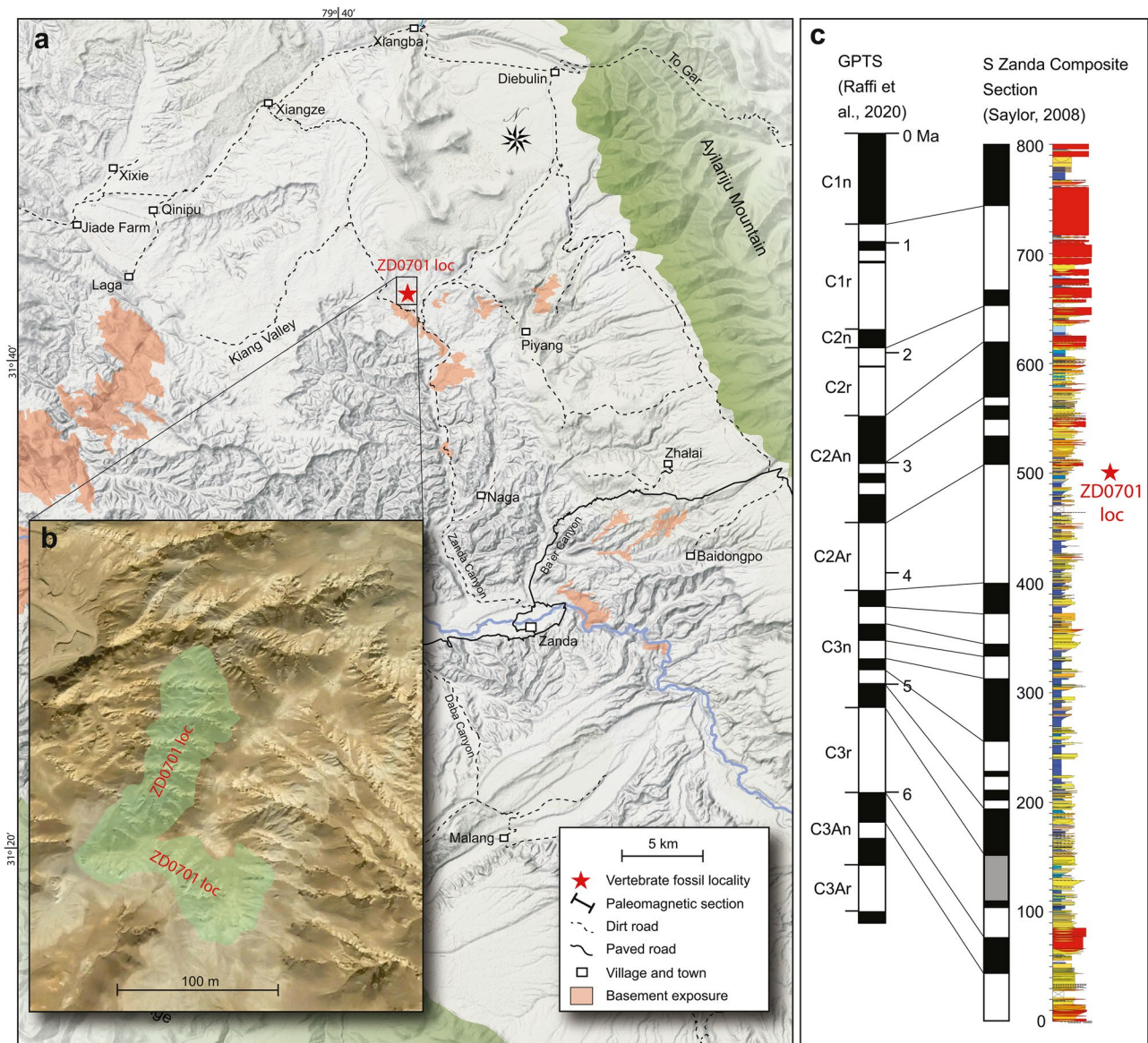


Fig. 2 Geographic and stratigraphic context. **a.** map of Zanda Basin and ZD0701 locality (red star), as modified from Wang et al. (2013: fig. 2). **b.** inset map of strata producing fossils from ZD0701 locality

(shaded green). **c.** generalized lithostratigraphic and magnetostratigraphic columns, as modified from Saylor (2008) and Wang et al. (2013: figs. 4, 5)

torsion on the right side”, which by Kostopoulos’s definition should be heteronymous.

Horncore keels: Keels refer to longitudinal crests or ridges along the length of horncores (Kostopoulos 2009). Other authors may use the term carina (Teilhard de Chardin and Piveteau 1930; Bai et al. 2019).

Ribbons: Ribbon 1 refers the longitudinally twisted zone running immediately above anterior keel and ribbon 2 that below the anterior keel (Bai et al. 2019).

3D models by laser scans

Individual bones were scanned using a NextEngine scanner (model 2020i) in combination with ScanStudio software

(version 2.0.2). Specimens were usually scanned in the highest resolution in the “Macro” setting, which has a 0.005” accuracy (~40,000–160,000 points/square inch or about 6,200–24,800 points/square cm). Typically, two sets of 360° scans (at intervals of 22.5°) were obtained, and manually aligned and fused into a single model. Scans were saved in the PLY format that preserves texture information. Size scale was captured by build-in calibrations of the NextEngine scanner.

Virtual cross sections of the horncores are derived from above 3D laser scan models using MeshLab’s (v2020.07; <https://www.meshlab.net/>) build-in function of “Compute Planar Section”. The cross-section outlines were then traced in Adobe Illustrator.

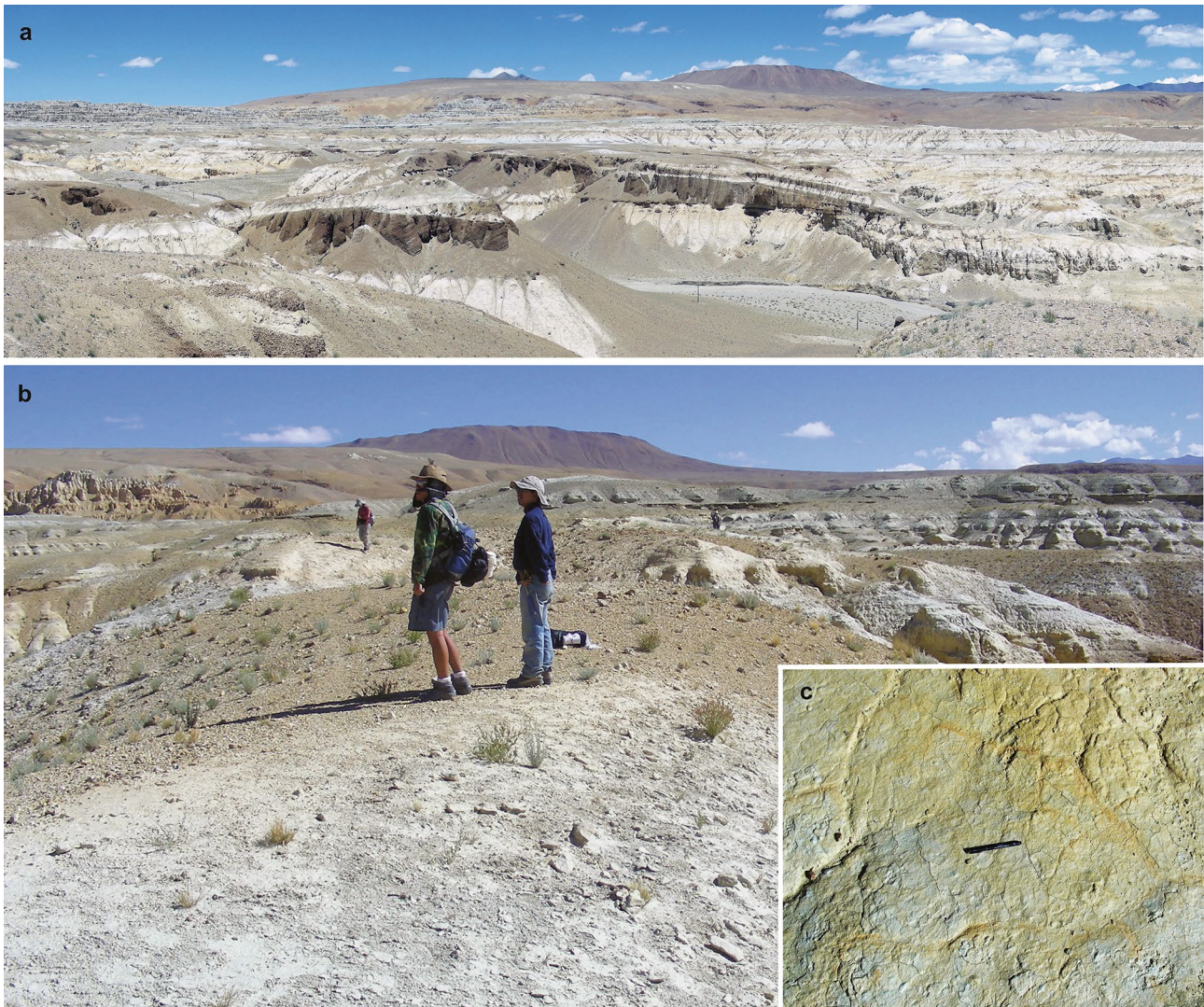


Fig. 3 Geological context. **a.** panoramic view (looking to the east) showing general stratigraphy near ZD0701 loc., photo taken at N 31° 41' 54" E 79° 43' 01", about 900 m south of ZD0701 locality. **b.** photo of ZD0701 locality looking toward east; fossil-rich exposures are along the edges of a small platform, where two persons in

foreground, ZJT and Gary Takeuchi, are standing. **c.** close up of fine-grained sediments with mud cracks, suggesting near-shore sedimentation; black pen in middle for scale. Photos by X. Wang on July 17, 2007

MorphoSource repository

MorphoSource is a repository platform (www.morphosource.org) that holds digital data of biological specimens and cultural heritage objects contributed by museums, researchers, and scholars. We have uploaded files pertaining to *Gazellospira tsaparangensis* to this site (<https://www.morphosource.org/projects/000510942?locale=en>) to make them broadly available.

