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The first discovery of *Hypsodontus* (Artiodactyla, Bovidae) from the Early Miocene of Linxia Basin, Gansu Province, China

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Abstract

Hypsodontinae is a highly specialized subfamily of Bovidae, primarily distributed across East and West Asia as well as Eastern Europe during the Miocene; however, the type genus *Hypsodontus* had not been documented in East Asia. Here, we report a new species of *Hypsodontus*, *Hypsodontus sinensis* **sp. nov.**, from the Dongxiang Formation at the Citan locality, Linxia Basin, China, dating to the late Early Miocene (~17.2 Ma). This marks the first definitive record of the type genus in China. The new material consists of a horn core that exhibits more than 1/3 circle of strong homonymous twisting, uniform elongation, and a smooth surface, displaying closer affinities to *H. pronaticornis*. The age of *Hypsodontus sinensis* **sp. nov.** represents the oldest known record, suggesting that this genus might have originated in China and radiated during the late Early Miocene or early Middle Miocene. The evolutionary relationships among the members of Hypsodontinae, i.e., *Hypsodontus*, *Kubanotragus*, and *Turcocerus*, are also discussed here. Materials from the Xishuigou locality and the Halamagai Formation of the Junggar Basin may represent an ancestral form of these genera mentioned above, possibly an early variant of *Kubanotragus*. The discovery of this new species at the Citan locality illustrates an early diversification of *Hypsodontus* in China and provides critical insights into the early evolution of Bovidae.

Key Words

Bovidae, horn core, Hypsodontinae, *Hypsodontus*, Linxia Basin, Miocene

Introduction

Bovidae, the most diverse group of living artiodactyls, encompasses numerous extinct and extant species (Wang 2023). They underwent a rapid radiation beginning in the Early Miocene (Li et al. 2020), or roughly 20 Ma (Matthee and Davis 2001; Bibi et al. 2009). However, the evolutionary and phylogenetic relationships among early bovids remain under debate and are not straightforward.

Hypsodontinae is a primitive and highly specialized extinct subfamily of Bovidae, characterized by homonymously twisted horn cores (with the left one twisted clockwise from the base upward) that stand upright above the orbit and feature an oval to round cross-section. This group reached peak diversity and became widespread during the Middle Miocene (Gentry 2010). Since its establishment by Köhler (1987), the subfamily has undergone several taxonomic revisions due to unresolved phylogenetic relationships among its genera. Some studies have examined the position of Hypsodontinae within Bovidae and concluded that it may not represent a monophyletic group (Bibi et al. 2009; Gentry 2010; Kostopoulos 2014; Geraads et al. 2023). In contrast, the evolutionary relationships among genera within Hypsodontinae have rarely been discussed (Geraads et al. 1995; Gentry 2003). Over the past three decades, the discovery of new fossil material has led to ongoing reclassifications (Gentry 1992; Chen and Zhang 2004, 2009; Dmitrieva 2007; Gentry

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2010; Li et al. 2020). The subfamily primarily includes the genera *Hypsodontus*, *Turcocerus*, and *Kubanotragus*. The latter two have previously been reported from China, while the type genus *Hypsodontus* had not been documented until this study.

The genus *Hypsodontus* is the earliest established genus within the subfamily. It includes *H. miocenicus* from Belometchetskaya (North Caucasus) in MN5 (Sokolov 1949; Dmitrieva 2007) or MN6 (Pickford et al. 2000); *H. serbicus* from Prebreza (Serbia) in MN6 (Pavlović 1969); and *H. pronaticornis* from Paşalar in MN5 (Köhler 1987) or MN6 (Pickford et al. 2000; Dmitrieva 2007), as well as from Çandır, Yukarı Kızılca, and Prebreza in MN5 (Kaya et al. 2003) or MN6 (Köhler 1987; Pickford et al. 2000), and from İnönü (Geraads et al. 1995) and Mordoğan (Turkey) in MN5 (Kaya et al. 2003). Notably, all known species have been restricted to the Middle Miocene, leaving a critical gap in our understanding of the early evolutionary history of this genus. *H. miocenicus*, erected by Sokolov (1949), was designated as the type species and initially classified within the tribe Oiocerini (Gabunia 1973). However, Köhler (1987) conducted a comprehensive taxonomic revision of highly specialized Miocene bovids, based on extensive fossil material from the Neogene of Turkey, and established the subfamily Hypsodontinae, with *Hypsodontus* as the type genus. Additionally, *H. pronaticornis*, distinguished by its larger size relative to the type species, was described based on fossil records of teeth and horn cores from Middle Miocene deposits in Turkey (Köhler 1987).

In this paper, we report a new bovid horn core from the base of the Dongxiang Formation at the Citan locality in the Linxia Basin, Gansu Province (Fig. 1), dated to the Early Miocene (~17.2 Ma). Based on measurements and morphological comparisons, we assign this specimen to a new species of *Hypsodontus*, which most closely resembles *H. pronaticornis*. This discovery has significant implications for clarifying the morphological and evolutionary relationships within the genus. Furthermore, it offers critical insights into the evolutionary trends of *Hypsodontus*, Hypsodontinae, and even Bovidae in China.