Institutional and fossil site abbreviations

DFN, Dafnero localities (DFN, DFN2, and DFN3), north-western Greece; **FP1**, Fonelas P-1 site, Granada, Spain; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology,

Chinese Academy of Sciences, Beijing, China; **PIN**, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; **THP**, Tianjin Huangho-Baiho Museum (now Tianjin Natural History Museum), Tianjin, China; **ZIN**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

History of studies on heteronymously twisted antelopes in Asia

There is a diverse assemblage of Plio-Pleistocene heteronymously torsioned and/or spiraled antelopes in Central and East Asia. Up to 16 species in 6 genera have been named or referred. Many of these have been mentioned in various degrees

of relatedness to *Gazellospira*. The following briefly review the history of studies of each genus in chronologic order.

Antilope Pallas, 1776 (Fig. 4f)

The living blackbuck, *Antilope* Pallas, 1776 (type species *Capra cervicapra* Linnaeus, 1758), is a monotypic species

from the Indian subcontinent. Genetic studies suggest that *Antilope* is embedded within or sister to *Gazella* (Bibi, 2013; Jana and Karanth, 2019). The long horns of *Antilope* stand out among *Gazella* spp. and other antilopines in its prominent spiral but its horncores are smooth and lacking a keel. Fossil records of *Antilope* are poor. Pilgrim (1937) erected a



Fig. 4 Examples of heteronomously twisted antelopes in Asia. **a.** *Lyrocerus satan* Teilhard de Chardin and Trassaert, 1938, holotype, No. 18932, from Yushe Basin, Shanxi Province, modified from Teilhard de Chardin and Trassaert (1938: fig. 58); **b.** *Sinoreas cornucopia* Teilhard de Chardin and Trassaert, 1938, holotype, No. 14292, from Yushe Basin, Shanxi Province, modified from Teilhard de Chardin and Trassaert (1938: fig. 56); **c.** *Antilospira licenti* Teilhard and Young 1931, holotype from Hefeng, Jingle County, Shanxi Province, modified from Teilhard de Chardin and Young (1931: fig. 11); **d.** *Spirocerus*

kiakhtensis (Pavlova, 1910), No. 36077 (1) from Tologya, modified from Sokolov (1961: fig. 3); **e.** *Gazellospira torticornis* (Aymard, 1854), Basel Museum Se. 1, from Senèze, modified from Pilgrim and Schraub (1939: pl. I, fig. 2); **f.** *Antilope cervicapra* (Linnaeus, 1758), an adult male blackbuck from the Mahavir Harini Vanasthali National Park, India, photo by Pranav Yaddanapudi, under Creative Commons Attribution 2.0 generic license, https://commons.wikimedia.org/wiki/File:Black_Buck.jpg; Sizes of each specimens are not scaled to be the same (e.g., the size of the living blackbuck is not known)

new species, *Antilope subtorta* from the Upper Siwaliks (near Siswan) of Pakistan, which has a rounded horncore cross section but with less spiral. Pilgrim (1939) named “(cf. *Antilope*) *planicornis*” from possibly Perim Island, which Pilgrim and Schaub (1939) thought to be related to *Antilope cervicapra*, but may form a link between living blackbuck and extinct *Antilospira* and *Gazellospira*. Gentry and Heizmann (1996: p. 387) suggested that “a *Prostrepsiceros* species somewhere in Eurasia must have been ancestral to the extant Indian blackbuck, *Antilope cervicapra*, while *Protragelaphus* may be related to later *Gazellospira* and *Spirocerus*.” Khan and Akhtar (2014) named a new species, *Antilope intermedia*, based on a single horncore from the upper Siwalik of Pakistan, but this horncore is too straight (lacking spiral) to resemble *Antilope*. Some recent authors also included *Parastrepsiceros koufosi* (Kostopoulos 1998) from the early Pleistocene Mygdonia Basin of Greece within the genus *Antilope* (Khan and Akhtar 2014; Hermier et al. 2020).

Spirocerus Boule and Teilhard de Chardin, 1928 (Fig. 4d)

While describing some fragmentary materials from the Pleistocene of Sjara-osso-gol in Ordos, Inner Mongolia, Boule and Teilhard de Chardin (1928) established the genus *Spirocerus* based on *S. kiakhtensis* (Pavlova, 1910). This species has a relatively straight, heteronymously torsioned horncores with stronger anterior keel and a variably present posterior keel. Shortly afterward, Teilhard de Chardin and Piveteau (1930) described a new species, *Spirocerus wongi*, from the early Pleistocene of Nihewan Basin in Hebei Province that has a single anterior keel. They distinguished *S. wongi* in its absence of a posterior keel in contrast to equally well-developed anterior and posterior keels in *S. kiakhtensis*. Regarding the origin of *Spirocerus*, Teilhard de Chardin and Piveteau envisioned that *S. wongi* directly gave rise to *S. kiakhtensis* by reduction in size and accentuation of the keels. Teilhard de Chardin and Trassaert (1938) referred additional materials of *S. wongi* from Yushe Basin, extending its range into late Pliocene. Bai et al. (2019 and citations within) added more materials to *S. wongi* from sediments similar to those of Nihewan but suggested a cladogram that is in opposite direction of evolution proposed by Teilhard de Chardin and Piveteau.

Young (1932) described a new species, *Spirocerus peii*, from the Zhoukoudian Locality 1, which has distinct anterior and posterior keels. Teilhard de Chardin and Trassaert (1938) also added to *S. peii* new materials from Nihewan and the Pleistocene of Harbin. The validity of this species was challenged by several Russian paleontologists (Sokolov 1961; Dmitrieva and Liskun 1981; Kalmykov et al. 2014) but was still considered distinct by Dong et al. (2009) and Bai et al. (2019). A more recently named species *S. hsuchiayacoccus* by Chia et al. (1979) from the Xujiayao Man Site is

generally considered intraspecific variations of *S. kiakhtensis* (Kalmykov et al. 2014; Bai et al. 2019).

Increasing records of *Spirocerus* show that this genus was present throughout northern China (Chia and Chai 1957; Chow and Hsieh 1958; Pei et al. 1958; Ting et al. 1965; Li et al. 1983; Zhou et al. 1984; Dong et al. 1999, 2009; Bai et al. 2019; Tong et al. 2022), the Lake Baikal area (Sokolov 1959, 1961; Germonpré and Lbova 1996), as well as Kazakhstan and Mongolia (Kalmykov et al. 2014). With these abundant records, *Spirocerus* has become not only the earliest established extinct genus of twisted horned antelopes but also the most widespread and best documented taxon.

Antilospira Teilhard de Chardin and Young, 1931 (Fig. 4c)

Teilhard de Chardin and Young (1931) established a new genus and species, *Antilospira licenti*, from the Hefeng (Houfeng) *Hipparion* red-clay in Jingle (Chinglo) County, Shanxi Province. The moderately spiraled, heteronymously torsioned horncores have a diamond-shaped cross-section with both anterior and posterior keels. Teilhard de Chardin and Trassaert (1938) figured a more complete specimen of *Antilospira licenti* from Yushe Basin. The Yushe specimens have striking parallel grooves along the length of the horncores. Teilhard de Chardin and Trassaert (1938) also described three other species, *A. gracilis*, *A. robusta* and *A. zdanskyi*, all questionably referred to *Antilospira*. In particular, *A. zdanskyi* is strikingly different from the type species of *Antilospira* without the longitudinal grooves of the latter. This species was later synonymized with *Spirocerus wongi* by Bai et al. (2019), but considered a valid species of *Gazellospira* by Hermier et al. (2020). Another Yushe horncore fragment (THP 14310) was referred to *Antilospira* cf. *torticornis*, which was included in *G. zdanskyi* as part of intraspecific variation by Hermier et al. (2020).

Tang (1980) named a new species *Antilospira yuxianensis* from Yuxian, Hebei Province based on a poorly preserved horncore. Chen and Zhang (2009) commented that *A. yuxianensis* is probably the same species as *A. gracilis*, but they nonetheless listed the former as a valid species. Chen and Zhang (2009) recognized all five of above species of *Antilospira* from Plio-Pleistocene of Shanxi and Hebei.

Sinoreas Teilhard and Trassaert, 1938 (Fig. 4b)

Teilhard and Trassaert (1938) named a new genus and species *Sinoreas cornucopia* from Yushe Basin. Horncores of this genus is straight without spiral (in contrast to those in *Antilospira*) but has tight torsions with distinct anterior keel and posterior grooves and convex ribbon 2. Teilhard de Chardin and Trassaert thought this genus to be a tragelaphin (within their “Pseudotragelaphinae”) but regarded the

Chinese forms as representing a special group belonging to a distinct faunal province.

Lyrocerus Teilhard de Chardin and Trassaert, 1938 (Fig. 4a)

Teilhard de Chardin and Trassaert (1938) erected a new genus and species *Lyrocerus satan* from Yushe Basin. This genus is even more specialized in its massive frontal platform elevated above the forehead, thick horncore rapidly tapering off, and a sharp anterior keel and a weak posterior keel, as well as distinct grooves.

Gazellospira Pilgrim and Schaub, 1939 (Fig. 4e)

Pilgrim and Schaub (1939) named the genus *Gazellospira* based on *Antilope torticornis* Aymard, 1854. They listed many similarities between *G. torticornis* and the living Indian blackbuck *Antilope cervicapra*, as also outlined in Pilgrim (1939). They advocated a gazelline relationship for the European *G. torticornis*. Pilgrim and Schaub (1939: p. 28) noted that a partial horncore from Yushe referred to *Antelope* cf. *torticornis* by Teilhard de Chardin and Trassaert (1938) had a dominant posterior keel, which is consistent with *Gazellospira*. In the ensuing years, *G. torticornis* was mostly regarded as a common European taxon until Hermier et al. (2020), who included *Antilospira zdanskyi* under *Gazellospira*. In addition, they also placed Teilhard de Chardin and Trassaert's (1938) *Antelope* cf. *torticornis* within *G. zdanskyi*. Furthermore, Hermier et al. synonymized *G. gromovae* (Dmitrieva 1975, 1977) from Kuruksay in Tajikistan under *G. zdanskyi*, in contrast to Rodrigo (2011) who retained as a distinct species for *G. gromovae*.