Geological settings

The Neogene strata in China are widely exposed and predominantly composed of terrestrial sediments, within which mammalian fossils have attracted the interest of paleontologists since the second half of the 19th century (Hou et al. 2021). The new specimens described here were excavated from a sandstone layer at the base of the Dongxiang Formation in the Citan locality (also known as "Guanfang"), Linxia Hui Autonomous Prefecture, Gansu Province. The Cenozoic sediments at the Citan locality comprise three Miocene units: the Shangzhuang Formation in the lower part, the Dongxiang Formation in the middle, and the Hujialiang Formation/Liushu

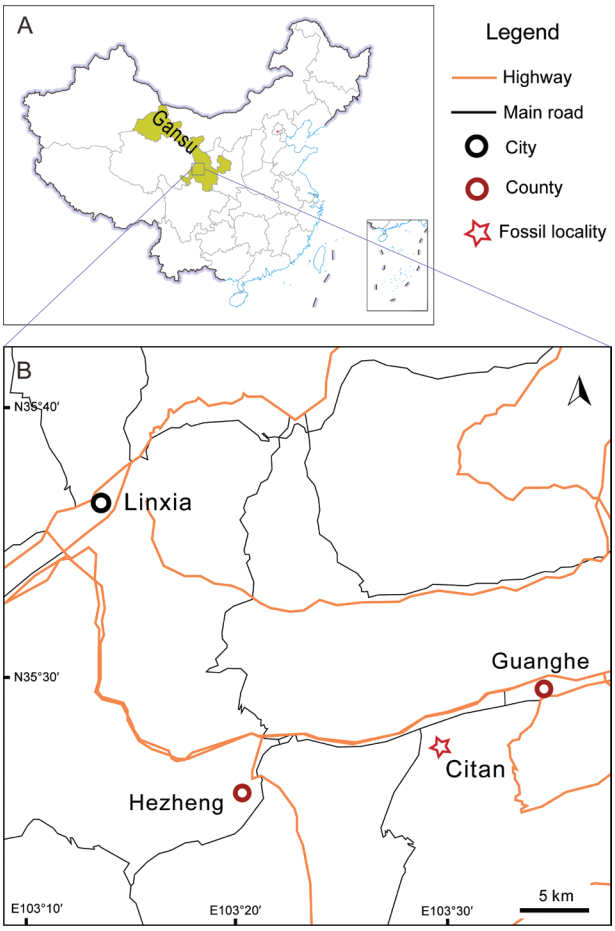

Figure 1. Geographical context of the new specimen discovered from the Citan locality. **A.** Map of China; **B.** A meso-scale view of Linxia Hui Autonomous Prefecture, and Citan area is located in the southeastern part of Linxia City.

Formation in the upper part. The Dongxiang Formation is mainly composed of reddish-brown clay or silty clay with multiple striped greenish marls ("zebra layers"), sharply delineated from the overlying Hujialiang Formation/Liushu Formation. Based on magnetostratigraphic investigations, the age of the sandstone layer at the base of the Dongxiang Formation has been determined to be the Early Miocene (~17.2 Ma) (Zheng et al. 2023).

The basal sandstone layer that produced the new fossil specimen also yields the Shinanu fauna, which comprises abundant mammalian fossils, including *Atlantoxerus junggarensis*, *Democricetodon tongi*, *Leptodontomys lii*, *Litodonomys minimus*, *Gobicricetodon flynni*, "*Protanancus*" *wimani*, *Platybelodon tongxinensis*, *Gomphotherium tassyi*, *Styriofelis guangheensis*, *Anchitherium gobiensis*, *Hispanotherium matritense*, *Percrocuta xixiaensis*, *Stephanocemas thomasoni*, "*Micromeryx*" *caoi*, *Hemicyon* sp., *Alicornops* sp., *Chalicotherium* sp., *Kubanochoerus* sp., etc. (Aiglstorfer et al. 2023; Jiangzuo et al. 2023; Qiu et al. 2023; Wang et al. 2023). Based on chronostratigraphic and biostratigraphic data, this fauna is assigned to the Early to Middle Miocene (~17–15 Ma) (Wang et al. 2023), correlating with the European upper MN4 to MN5 zone (Deng 2006; Jiangzuo et al. 2023).

Materials and methods

The holotype, IVPP V34116, housed in the Institute of Vertebrate Paleontology and Paleoanthropology (**IVPP**), is a nearly complete right horn core with a portion of the frontal bone. Comparative materials from other institutions (see abbreviations below) were scanned as 3D models for observation and data analysis using MeshLab. All measurements are given in millimeters. Cranial and horn core terminology follows Gentry (1992), while cheek tooth terminology follows Bärmann and Rössner (2011). Specimens were photographed using a Canon EOS 6D Mark II, and figure preparation was conducted using Illustrator 2023, Adobe Photoshop CC 2019.

Abbreviations used throughout the paper are as follows: **AMNH** – American Museum of Natural History, New York; **KNM** – the National Museum of Kenya, Nairobi; **PIN/IP** – Paleontological Institute of the Russian Academy of Sciences, Moscow; **IVPP V** – catalogue number prefix for fossil mammals of the IVPP; **MN** – Mammal Neogene, a unit of the European Land Mammal Ages; **APD** – antero-posterior diameter; **TD** – transverse diameter.

Results

Systematic paleontology

Order Artiodactyla Owen, 1848
Suborder Ruminantia Scopoli, 1777
Family Bovidae Gray, 1821
Subfamily Hypsodontinae Köhler, 1987

Genus *Hypsodontus* Sokolov, 1949

Type species. *Hypsodontus miocenicus* Sokolov, 1949

Type locality. the Chokrak sediments of the Middle Miocene in the Belometchetskaya, northern Caucasus

Included species. *Hypsodontus serbicus* Pavlović, 1969; *H. pronaticornis* Köhler, 1987; *H. sinensis* sp. nov.

Diagnosis. Medium-sized bovids (comparable to medium- and small-sized antelopes), possessing a long face and narrow occipital bones with an inverted "V" shape. Horn cores exhibit pronounced homonymous twisting and are inserted vertically above the orbital roofs, which prominently protrude from the sides of the skull. They uniformly taper from the base to the tip, and the surface is covered with small, shallow furrows without keel. The pedicles are long, with a diameter equivalent to the horn core bases. Dentition is moderately hypsodont, with relatively short lower premolar rows. The lower molars lack pillars (ectostylids) and exhibit flattened lingual walls; the distinctive goat-folds are present on the anterior part of the m3 (Sokolov 1949; Gabunia 1973; Köhler 1987; Dmitrieva 2007; Solounias 2007).

Differential diagnosis. *Hypsodontus* differs from *Gobiocerus* in possessing relatively hypsodont teeth with smoother lingual walls, fully developed goat-folds, and the absence of supplementary elements at the base of crescents; further from *Turcocerus* in the larger size (except for *T. grangeri*), more slender and consistent horn cores with a well-developed homonymous twisting and weak longitudinal grooves, and the dimensions of teeth are larger and lower molars that lack basal pillars (ectostylids). Additionally, horn cores differ from *Kubanotragus* in being more robust and displaying a remarkable homonymous twisting.

***Hypsodontus sinensis* sp. nov.**

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Etymology. From China, where the species was first discovered.

Holotype. IVPP V34116, a right horn core with a broken frontal bone (Fig. 2).

Type locality. Citan locality, Linxia Hui Autonomous Prefecture, Gansu Province, China (Fig. 1)

Age. Late Early Miocene (~17.2 Ma), possibly correlated to the early age of MN4 in Europe.

Description. IVPP V34116 is a well-preserved right horn core, with only the lateral part of the base of the horn core and the pedicle slightly broken. As a whole, the horn is elongated (~126.4 mm in length) and evenly tapered upward, giving it a cylindrical appearance; the horn core is only slightly larger in diameter than the pedicle at the transition ring. It is uprightly inserted into the orbit and slightly inclined backward, whereas the tip of the horn core curves anteriorly. In medial view, a fragment of the frontal bone posteromedial to the horn core is preserved, exhibiting a slight inward tilt, resulting in a depression on the posteromedial aspect between the horn cores. In rostral view, the horn core displays marked homonymous twisting, exceeding 1/3 circle but less than 1/2 circle. The basal cross-section is nearly circular (Fig. 2A), with a transverse diameter (TD) to anteroposterior diameter (APD) of approximately 87.8% (a length of 31.1 mm in APD and a length of 27.3 mm in TD). On the surface of the horn core, some faint longitudinal grooves are present, and the horn core surface is porous, especially along the transition ring between the horn core and the pedicle. A short anterior rib is present near the tip (Fig. 2C). The pedicle is rather long (~18.2 mm), with an oval supraorbital foramen at its base. Additionally, two sinuses occur at the bottom of the horn core: one is large and deep on the lateral side, and the other is small and shallow on the medial side (Fig. 2E); it is an advanced morphological trait in bovids as the frontal sinus enters the horn core (Gentry 2010).