Systematic paleontology

Order ARTIODACTYLA Owen, 1848

Family BOVIDAE Gray, 1821

Subfamily ANTILOPINAE Gray, 1821

Tribe ANTILOPINI Gray, 1821

Genus *Gazellospira* Pilgrim and Schaub, 1939

Type species: *Antilope torticornis* Aymard, 1854

Included species: *Gazellospira torticornis* (Aymard, 1854); *G. zdanskyi* (Teilhard de Chardin and Trassaert, 1938); *G. tsaparangensis* sp. nov.

Differential diagnosis: Different from *Antilope* in the presence of a posterior keel. Differ from *Spirocerus* in more spiraling (twisted central axis) of the horncore, a relatively better-developed posterior keel compared to the anterior keel, and a more compressed cross section (along a plane between anterior–posterior keels). Distinguishable from

Antilospira in a lack of an anterior keel (except in *G. zdanskyi*) and absence of deep grooves along the keels. Differ from *Sinoreas* in a more spiraled horncore and convex ribbon 1 and from *Lyrocerus* in the lack of an elevated frontal platform and very sharp anterior keels.

Remarks: Based on *Antilope torticornis* (Aymard 1854) from European early Pleistocene sites of Pardines, Senèze, and Coupet, Pilgrim and Schaub (1939) erected the genus *Gazellospira*, comparing extensively with living gazellines. By late 20th Century, *G. torticornis* was widely recognized in the Plio-Pleistocene of Europe. Because of the abundant fossil records in Europe and western Asia, *Gazellospira* was adopted as a species with zoogeographic and biochronologic significance (Duvernois and Guérin 1989; Masini and Torre 1989; Van Couvering 1997; Gliozzi et al. 1998; Geraads 2010; Rook and Martínez-Navarro 2010; Raffi et al. 2020). Agustí et al. (2001) listed *Gazellospira torticornis* as a defining first appearance taxon in the MN16 (3.2–2.5 Ma as defined by Agustí et al. 2001), as did Cregut-Bonnoure (2007: fig. 1) who also compiled a combined (western and eastern zones) chronologic range of MNQ16–MNQ20 for this species. Hermier et al. (2020), on the other hand, placed its stratigraphic range in MNQ16–19, with the possible extension to MNQ15 (Çalta, Turkey).

Knowledge about the cranial, dental, and postcranial anatomy of *Gazellospira* also steadily increased. From the early Pleistocene (MNQ18) site of Fonelas P-1 in Granada, Spain, Garrido (2008) described the largest collection of *Gazellospira* and named a new chronosubspecies *G. torticornis hispanica* as the smallest individuals in Mediterranean. This late Spanish population has relatively long horns with more spiral turns, suggesting the general trend of lengthening of horns.

Sotnikova et al. (1997) mentioned (without description) *Gazellospira* sp. in the Akterek section in Issyk-Kul' Basin in Kazakhstan and *G. gromovae* from Kuruksay Suite of Tajikistan. The latter from Kuruksay was referred to *G. zdanskyi* by Hermier et al. (2020) but retained as a distinct species by Rodrigo (2011). *G. gromovae* was also mentioned in the Khapry faunal assemblage in Liventsovka of the Sea of Azov Region (Titov 2008).

Instead of the previous notion that these European late Pliocene to early Pleistocene forms being related to the African tragelaphines, Pilgrim and Schaub (1939), in establishing their new genus *Gazellospira*, explicitly pointed its affinity to the antilopines in general and *Gazella* in particular. More specifically, they suggested that this genus is related to the living Indian blackbuck, *Antilope cervicapra*. Phylogenetically, modern Indian blackbuck, *Antilope cervicapra*, is either just outside of all gazelles (*Gazella*, *Eudorcas*, *Nanger*) as evidenced from mtDNA (Bibi 2013) or embedded within genus *Gazella* as evidenced from select nuclear DNA (Jana and Karanth 2019). Either way, it seems clear that the spiral

horned clade must have evolved from a morphotype similar to that of *Gazella*, which may serve as an outgroup for character polarity determinations.

Duvernois and Guérin (1989) suggested that *Gazellospira* was descended from *Protragelaphus*. Gentry and Heizmann (1996: p. 387) stated that “a *Prostrepsiceros* species somewhere in Eurasia must have been ancestral to the extant Indian blackbuck, *Antilope cervicapra*, while *Protragelaphus* may be related to later *Gazellospira* and *Spirocerus*.” Hermier et al. (2020) has placed the Greek species *Parastrepsiceros koufosi* under the genus *Antilope*.

Gazellospira tsaparangensis sp. nov.

(Figs. 5, 6, 7, 8, 9; Table 1).

Antilospira sp. Wang et al., 2013: p. 87, fig. 4

Antilospira sp. Wang et al., 2014a, b: p. 1342, table 2.

Antilospira sp. Wang et al., 2022

Holotype: IVPP V31668, a nearly complete left horn-core, collected by Qiang Li on July 17, 2007.

Type locality: IVPP ZD0701 locality (Figs. 2, 3), N 31° 42' 21" E 79° 43' 05", elevation 4,223 m., in northern end of Zanda Canyon, Zanda County, Gar District, Tibetan Autonomous Region. Sediments in the general area consist of fine-grained lacustrine beds interbedded with dark brown, cross-bedded sandstones and conglomerates of channel fills (Fig. 3a), up to 3–5 m thickness in individual layers. Rich vertebrate fossils at ZD0701 loc. are mostly found in yellowish to greenish mudstones containing a thin layer of dark brown fine gravel bed (about 10 cm to 1 m in thickness), although some large bones are present within the gravel layers. Fossils were collected from a 2–3 m band along the southern and western escarpments of a ~50 × 100 m platform (Fig. 2b), in near-shore depositional environments as evidenced by mud cracks (Fig. 3c).

Referred specimens: IVPP V31669, a partial left horn-core from the IVPP ZD0701 locality.

Etymology: Tsaparang (Tsaprang, Chaparangué, Rtsa pa rang), legendary capital and fortress of ancient Guge Kingdom in modern Zanda area.

Differential diagnosis: Differing from *Gazellospira torticornis* in the following characters: smaller size, shorter horn-cores, small supraorbital foramina lacking a large supraorbital fossa, thin frontal bones lacking sinuses, faster twisting per unit length of horn-core and also faster tapering off toward the tip. Distinguishable from *G. zdanskyi* in smaller size, lacking a distinct anterior keel, and smaller supraorbital foramina.

Fauna and age: *Gazellospira tsaparangensis* is known in a single locality, ZD0701, which was correlated to the top of C2Ar (Gilbert) magnetochron based on re-calibrations of measured sections by Saylor et al. (2010a, b). Wang et al. (2013: table 1) arrived at a calibrated age of 3.62 Ma for

Loc. ZD0701 based on the GTS2004 (Lourens et al. 2004), which is the same as in GTS2020 (Raffi et al. 2020). If correct, this would place the Tibetan species as one of the earliest occurrences of this genus, with the possible exceptions of late Ruscinian (MN15) records from Çalta and Akçaköy (Hermier et al. 2020: fig. 11). The most updated faunal list of Zanda Basin fossil vertebrates include (excluding Pleistocene taxa): order Eulipotyphla: Soricidae indet.; order Rodentia: family Sciuridae: *Aepyosciurus* sp.; family Cricetidae: *Nannocricetus qiui* *Aepyocricetus liuae*, *Mimomys* (*Aratomys*) *bilikeensis*; family Spalacidae: *Prosiphneus eriksoni*; family Muridae: *Apodemus* sp.; order Lagomorpha: family Leporidae: *Trischizolagus mirificus* and *Trischizolagus* cf. *T. dumitrescuae*; family Ochotonidae: *Ochotona* sp. A–D; order Carnivora: family Mustelidae: *Meles* sp.; family Felidae: *Panthera blytheae*; family Canidae: *Vulpes qiuzhudingi*, *Nyctereutes* cf. *N. tingi*, and *Sinicuon* cf. *S. dubius*; family Hyaenidae: *Chasmaporthetes gangsriensis* and *Pliocrocota perrieri*; order Artiodactyla: family Bovidae: *Qurlignoria hundesiensis*, *Protovis himalayensis*, and *Gazellospira tsaparangensis* sp. nov.; family Cervidae: *Metacervulus* sp.; family Giraffidae: *Palaeotragus* sp.; order Perissodactyla: family Equidae: *Hipparion zandaense*; family Rhinocerotidae: *Coelodonta thibetana*; order Proboscidea: Gomphotheriidae indet.; and class Aves: family Struthionidae: *Struthio* sp. (Li and Li 1990; Deng et al. 2011; Tseng et al. 2013a, b, 2016; Wang et al. 2013, 2014a, b, 2016, 2022; Li and Wang 2015; Li et al. 2017). See also Wang et al. (2020) for a history of explorations in the Zanda Basin.

Description

Both Zanda horncores (Figs. 5–7) have suffered extensive postmortem, pre-burial erosions. The pitted surface textures in the braincase and orbit are indicative of transport of a long distance before burial and/or in high-energy fluvial settings. The horn-core surfaces themselves are less eroded, presumably due to the protection of the horn sheath during transportation because horn sheaths are more securely attached in spiral forms compared to straight forms. We may thus envision that the individual horncores have been detached from the skulls while undergoing transport, and that the horn sheaths were largely intact and buried together with the horncores before the horn sheaths disintegrate during fossilization.