Comparison. Up to now, the subfamily Hypsodontinae consists of four genera, among which all except *Gobiocerus* have yielded a considerable number of horn core specimens. As shown in Fig. 2, the right horn core unearthed from the Citan locality exhibits pronounced homonymous twisting, indicating this specimen belongs to *Hypsodontus*. Contrasted with the type species, *Hypsodontus miocenicus*, the horn cores of *Hypsodontus sinensis* are moderately

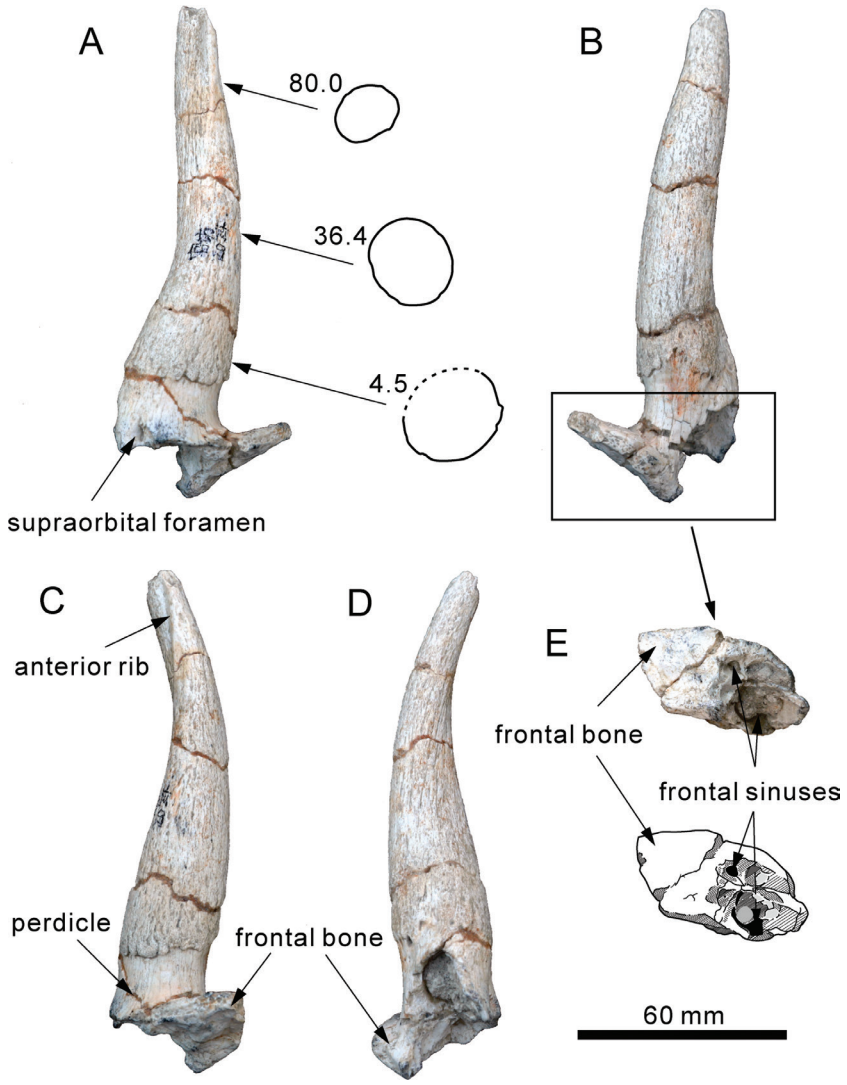

Figure 2. *Hypsodontus sinensis* sp. nov. from the Early Miocene of China. **A.** Anterior, with the cross section at 4.5, 36.4, and 80.0 mm distal to the base of the horn core; **B.** Posterior; **C.** Medial; **D.** Lateral; **E.** Bottom, represented by a photograph and sketch, with the medial side of the horn core facing left.

more robust, exhibit a smoother surface, and demonstrate stronger homonymous twisting, thereby precluding its assignment to *H. miocenicus*.

The earliest record of *Hypsodontus* in Europe west of the Belomechetskaya in the North Caucasus (Stefanović and Mijovic 2004) was reported by Pavlović and Thenius (1959) from the Miocene strata at Prebreza, southern Serbia (the former Yugoslavia), where they documented an indeterminate species of this genus. Subsequently, Pavlović (1969) provided a comprehensive description of those materials and formally designated it as *H. serbicus*, despite some disagreements (Cirić and Thenius 1959; Cirić 1960; Gentry 1970). The new specimen from the Citan locality actually does not differ much from *H. serbicus*, referring to the illustration plates (Pavlović 1969; Tafel XVII-XVIII), but further comparisons are hindered by the lack of detailed morphological description and measurement data of *H. serbicus*.

H. pronaticornis is represented by the most extensive fossil record in this genus, and the horn cores of *Hypsodontus sinensis* share with the former several morphological features in terms of the shape of the cross-section and the degree of the upward tapering. Nevertheless, several diagnostic differences are evident: (1) the horn cores of *Hypsodontus sinensis* are significantly shorter than those of adult individuals of *H. pronaticornis* (measurements of horn cores in Köhler 1987, pp. 148), (2) the former exhibits less pronounced medial inclination; (3) there is no younger growth ring on the *Hypsodontus sinensis*, whereas always remarkably occurs in *H. pronaticornis* (manifesting as an obliquely outwards projection at ~30° on the posterior; Köhler 1987, fig. 16); (4) the growth trend and proportional length of the juvenile *H. pronaticornis* are comparable to those of *Hypsodontus sinensis*, whereas the presence of well-developed sinuses at the bottom of the *Hypsodontus sinensis* ruled out the possibility of juvenile *H. pronaticornis*. These collective morphological attributes support

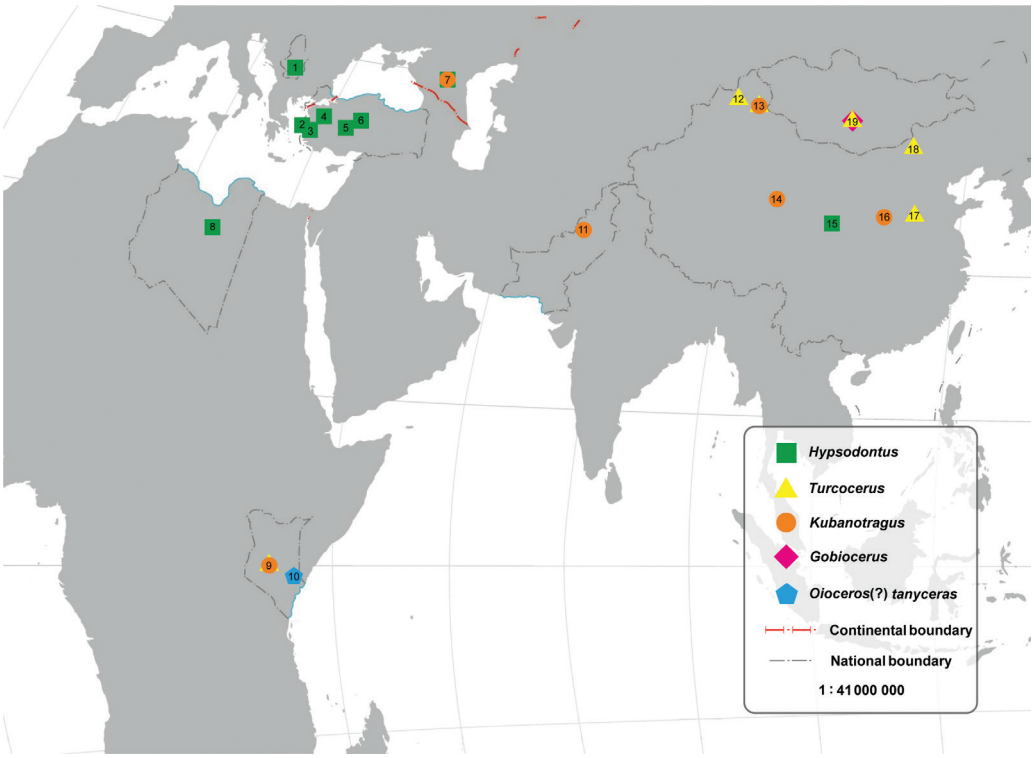

Figure 3. Distribution of the subfamily Hypsodontinae. Numbers refer to the following localities: 1, Prebreza, Serbia (Pavlović 1969); 2, Mordoğan, Turkey (Kaya et al. 2003); 3, Yukari Kizilca, Turkey (Köhler 1987); 4, Paşalar, Turkey (Köhler 1987); 5, Inönü, Turkey (Geraads et al. 1995); 6, Çandir, Turkey (Köhler 1987); 7, Belometchetskaya, North Caucasus (Sokolov 1949; Gabunia 1973); 8, Gebel Zelten, Libya (Gentry 2010); 9, Maboko, Kenya (Geraads et al. 2023); 10, Fort Ternan, Kenya (Gentry 1970); 11, Cheskewala, Pakistan (Thomas 1984); 12, Duolebulujin, Xinjiang (Ye 1989; Ye et al. 1999); 13, Botamoyin, Xinjiang (Ye 1989; Li et al. 2020); 14, Xishuigou, Subei Mongolian Autonomous County, Gansu (Li et al. 2020); 15, Citan (also known as "Guanfang"), Gansu (in this paper); 16, Gaopo, Lantian, Shaanxi (Chen 1990); 17, Jiulongkou, Cixian, Hebei (Chen and Wu 1976); 18, Tonggur, Inner Mongolia (Pilgrim 1934); 19, Ulan-Tologoi, Mongolia (Sokolov 1952; Dmitrieva 2007)

the recognition of *Hypsodontus sinensis* as a distinct species of *Hypsodontus*; despite this, there is a closer phylogenetic affinity to *H. pronaticornis* than to other species.