Although both specimens from Zanda were broken close to the base of the horncores that make their orientations difficult, we think both of the horncores are left ones for the following three reasons. Firstly, nutrient foramina are much more common on the lateral and posterolateral sides at the base of the horns in spiral horned antelopes; this is the case in both Zanda specimens. Secondly, the supraorbital foramina are more commonly located at the anterolateral aspect of the anterior keels of the

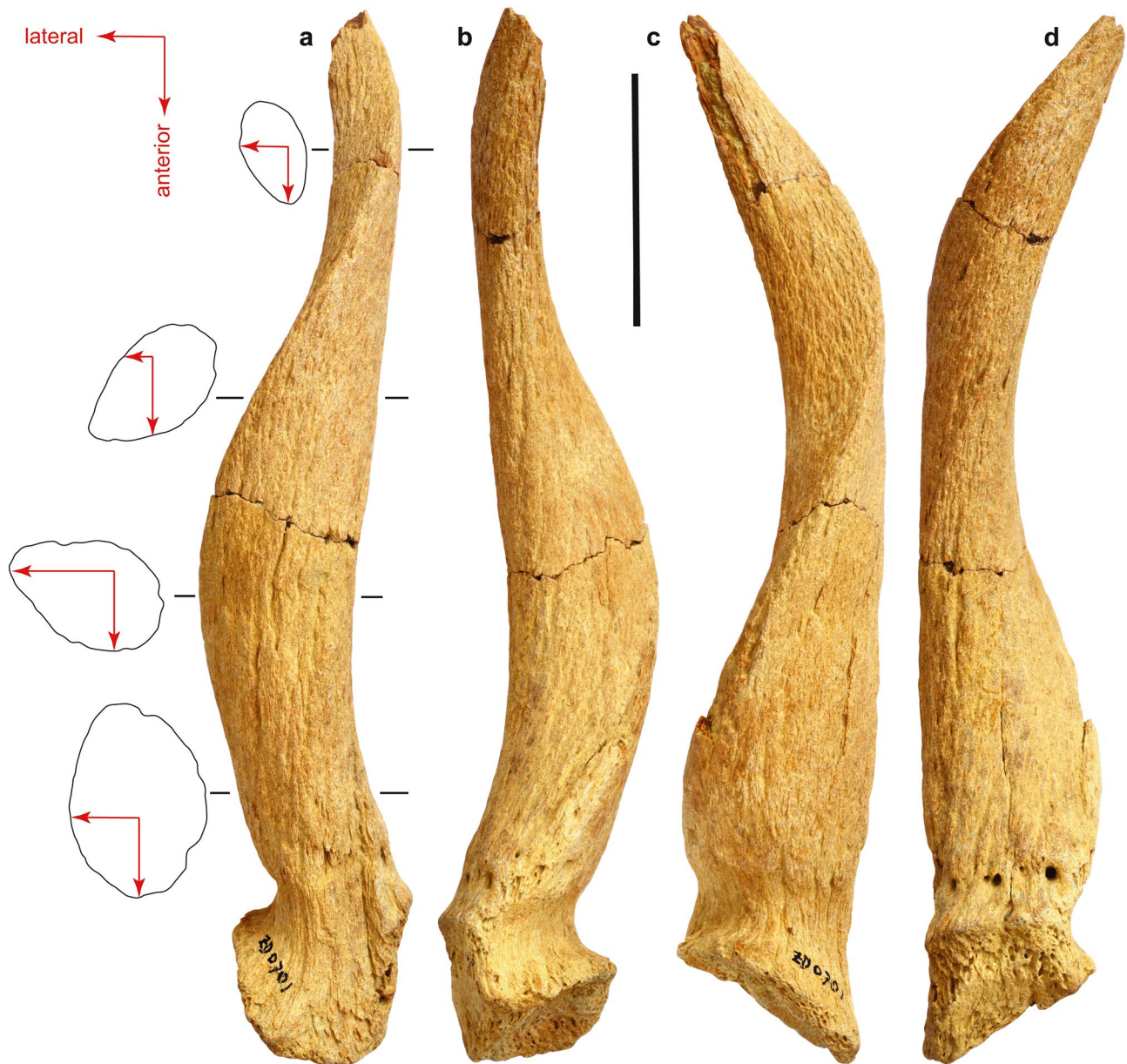


Fig. 5 *Gazellospira tsaparangensis* sp. nov., IVPP V31668, left horncore, holotype. **a.** anterior; **b.** posterior; **c.** medial; and **d.** lateral views. Horncore cross sections are derived from 3D models of laser scans (see [Materials and methods](#)). Scale bar equals 50 mm. Photos by X. Wang

horncores (or the central sagittal plane of the horncores if the anterior keel is lacking). In both Zanda specimens, the foramina are located near the orbit side of the frontal bones. Thirdly, the internal surfaces of the presumed braincases, although pitted due to pre-burial erosions, preserve enough of the original brain texture to suggest their corresponding gyri and sulci on the endocast. This is in contrast to a smoother surface texture on the orbit side, although the orbits are also extensively eroded, more so in the holotype. The above three factors thus provide enough evidences that IVPP V31668 and V31669 are both left horncores, and as a result, having heteronymous torsions.

IVPP V31668 (holotype): Although the frontal bone is eroded, the horncore is reclined from the skull roof judging by the medial rim of the frontal, but the exact angle of inclination is difficult to estimate. The medial edge of the frontal is thin, ranging from 4–6 mm in thickness. On the exposed edges of the frontal, there is no sign of frontal sinus. The inner surface of the frontal still preserves some external brain morphology, although extensive erosion on bone surface is clearly shown in the cancellous bone texture. Because of the missing medial margin of the frontal, it is not possible to accurately estimate the lateral divergence of the horncore.



Fig. 6 *Gazellospira tsaparangensis* sp. nov., IVPP V31669, left horncore. **a.** anterior; **b.** posterior; **c.** medial; and **d.** lateral views. Horncore cross sections are derived from 3D models of laser scans (see [Materials and methods](#)). Scale bar equals 50 mm. Photos by X. Wang

On the lateral side, the orbital wall is preserved on the lower half of preserved frontal bone, whereas the upper half is heavily eroded. As a result, the orbital rim is not preserved, exposing the underlying cancellous bone.

The anterior aspect of the frontal bone is extensively damaged. Two tiny supraorbital foramina are nevertheless preserved, each measuring no more than 2 mm in diameter (Fig. 7). These two foramina are separated from each other by about 6 mm. There is no sign of a fossa on the preserved surface, although a shallow fossa may have existed if that in IVPP V31669 is any guidance. The supraorbital foramina do not open into the orbital wall. There are three large nutrient foramina along the lateral rim of the horn sheath.

Suffering from slight damage at the tip, the total horncore length is about 212 mm (Table 1), with the missing tip being about 10–20 mm. The horncore has a moderate spiral that falls outside of a hypothetical axis of the horn. The twisting is faster than in *Gazellospira torticornis*, ranging from 79°

to 84° per 50-mm segment of the horncore and with a total twisting of > 250° (Fig. 8).

The surface texture of the horncore is pitted with numerous shallow parallel grooves but lacks a deep furrow seen in some homonymously spiraled forms (Kostopoulos 2014). The horncore has a compressed cross section throughout. An anterior keel is absent at the base, but a narrow and low ridge is visible in the middle one-third of the horncore, which becomes less visible near the top. By contrast, a posterior keel is distinct throughout the length of the horncore and forms a prominent ridge. The posterior keel begins at the posterolateral aspect of the horncore base. Ribbons 1 and 2 are convex. As in the type species, a postcornual fossa is absent.

IVPP V31669: The frontal bone is slightly thicker than that in the holotype, being up to 9 mm thick in the central portion. As in the holotype, there is no sign of a frontal sinus. Also like the holotype, the inner surface that contacts

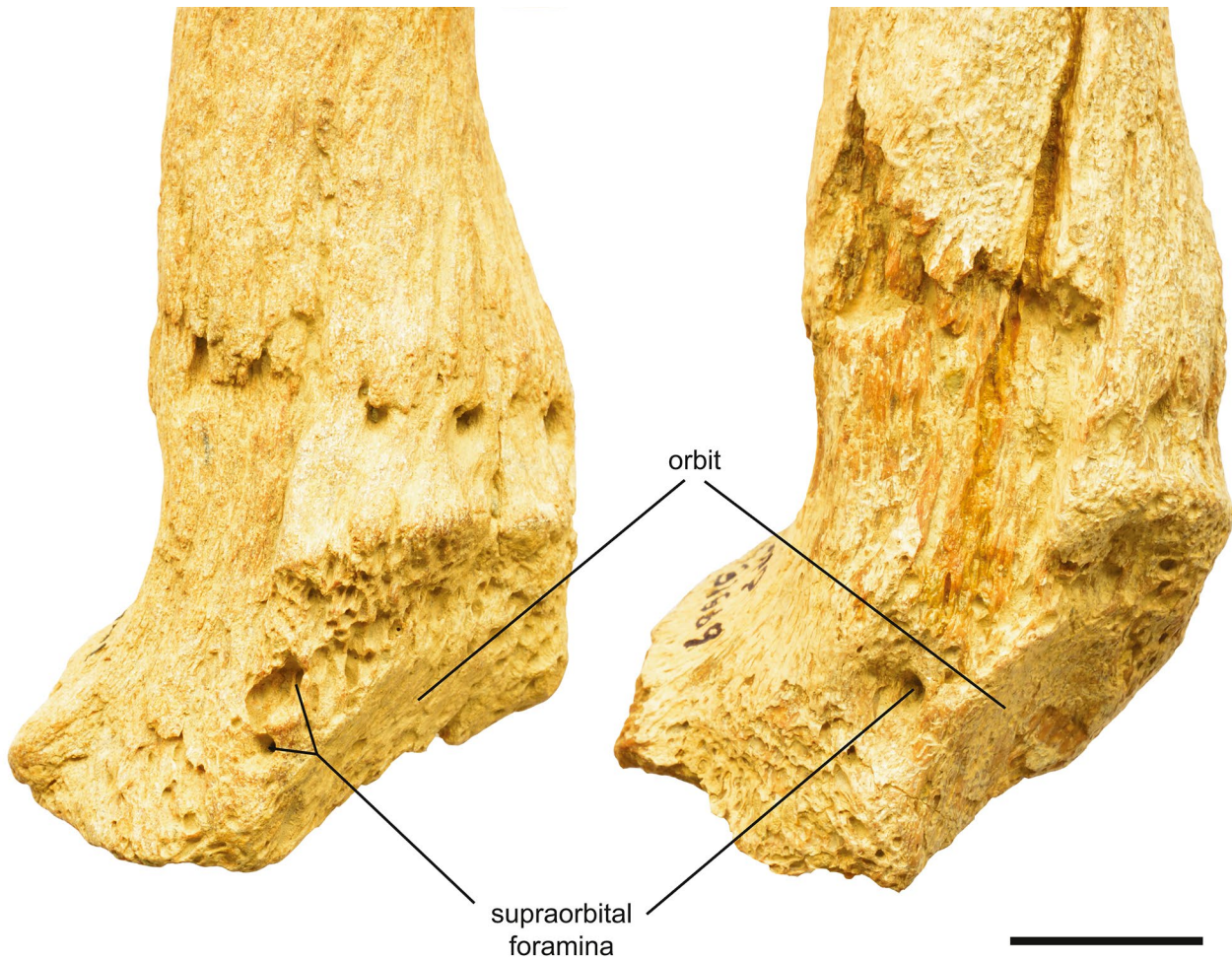


Fig. 7 *Gazellospira tsaparangensis* sp. nov., IVPP V31668 (left) and V31669 (right), anterolateral views of lower part of horncores showing supraorbital foramina and fossa. Scale bar equals 20 mm. Photos by X. Wang