Turcocerus was erected as a distinct genus by Köhler (1987) to distinguish it from *Oioceros*, which was widely recorded in Turolian (Late Miocene) deposits across Eurasia (Chen 1988). The horn core of *Hypsodontus sinensis* differs from *Turcocerus* not only in terms of length and thickness but also in the twisting degree and the surface ornamentation: (1) among the various forms of *Turcocerus*, their horn cores are consistently shorter and thicker than those of *Hypsodontus sinensis*. For instance, *T. grangeri*, possessing the longest recorded horn cores within this genus so far, measures only approximately 110 mm in length (Pilgrim 1934, pp. 25); (2) the horn cores of *Turcocerus* taper sharply from the base to top, displaying a conical profile in the lateral view, and they generally twist about 1/4 loop (Ye et al. 1999) or less (Köhler 1987), which is much weaker than those of the *Hypsodontus sinensis*; (3) the horn cores of *Turcocerus* are characterized by prominent longitudinal grooves resulting in a rougher horn core surfaces; for example, there are covered with numerous anastomosing crests on the horn cores surface of the *T. kekemaidengensis* (Ye et al. 1999), and posterior longitudinal grooves occur between two well-demarcated ridges on the horn cores of *T. grangeri*, *T. noverca*, *T. halamagaiensis* and *T. africanus* (Li et al. 2020; Geraads et al. 2023), while those of *Hypsodontus sinensis* are flat and smooth, with only a few short and indistinct grooves. Therefore, the new material from the Citan locality must not be affiliated with the *Turcocerus*.

Kubanotragus is characterized by the slender and well-proportioned horn cores, with a very weak homonymous twisting (Gabunia 1973; Chen 1990). Although the length of the horn cores of *Kubanotragus* resembles that of *Hypsodontus sinensis*, the latter is distinguished by a more intense twisting. Additionally, the two taxa differ in basal cross-sections; the type species *K. sokolovi* displays a symmetrically elliptical cross-section with transverse compression (Gabunia 1973), while *Hypsodontus sinensis* is nearly circular. Previous taxonomic uncertainty regarding the distinction between *Hypsodontus* and *Kubanotragus* stemmed from limited fossil records. Given this paucity of available data, the genera *Hypsodontus* and *Kubanotragus* were initially considered synonymous (Gentry 1990). The differences in their horn corns have been variably interpreted as either a manifestation of ontogeny (Köhler 1987) or sexual dimorphism (Thomas 1984; Bonis et al. 1998). However, Geraads et al. (1995) argued the two share very few derived characters. Comparisons between the horn corns of *H. sinensis* and those of *Kubanotragus* species (Gabunia 1973, fig. 34; Chen 1990, Plate I, fig. 1–8) also provide no clear evidence that would support the synonymization of the two genera.

Discussion

Evolutionary relationships of Hypsodontinae

Understanding the evolution of early bovids primarily centers on the horn cores, as they serve as the most reliable and diagnostically unambiguous feature for determining a ruminant as a bovid (Solounias et al. 1995). Although bovid horn cores tend to diversify, the changes generally progress from short, robust ancestral forms to more derived morphologies characterized by increased length and varying degrees of inclination, divergence, curvature, and torsion (Gentry 2010). The three genera *Hypsodontus*, *Turcocerus*, and *Kubanotragus* from the Miocene epoch all possess homonymously twisted horn cores, representing a highly specialized morphological characteristic compared to other contemporaneous bovids. Remarkably, the degree of twisting shows significant interspecific variation among these taxa, with *Hypsodontus* exhibiting the most pronounced twisting, followed by *Turcocerus*, while *Kubanotragus* displays the least developed form. In summary, we suggest that the slight homonymous twisting in *Kubanotragus* represents a plesiomorphic trait within Hypsodontinae, whereas the more intense twisting seen in *Hypsodontus* and *Turcocerus* is a derived characteristic, reflecting an evolutionary adaptation that contributed to bovid diversification.

Fossil materials from the middle to late Early Miocene (MN3−4) of the Tiejianggou Formation at the Xishuigou locality in Gansu Province (Li et al. 2020) and the Halamagai Formation in the northern Junggar Basin, Xinjiang Uygur Autonomous Region (Ye 1989), share several morphological similarities with the aforementioned genera (*Hypsodontus*, *Turcocerus*, *Kubanotragus*). These similarities include horn cores inserted directly above the orbits with homonymous twisting, more high-crowned cheek teeth, a relatively short lower premolar row, and well-developed goat folds. Further detailed comparisons reveal that the key diagnostic features observed in the Xishuigou and Halamagai specimens—such as a distinct horn core contour (concave anterior and convex posterior margins in lateral view), slight homonymous twisting with uniform upward tapering, oval basal cross-sections (mediolateral compression) with comparable TD/APD ratios (Table 1), and rugose surfaces bearing longitudinal grooves and ribs—strongly align them with the type species *Kubanotragus sokolovi*. In addition, the horn cores of the Xishuigou and Halamagai specimens are relatively short and stumpy, consistent with early-stage bovid morphology. These specimens also retain several primitive traits, including relatively lower-crowned teeth, weakly developed styles or stylids, and the presence of basal pillars (ectostylids) on the lower molars. We therefore hypothesize that the fossil remains from Xishuigou and Halamagai likely represent an early variant of *Kubanotragus*, possibly the earliest members among the three genera within Hypsodontinae. The more derived genera, *Hypsodontus* and *Turcocerus*, may have diverged from early *Kubanotragus* taxa during the transition from the Early to Middle Miocene.

As for the genus *Gobiocerus*, which first appeared in the Early Miocene (MN4) (Dmitrieva 2007), we have no definite hypothesis on its evolutionary relationships due to the absence of preserved horn core material. However, several primitive dental features—including relatively brachyodont teeth with rounded and smoothed ribs, poorly developed styles and goat folds, the absence of supplementary elements on both upper and lower teeth, and a slightly striated tooth surface (Dmitrieva 2007, Plate 11, fig. 6–8)—suggest that this genus occupies a basal position closer to the ancestral bovid in the phylogenetic tree.

Origin and migration patterns of *Hypsodontus* in the Miocene

During the Miocene epoch, Hypsodontinae were widely distributed across East Asia (including China and Mongolia), West Asia (notably Turkey), and the Balkan region of eastern Europe, with limited occurrences documented in Central Europe, Africa, the Arabian Peninsula, Pakistan, and India (Fig. 3). In contrast, the genus *Hypsodontus* appears to have been predominantly restricted to the Anatolian region of modern-day Turkey.

Due to the ambiguity of the past geological record, the stratigraphic resolutions of the discovered *Hypsodontus* remain contentious (Geraads et al. 1995; Pickford et al. 2000; Kaya et al. 2003; Stefanović 2004). Notably, non-Chinese records are typically dated to the Middle Miocene (MN5 to MN6 zones in Europe). Of particular significance is the newly discovered *Hypsodontus* from the Citan locality in the Linxia Basin, Gansu Province, which predates all other known species. This temporal precedence suggests a potential origin in China. This hypothesis is further supported by the more derived morphology observed in the Turkish specimens, which would be consistent with a subsequent westward dispersal.

Table 1. Dimensions of the basal cross-section of horncores from Kubanotragus sokolovi and the other two forms. The measurements of TD and APD are in mm.

Locality	North Caucasus (Gabunia 1973)			Xishuigou locality (Li et al. 2020)	The northern Junggar Basin (Ye 1989)									
Specimen	PIN №428/10	IP №5/10	IP №5/210	IVPP V 25523.1	V 8595.2	V 8595.3	V 8595.4	V 8595.6	V 8595.7	V 8595.8	V 8595.9	V 8596.1	V 8597.1	V 8597.2
TD	14	16.1	16	21.2	13.7	15.5	16.8	17.8	20.9	16.7	17.3	20.7	14.5	16.1
APD	18	19	20	26.7	17.1	19.1	20.4	22.5	24.5	21.5	20	23.9	17.2	19
TD/APD (%)	78.7	84.7	80	79.4	80.1	81.2	82.4	79.1	85.3	77.7	86.5	86.6	84.3	84.7

It remains a fascinating question what plausible factors contributed to the origin of *Hypsodontus* in East Asia and its subsequent dispersal into West Asia, Europe, and Africa. One of the key factors for the origin of the genus in China may be the uplift of the Tibetan Plateau. Affected by the Cenozoic Himalayan orogeny, multiple regions—including the Lunpola and Hoh Xil basins in the central to northern Tibetan Plateau—underwent continuous uplift, reaching approximately 3000 meters by the Miocene (Deng et al. 2024), effectively blocking the inflow of water vapor transported by the Indian Ocean. Consequently, aridification commenced during the Early Miocene, particularly impacting the northern Tibetan Plateau region (northwestern China), including the Linxia Basin. These environmental changes may have created ecological conditions favorable for the evolution of the grazer *Hypsodontus*, with high-crowned teeth that emerged in response to a shift toward a semi-arid, savanna-like ecosystem.

Moreover, the occurrence of dry summers and the development of a distinctive arid belt in the middle latitudes—likely driven by the predominant planetary wind patterns (Oligocene-like) (Liu et al. 2009)—combined with the emergence of land bridges along the Mediterranean and Paratethys seaways during the Early Miocene (Fig. 4A, B), created moderately favorable conditions for *Hypsodontus* dispersal. This mid-latitude arid belt was temporarily subdued during the Middle Miocene Climatic Optimum (MMCO, ~16.9–14.7 Ma) but intensified with global cooling in the late Middle Miocene, persisting into the Late Miocene (Liu et al. 2009). Although these land bridges were temporarily disrupted during the Langhian (Fig. 4C), their reconnection in the early Serravallian (Fig. 4D) likely facilitated *Hypsodontus* migration. Therefore, we propose that the genus *Hypsodontus* originated in China and subsequently dispersed across Eurasia and the Afro-Arabian regions during the transition from the early to the Middle Miocene.