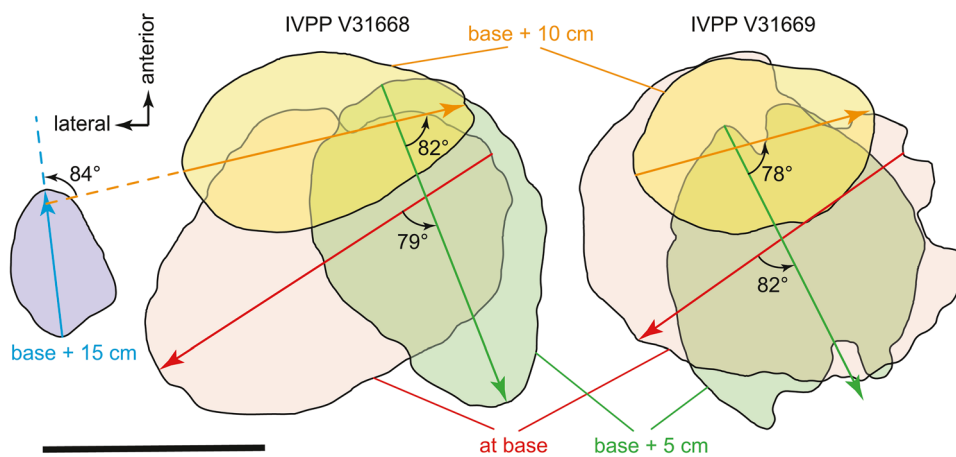


Fig. 8 Cross sections of left horncores in *Gazellospira tsaparangensis* sp. nov. Four sections are shown for IVPP V31668: at base (pink), base+5 cm (green), base+10 cm (yellow), and base+15 cm (blue). Three sections are shown for IVPP V31669: at base (pink), base+5 cm (green), and base+10 cm (yellow). Color arrows indicate

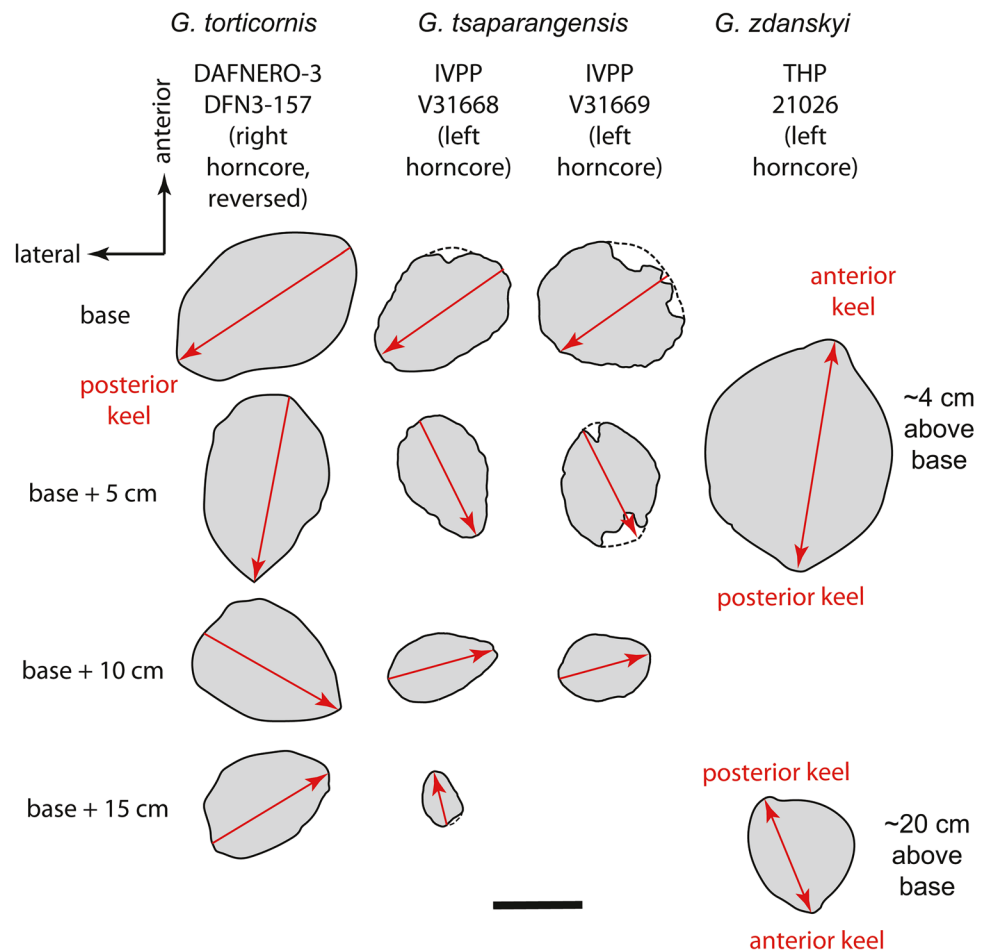
directions of posterior keel and black curved arrows indicate twisting between successive cross sections. Cross sections are made by Compute Planar Section function in MeshLab and the outlines are traced in Adobe Illustrator. See Online Resource 1: Figs. S1–S4 for location and orientation of the cross sections. Scale bar equals 20 mm

Table 1 Horncore measurements of *Gazellospira* (in mm). Definitions of measurements adopted from Hermier et al. (2020) and related personal data from Dimitris Kostopoulos. For anteroposterior and mediolateral horncore diameters, the Zanda specimens are oriented with the medial wall of the orbit facing laterally (i.e., the medial wall is assumed to be oriented along anteroposterior direction). Most of the measurements from the Greek Dafnero fossil sites (Hermier et al. 2020) and Fonelas P-1 site (Garrido 2008) are averages of left and right sides where available. Those for *G. zdanskyi* is from Teilhard de Chardin and Trassaert (1938). See Rodrigo (2011: table 4.22) for measurements of specimens from additional European localities

Species	<i>G. isaparangensis</i>						<i>Gazellospira toricornis</i>						<i>G. zdanskyi</i>			
	Zanda ZD0701		IVPP		V31669		Dafnero 1	Dafnero 3		Fonelas P-1		Yushe		Kuruksay		
Locality	IVPP	IVPP	DFN	DFN	DFN3	DFN3	DFN3	FPI-2001	FPI-2001	FPI-2001	FPI-2001	FPI-2001	FPI-2001	THP	THP	PIN
Catalogue Number	V31668	V31669	156	157	158	0094	0164	0357	0357	21026	14310	3120–54				
Basal internal distance between the horn-cores			49.9	59.0	56.3	54.4	62.8	53.0	53.0	53*						
Cranial breadth at the basal external sides of the horncores			126.9	124.4	134.0	120.1	113.3	116.0	116.0	149*						
Internal horncore distance at the apex			340.4	279.7												
Minimum horncore basal diameter	25.7	26.6	27.9*	34.2	34.3	39.5	33.4	35.6	35.6	29.4	45.0	39.0	27.4–41.5			
Maximum horncore basal diameter	35.7	34.7	48.1	44.9	47.4	39.0	38.0	35.7	35.7	60.0	45.0	42.0–49.5				
Basal horncore circumference	111.0	113*	132.5	141.0												
External straight horncore length	173.8	132*	203.0													
Full length following the torsion	212.0	152*	276.0													
Anteroposterior horncore diameter at 5 cm from the base	28.2	27.1	30.5	29.4	33.9											
Mediolateral horncore diameter at 5 cm from the base	28.2	29.2	41.2	41.2	40.6											
Anteroposterior horncore diameter at 10 cm from the base	22.0	22.9	35.3	31.5	32.5											
Mediolateral horncore diameter at 10 cm from the base	22.1	16.9	27.1	31.1	33.1											
Anteroposterior horncore diameter at 15 cm from the base	12.5		25.4	30.6	36.2											
Mediolateral horncore diameter at 15 cm from the base	10.4		19.5	20.6	21.6											
Horncore circumference at 5 cm from the base	90.0	91.0	118.0	114.0	120.0											
Horncore circumference at 10 cm from the base	68.0	64.0	99.0	99.5	106.5											
Horncore circumference at 15 cm from the base	38.0		81.0	83.0	94.0											

* Indicates an estimate

Fig. 9 Comparison of cross section shapes and orientations in species of *Gazellospira*. Cross sections for *G. torticornis* were redrawn from Hermier et al. (2020: app. G, fig. S5), those for *G. tsaparangensis* sp. nov. were adopted from Fig. 8, and those for *G. zdanskyi* were redrawn from Teilhard de Chardin and Trassaert (1938: fig. 53). Scale bar equals 20 mm



the brain is eroded to show cancellous bone textures. The orbital wall, however, is better preserved, with the surface texture resembling smooth cortical bones. A single supraorbital foramen is about 2 mm in diameter and is enclosed by a fossa of modest size (~8 mm across) (Fig. 7). The foramen sinks inside this fossa by about 4 mm. As in the holotype, the supraorbital foramen does not show any connection with the orbit.

The horncore in V31669 is more damaged than the holotype and a significant part of its tip is missing. In addition, both the anterior part of the base and medial side of the middle segment has large pieces missing, making it difficult to observe the cross-section shape. Despite these damages, it is clear that V31669 has a more rounded cross section than shown in the holotype (Figs. 8, 9). This roundedness makes both anterior and posterior keels less distinct. Nevertheless, the posterior keel is more distinct than the anterior one. Perhaps also because of this roundedness in cross sections, the spiraling of the horncore is also less prominent than in the holotype and the successive cross sections of the horncore are less deviated from the center, in contrast to that in the holotype (Fig. 8). The rate of twisting is 78° to 82° per 50-mm segment of the horncore (Fig. 8). The ribbon 1 has a very

indistinct ridge along much of its length, whereas the ribbon 2 has shallow groove in the upper two-third of the horncore.

Comparison

Horncore size and length: Fig. 10 shows that *Gazellospira tsaparangensis* has the smallest horncore diameters among species of the genus, falling just below the smallest individuals from Fonelas P-1 site, Granada, Spain. This latter Spanish sample was the material basis of a chronosubspecies *G. torticornis hispanica* (Garrido 2008) and represents some of the smallest *G. torticornis* individuals in western Europe. Even if discounting such a size difference, the horncores of *G. torticornis* are still almost twice as long as those in *G. tsaparangensis* as well as having considerably more twist given the extra length. In addition, the much-lengthened horncores in *G. torticornis* tapers slowly (i.e., slower decrease in horncore cross sections in Table 1) as compared to those in *G. tsaparangensis* (compare left column with two middle columns in Fig. 9). The Zanda form is thus readily distinguishable from the European and western Asian *G. torticornis* in these dimensions.

Sexual variations in frontal sinus: As described above, there are significant variations between the two Zanda

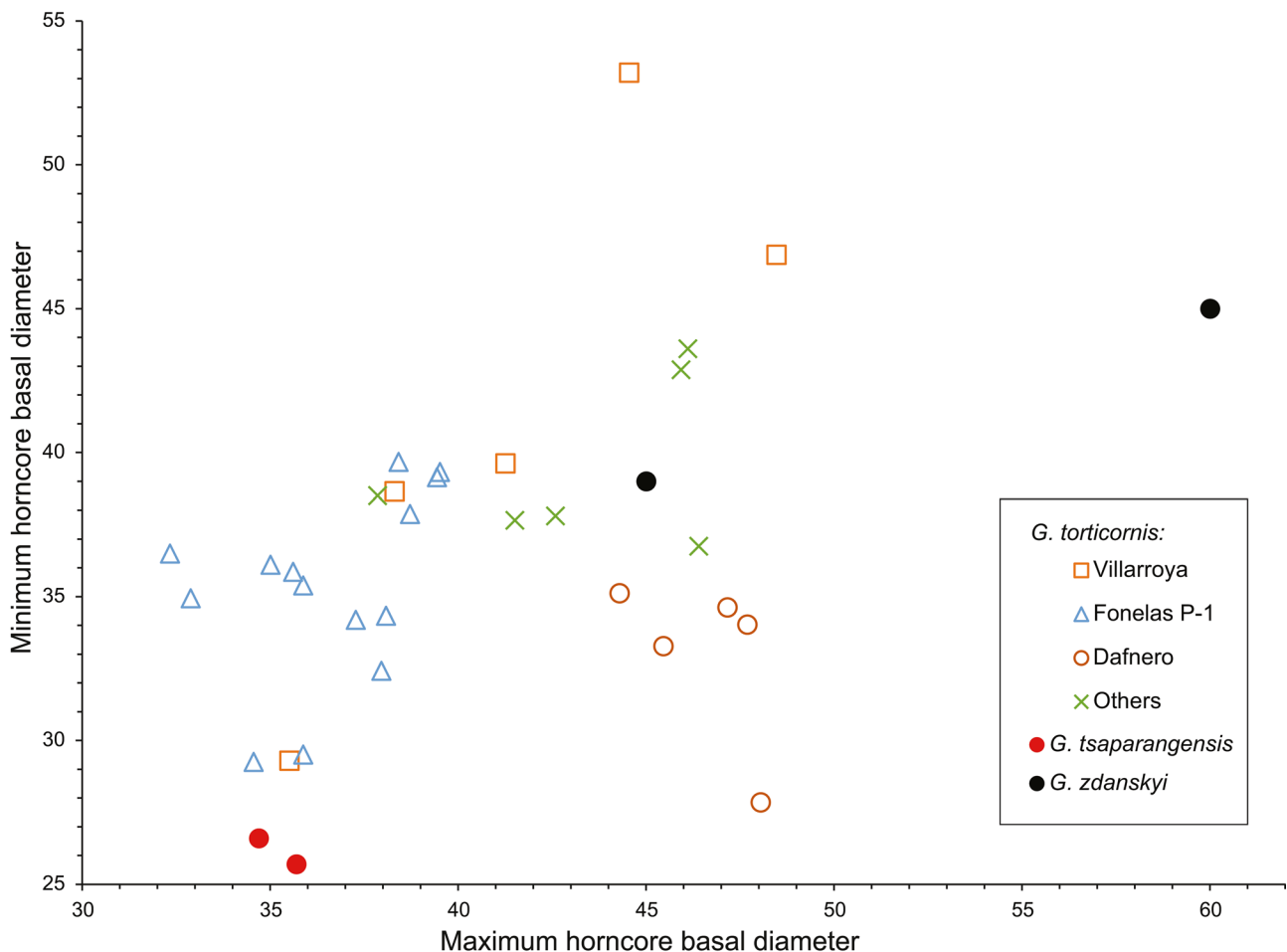


Fig. 10 Scatter diagram showing size and proportional relationships of horncores in three species of *Gazellospira*. Data for *G. torticornis* are from Garrido (2008), Rodrigo (2011), and Hermier et al. (2020), and those for *G. zdanskyi* are from Teilhard de Chardin and Trassaert (1938)

horncores in terms of cross-sectional shapes and degree of spiraling (deviation from the center). Despite these variations, the rates of torsion are very similar, which, along with their similar size, suggest that these two specimens belong to the same species. With only two incomplete horncores, however, it is not easy to determine if these variations are due to age or sexual differences.

Hermier et al. (2020) postulated sexual dimorphism in frontal sinuses within their Dafnero sample of *Gazellospira torticornis* from northern Greece, with the males having more extensive sinuses presumably because of their clashing behaviors in intraspecific competitions during rutting seasons. They observed much larger and deeper sinuses in DFN3-158, assigned as a potential male individual, than in DFN3-157, assigned as a female. By this criterion, the somewhat thicker frontal bones in IVPP V31669 may thus indicate a male when compared to that in IVPP V31668.

The sexual variations aside, as shown in their illustration (Hermier et al. 2020: fig. 2), the presumed males and females from Dafnero both have substantial sinuses. Pilgrim

and Schaub (1939: pl. 1, fig. 4) observed strong frontal sinuses, with a total thickness of 13–30 mm in their Coupet specimen. Extensive frontal sinuses are also readily visible in the Senèze specimens (Pilgrim and Schaub 1939: pl. 1, figs. 2, 3). In contrast, the complete lack of any indication of a frontal sinus, along with the thin frontal bones in *Gazellospira tsaparangensis* is probably not a result of individual variations and suggests that the Zanda form is at a more primitive stage of evolution.

Supraorbital foramen: Of the illustrated specimens of *Gazellospira torticornis*, only FP1-2001-0164 (Garrido 2008: fig. 1) clearly shows the supraorbital foramina. They are paired small foramina located within a fossa of modest size, bordered on either side by roughened areas of bones that form slightly elevated ridges enclosing a fan-shaped supraorbital fossa. By contrast, the small supraorbital foramina in the Zanda form are enclosed either by a very small fossa or not at all, and they are located more laterally, close to the orbital wall (Fig. 7). Such a condition seems also a primitive state. Most other spiral horned antelopes also have a large fossa

that houses two or more supraorbital foramina, including *Spirocercus*, *Antilospira*, as well as living *Antilope cervicapra*.

Antilospira (*A. licentigracilis* and *A. robusta*) from Yushe Basin described by Teilhard de Chardin and Trassaert (1938) all have a modest to large supraorbital fossa, within which lies a single supraorbital foramen (but *A. robusta* seems to have an additional small foramen just above the main one, both within the same pit). This is in contrast to a much-enlarged supraorbital fossa containing two supraorbital foramina in *Spirocercus*, seen in Russian materials (Sokolov 1961) and in Nihewan specimens (Teilhard de Chardin and Piveteau 1930).

Anterior and posterior keels: Development of a strong posterior keel and weak or absent anterior one in the Zanda specimens are almost identical to those *Gazellospira torticornis* described by Pilgrim and Schaub (1939). Such a pattern is further confirmed by recent authors with greater sample size, more distant geographic locations, and larger chronologic ranges (Garrido 2008; Rodrigo 2011; Hermier et al. 2020). Horncore morphology for *G. torticornis* is consistent across the Plio-Pleistocene of Europe and western Asia.

The present addition of a Tibetan species, *Gazellospira tsaparangensis*, is also consistent with this horncore pattern, despite its small size and short horncores. Hermier et al.'s (2020) transfer of *Antilospira zdanskyi* to *Gazellospira*, however, breaks this pattern—*G. zdanskyi* has a distinct anterior and posterior keels. It remains to be seen if Hermier et al.'s referral will be confirmed by better materials from China (see further Discussion below).

Torsion and spiral: Chinese Plio-Pleistocene twist-horned antelopes can be divided into two major types: horncores with torsion of keels that have a straight central axis and horncores with twisting keels around a central axis in a helicoidal spiral. The spiraling may cause the body of the horncore to fall outside the central axis, i.e., in an open spiral. Torsioned forms include *Spirocercus* and *Sinoreas*, whereas spiral forms include *Antilospira*, *Lyrocercus*, and *Gazellospira*. Indeed, as pointed out by Pilgrim and Schaub (1939), one of the key differences between *Gazellospira* and *Spirocercus* is the spiral of the horncores in the former.

Kostopoulos (2014) suggests that torsion tends to be a primitive state predating spiral based on both ontogenetic and paleontologic evidences. Such may be the case for materials from Shuichongkou that were referred to *Spirocercus wongi* by Bai et al. (2019). For example, horncores in their IVPP V24483.1 and V24483.3 are quite straight, consistent with diagnosis of *S. wongi*, whereas others, such as IVPP V25878.1 and V25878.2, feature a noticeable spiral, with IVPP V24483.2 falling in between (Bai et al. 2019: figs. 1, 2). Bai et al. (2019: p. 96) described these specimens as all twisting “around an ideal axis inside the core”, although it is obvious that there is a spectrum of spiral among their

samples. If their assignment of the Shuichongkou materials to *S. wongi* is correct and assuming torsioned conditions being primitive as suggested by Kostopoulos (2014), it is possible to envision a scenario of an initial spiral arising from largely torsioned forms within the Shuichongkou population of *S. wongi*. If this is the case, the Shuichongkou materials seem to represent the start of a novel direction of evolution within *Spirocercus*.

Bai et al. (2019: p. 95) defined spiral forms (such as *Antilospira*) as “the axis of torsion becomes tangent or external to the surface of the horn”, whereas the torsioned form (such as *Spirocercus*) as “ideal axis of torsion of the horn keeps inside of the bony mass of the core.” How their ideal axis was defined was not clear, but it seems to boil down to slight degrees of differences in spiraling between these two genera. By placing their Shuichongkou materials into *S. wongi*, they have greatly enlarged the concept of this species, and by implication, the genus as well.

Sokolov (1961) suggests that the degrees of twisting turns is likely ontogenetically or sexually variable, with older and male individuals having greater degrees of torsion as more horn materials are added to the base. He thus casted doubt on the usefulness of the degrees of torsion. He pointed out that *Spirocercus peii* displays different degrees of torsion from Zhoukoudian Locality 1, and Russian materials of *S. kiakhtensis* also show substantial variations. Sokolov concluded that such a variation can be accounted for by age and possibly also sexual differences, with individuals making a full turn belonging to old males. Such a suggestion may possibly be supported by Dong et al. (2009: figs. 4, 5), who illustrated a possible juvenile or female skull in contrast to an adult skull with more torsion, although they assign the two skulls to different species, *Spirocercus kiakhtensis* and *S. peii*.

Controversies regarding the amount of intraspecific variation will likely remain until a sufficiently large sample become available. Lumping everything into a single species by Dmitrieva and Liskun (1981) and Kalmykov et al. (2014) seems extreme and obscure evolutionary trends, even if they truly belong to a single lineage. In the meantime, an intermediate approach (recognizing three species) by Bai et al. (2019) may be more sensible and allow easy discussions of chronological and morphological changes.

Of the two specimens of *Gazellospira tsaparangensis*, although both have about the same rate of twisting, the holotype (IVPP V31668) has more spiraling (i.e., deviating from the main central axis) than the referred specimen (IVPP V31669). Interestingly, IVPP V31669 is more robustly built with less compressed horncores and has a thicker frontal bone, features possibly enhancing male combats. However, greater spiral in the holotype may also be an adaptive feature for male displays (Walther 1962).

Discussion

Questions about *Gazellospira zdanskyi*

Teilhard de Chardin and Trassaert (1938) described two specimens (THP 21026, holotype, and 21027) from Loc. 67 (Mientsekuo) in Yushe Basin, southeastern Shanxi Province. They named it ?*Antilospira zdanskyi*. Sokolov (1961) remarked that this species seems closest to *Spirocerus* in terms of its double keel horncores, but he concluded that the Yushe species cannot be recognized as a direct ancestor to the genus *Spirocerus*. For much of the ensuing years, *A. zdanskyi* was occasionally questioned about its generic assignment (Chen and Zhang 2009) or mostly ignored. Bai et al. (2019) subjected *A. zdanskyi* to a phylogenetic analysis and concluded that it is clustered within a broader *Spirocerus wongi* clade. Hermier et al. (2020), on the other hand, placed *A. zdanskyi* under *Gazellospira*. In addition, they also included Teilhard de Chardin and Trassaert's (1938) *Antelope* cf. *torticornis* from Yushe (THP 14310) within *G. zdanskyi*, similar to an earlier suggestion by Pilgrim and Schaub (1939: p. 28) that this species seems related to *Gazellospira*. Pilgrim and Schaub even suggested the name *Gazellospira teilhardi* for this specimen, but lacking a formal diagnosis, Pilgrim and Schaub's name probably should be considered a *nomen vanum*. Furthermore, Hermier et al. (2020) synonymized *G. gromovae* (Dmitrieva 1975, 1977) from Kuruksay in Tajikistan under *G. zdanskyi*, in contrast to Rodrigo (2011) who retained *G. gromovae* as a separate species.

Stratigraphically, the type locality for *Gazellospira zdanskyi* (Loc. 67 in Yushe Basin) was placed in "Zone II" by Teilhard de Chardin and Trassaert (1938), but this locality (Mientsekuo) was not mentioned in recent summaries of the history of studies in Yushe Basin (Qiu and Tedford 2013). In the most recent stratigraphic synthesis where *Antilospira* was mentioned, Tedford et al. (1991: table 1) placed it in the Mazegou Formation, which is ~3.7–2.8 Ma (Flynn and Qiu 2013).

Teilhard de Chardin and Trassaert (1938) stated that the frontal bone in their ?*Antilospira zdanskyi* is very thick and the supraorbital foramina large and sunken. A thick frontal, typically associated with extensive frontal sinuses, seems to be a necessary condition for a large and sunken foramen. Such a condition is seen in *Gazellospira torticornis* and *G. zdanskyi*. On the other hand, a thin frontal bone with no sign of sinuses nor enlargement of the supraorbital foramina in *G. tsaparangensis* is here interpreted as a primitive character within the genus, as thickening and pneumatization in the frontal bone and horncore is likely an adaptation against breakage during intraspecific fights while maintaining a minimum weight

(Kitchener 1988). Where *G. zdanskyi* eventually falls will depend on better knowledge about its skull and teeth.

Relationship of Eurasian Plio-Pleistocene twist-horned antelopes

In their latest nuclear DNA analysis, Jana and Karanth (2019) suggested that the Indian blackbuck (*Antelope cervicapra*) is embedded within a paraphyletic *Gazella* and has a sister relationship with *G. dorcas*. Furthermore, they calculated a 2.16 Ma divergence time between *A. cervicapra* and *G. dorcas*. This is in contrast to Bibi (2013) who proposed a late Miocene divergence between *A. cervicapra* and the rest of the antelope clade at around 6.5–6 Ma. In any case, the case for a close relationship between *Gazellospira* and *Antelope*, as argued by Pilgrim and Schaub (1939), seems less likely because the latter has no development of a keel. If so, the *Gazellospira* lineage probably has no living survivor.

Phylogenetic relationships among Eurasian Plio-Pleistocene twisted horned antelopes have not been studied in detail. Bai et al. (2019) presented the first attempt at a partial cladistic analysis on selected taxa. They suggested that the spiral-horned *Gazellospira* and *Antilospira* form a clade, which in turn, has a sister relationship with the torsion-horned *Spirocerus*. This clade of extinct twisted-horned forms, (*Spirocerus* (*Gazellospira*, *Antilospira*)), forms a sister clade to the tragelaphines and boselaphines; *Gazella* and *Antelope* are placed further outside. However, modern molecular systematics show that antilopines (including *Gazella* and *Antelope*) are far removed from tragelaphines and boselaphines (Bibi 2013; Calamari 2021), so many of the relationships in Bai et al. (2019) may be questionable. Bai et al. (2019) further speculated that *Antilospira* was possibly derived from a *G. torticornis*-like ancestor during the late Pliocene in northern China. Hermier et al. (2020), however, pointed out that Bai et al. have misinterpreted their characters 8 (horncore divergence at the base) and 12 (sinuses at fronto-pedicle region) and did not take into account the variability in *G. torticornis* (characters 11 and 12, i.e., distances in horncore insertions and sinuses at fronto-pedicle region). These suspected deficiencies may have contributed to Bai et al.'s (2019) decision to synonymize *Antilospira zdanskyi* with *Spirocerus wongi*, making their concept of *S. wongi* far broader than that of Hermier et al. (2020). Unfortunately, Hermier et al. (2020) did not produce a phylogeny of their own.

Function of horncore twisting

Bovids with twisted horns have evolved numerous times with many examples in the fossil records as well as among

living taxa (Kostopoulos 2014). Many of these groups feature male dominance behaviors such as pushing, wrestling and clashing. Twisting of the horns as well as other ornamentations, such as ridges, are presumed to help lock-in during horn-to-horn pushing and wrestling, although it is conceivable that spiraled horns may also be more impressive in broadside displays (Walther 1962).

Kostopoulos (2014) separates twisted horncores into two types, torsioned (with a “screw” type of twisting) and spiraled (with helicoidally twisted horncores). He further speculates that torsion predates true spiraling in evolution based both ontogenetic and paleontological evidence. Kostopoulos (2014) suggests that heteronymous twisting (see definition below) appears to be a highly convergent character occurring repeatedly in nine out of thirteen living bovid tribes (or in 34% of extant bovid species). By contrast, homonymously twisted horns only constitute about 13% of the living record, but are the rule in Alcelaphini, Caprini, and some Bovini, all of which display ramming as their predominant fighting behavior.

In terms of the functions of the horns, Köhler (1993: fig. 6) regards the twist-horned ruminants as the large-sized pushers and open-habitat, small- to medium-sized wrestlers, with the former being mostly in wooded habitat and the latter being predominantly in open grasslands. Caro et al. (2003) suggests that taxa with twisted horns and tips facing inwards are likely to wrestle with their horns, be monogamous and solitary. In contrast to the environmental correlation suggested by Köhler (1993), Caro et al. (2003) found little support for horn shapes to be related to the environmental conditions.

Limb proportions

At the Mount Tologoi site near Ulan-Ude, Sokolov (1959, 1961) described a partial skeleton and associated cranial materials, which can be unambiguously identified as *Spirocerus kiakhtensis*. Although excavations of the skeleton and skull with horncores were carried out in different field seasons (1951 and 1952, respectively), Sokolov (1961) judged the cranial and postcranial skeletons as belonging to the same individual because the skull was excavated in the same stratigraphic horizon and adjacent to the skeleton. Assuming a correct association, this individual [including ZIN 26077(1), 26077(2), 26077(3)] furnishes the best representation of *Spirocerus kiakhtensis*. A complete reconstruction was published by Sokolov (1959, 1961) with remarkably short legs and stout built, similar to that of a goat adapted for scaling steep cliffs.

Teilhard de Chardin and Piveteau (1930: pl. XII, fig. 4) figured an isolated metatarsus of *Spirocerus wongi* with a slender and elongated proportion. Bai et al. (2019: fig. 4A) also published a right metatarsus (IVPP V24483.5) of *S.*

wongi from Shuichongkou. This metatarsus is also very slender and bears no resemblance to those figured by Sokolov (1959, 1961). Bai et al. made no comment about such a stark difference. Given that the Mount Tologoi skeleton is based on considerably more substantial materials, the isolated metatarsals from Nihewan and Shuichongkou seem more likely an error in association. Similarly, long and slender metatarsus from Shuichongkou (Bai et al. 2019: fig. 4) were also referred to *Spirocerus wongi*, in stark contrast to those from Mount Tologoi.

On the other hand, Eurasian *Gazellospira torticornis* possesses relatively slender metapodials (Pilgrim and Schaub 1939; Garrido 2008; Rodrigo 2011; Hermier et al. 2020). Such a limb bone proportion is closer to those of modern antelopes such as *Gazella*, adapted to cursorial locomotion in open terrains, in contrast to the goat-like proportions in *Spirocerus* as illustrated by Sokolov (1959, 1961).

Regarding the paleoenvironments of Zanda Basin, Deng et al. (2012) suggested a landscape of alpine steppe above timberline based on the cursoriality of the three-toed horses *Hipparion zandaense*. However, a primitive giraffid, *Palaeotragus microdon*, from Zanda Basin (Zhang et al. 1981) may be a mixed feeder (Danowitz et al. 2016) and thus seems to suggest the presence of at least patches of trees. Although available evidences are unable to eliminate one of the two scenarios above, or possibly supports a heterogeneous landscape inference where open terrains and wooded areas were both present, it does seem that *Gazellospira tsaparangensis* may have been more adapted to open terrains if the limb bones of its European relatives are any indication (Hermier et al. 2020).

Out of Tibet

While commenting on fossils from the early Pleistocene Crimea, Vislobokova et al. (2020) speculated that the immediate ancestor for *Gazellospira* and *Pontoceros* are not yet known but may be sought in Asia. Previously we have proposed an out-of-Tibet hypothesis for the origins of the Ice Age megafauna from Tibetan Plateau (Deng et al. 2011). Initially based on the ancestral woolly rhinoceros from Zanda Basin (Deng et al. 2011), several other large mammals have subsequently been also shown to be consistent with this hypothesis, including an early snow leopard *Panthera blytheae* (Tseng et al., 2013b), an ancestral sheep *Protovis himalayensis* (Wang et al., 2016), a stem arctic fox *Vulpes qiuzhudingi* (Wang et al. 2014b), and possibly a basal dhole *Sinicuon* cf. *S. dubius* (Wang et al., 2014a), although each taxon probably came out of Tibet at different time and in its unique ways. To this list we may add *Gazellospira tsaparangensis*. The small size and primitive morphology of *G. tsaparangensis* from Zanda once again seems to fit an out-of-Tibet model—an earlier, more primitive form from the high

Tibet giving rise to descendants in western Asia and Europe during the late Pliocene to Pleistocene. The morphologic case for *Gazellospira tsaparangensis* seems strong, with its smaller size, shorter horncore and fewer turns in twist, less-developed frontal sinuses, and smaller supraorbital foramina, all of which are probably primitive characters for the genus.

The case for chronologic occurrences, however, is less certain. That *Gazellospira torticornis* first appeared in western Europe during the MN 16 seems well-established (Cregut-Bonnoure 2007: fig. 1). Hermier et al. (2020: fig. 11), on the other hand, extended its range to possibly Çalta and Akçaköy in Turkey during MN 15, i.e., ~4 Ma. However, the Çalta records are based on fragmentary jaws and limb bone fragments of *Gazellospira* sp. (Bouvrain 1998), whereas those from Dinar-Akçaköy seems also based on inconclusive materials (identified as “Antilopinae indet. ex. gr. *Gazellospira*” or “?*Gazellospira* sp.”) (Sickenberg et al. 1975; Bouvrain 1998). Until better materials become available, we follow Hermier et al. (2020) in tentatively treating these early records from

Turkey as *Gazellospira* sp. (Fig. 11). The next oldest records are somewhat more securely assigned to *G. torticornis* from near the village of Csarnóta in Villány Mountains of southern Hungary based on more definitive materials, such as skull fragments (Kretzoi 1956; Jánossy 1986; Hermier et al. 2020). The age for Csarnóta no. 3 locality, where *Gazellospira* cf. *torticornis* has been documented, is early Villafranchian (Jánossy 1986) and used as the earliest confirmed European record of *G. torticornis* (Hermier et al. 2020).

Based on the above analysis, the Zanda occurrence of *Gazellospira tsaparangensis* is either similar in age to the first appearance of European *G. torticornis* or slightly later if the Turkish materials are indeed early progenitors of *G. torticornis* (Fig. 11). It is worth noting that *G. tsaparangensis* is known from a single locality in the Zanda Basin and future discoveries may expand its stratigraphic range. Because the morphologic case for an out-of-Tibet model for *Gazellospira* origin seems reasonable, we may thus assume that ancestral *Gazellospira* came out of Tibet during the Pliocene,

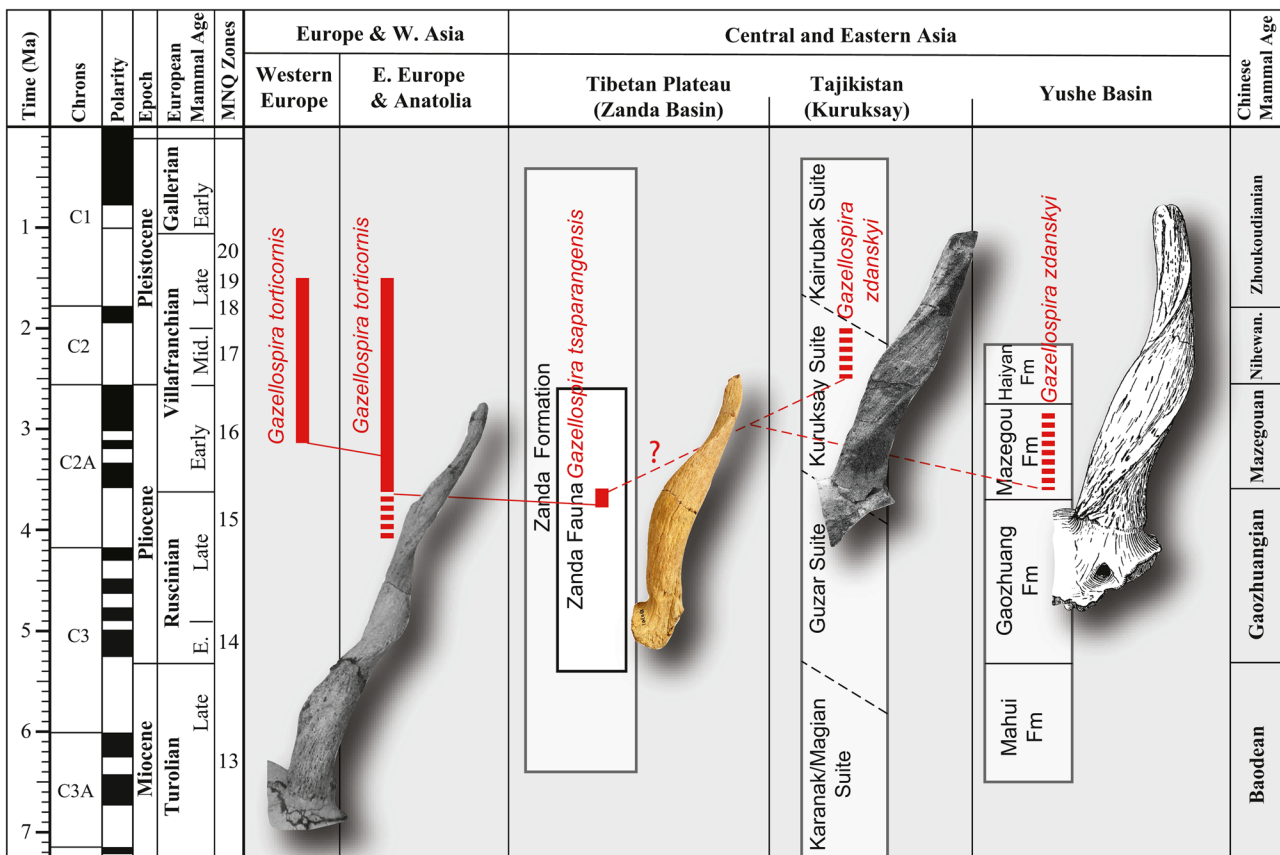


Fig. 11 Geologic and geographic occurrences and evolution of *Gazellospira*. Geochronology of Zanda Basin strata and fauna is based on Wang et al. (2013), and those for European records is adopted from Hermier et al. (2020). The Yushe records of artiodactyles still lack a modern revision and its stratigraphic range is esti-

mated in Tedford et al. (1991). The image for *G. torticornis* is modified from Garrido (2008: fig. 1), for *G. gromovae* modified from Dmitrieva (1977: pl. XVI), and for *G. zdanskyi* modified from Teilhard de Chardin and Trassaert (1938: fig. 53); all are in anterior view and sized to approximately the same scale

substantially earlier than for other megafauna species that fit in the out-of-Tibet scenario, and quickly established itself in the Mediterranean area.

Conclusion

We document in detail a new species of *Gazellospira* Pilgrim and Schaub, 1939, a spiral-horned antelope (tribe Antilopini) previously widely known in the Plio-Pleistocene of Europe and western Asia. *G. tsaparangensis* sp. nov. is collected from the Plio-Pleistocene Zanda Basin in Himalaya Mountains and is characterized by a heteronymous spiral with a distinct posterior keel. The new Tibetan species is easily distinguishable from the type species, *G. torticornis*, in its small size and primitive morphology, such as relatively short horncore with less twisting, thin frontal bones, a lack of frontal and horncore sinuses, small size of supraorbital foramina, and lack of an anterior keel. Such a primitive condition suggests a basal position in the genus *Gazellospira*.

The geologic age for *Gazellospira tsaparangensis* is estimated to be ~3.62 Ma, which makes it one of the earliest occurrences in Eurasia. Given such an early appearance and primitive horncore morphology, *G. tsaparangensis* seems to fit in an out-of-Tibet model of megafauna origin, i.e., it was adapted to cold and harsh environments in high Tibet (elevation 3,800–4,500 m above sea level) before expanding their range to the rest of Eurasia.

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Author contributions XW, QL, and ZJT led the field works that collected the materials in this study. XW collected and analyzed the data. XW drafted the manuscript. All authors discussed, revised, and reviewed the paper.

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Data availability 3D models of specimens described are available for download at <https://www.morphosource.org/projects/000510942?locale=en> (see **Material and methods** section).

Declarations

Competing interests The authors declare no conflicts of interest.

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