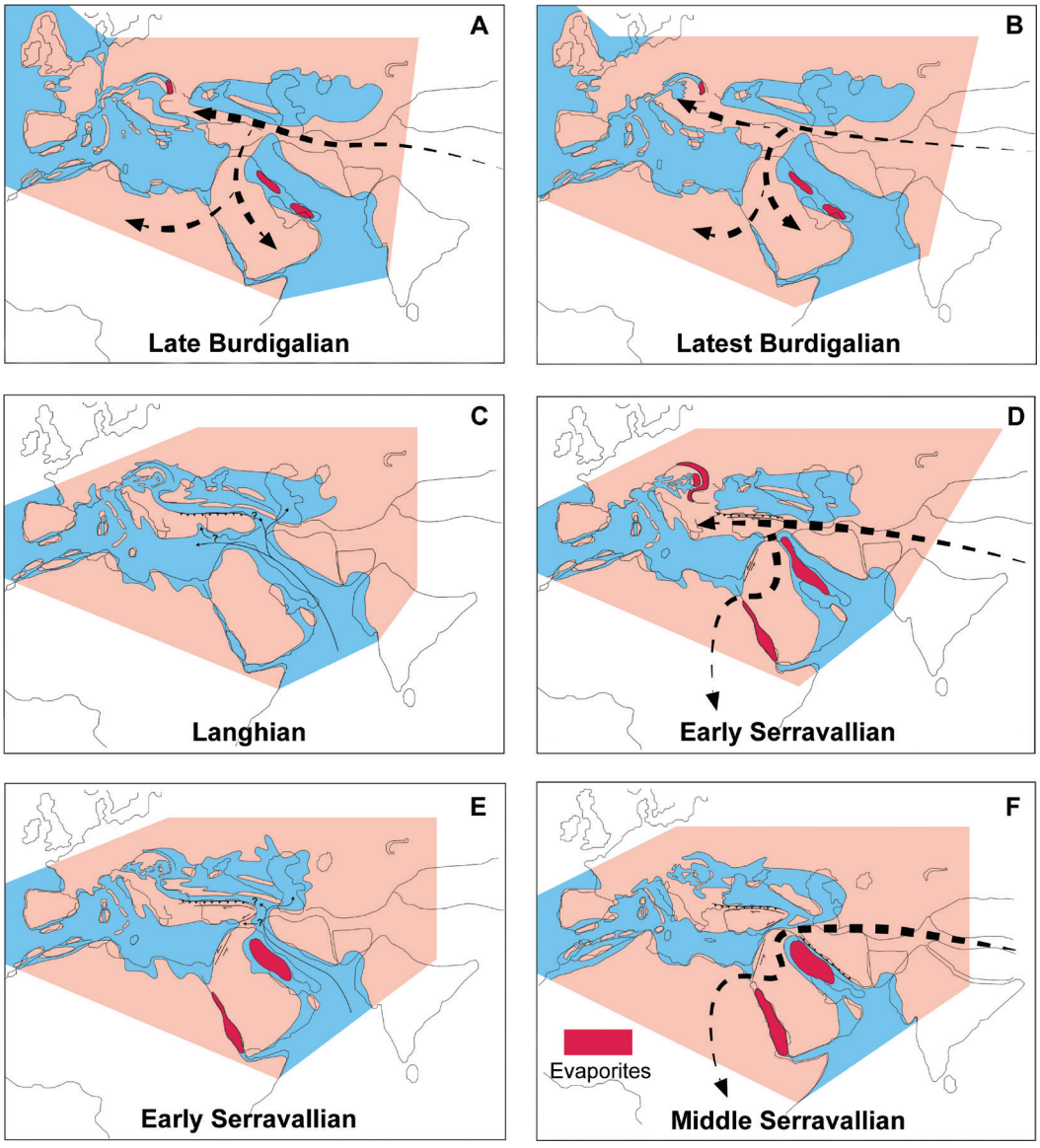

Figure 4. Movements of continental plates in the Paratethys, modified from Rögl (1998). The black dotted lines with black arrows suggested migration routes of *Hypsodontus*, and the question marks represent uncertainty of the land bridges.

Conclusion

We describe herein a new species of *Hypsodontus* from the late Early Miocene Dongxiang Formation at the Citan locality in the Linxia Basin, Gansu Province, designated as *Hypsodontus sinensis* sp. nov. This specimen (IVPP V 34116), comprising a well-preserved right horn core, represents the first definitive record of this genus in China. Notably, the age of this specimen predates all previously known *Hypsodontus* species, suggesting a probable origin in China. We propose that *Hypsodontus* subsequently dispersed westward into West Asia, Europe, Africa, and the Arabian Peninsula during the late Early Miocene or early Middle Miocene, likely facilitated by the mid-latitude arid belt and land bridges formed by tectonic activity in the Paratethys region.

Based on comparative morphological analyses, the fossil specimens collected from Xishuigou in the Tabenbuluk area of Gansu Province represent an early form of *Kubanotragus*, which likely gave rise to two more derived genera: *Hypsodontus* and *Turcocerus*. As for *Gobiocerus*, which is only known from dental remains, its evolutionary relationship with the other three genera in the subfamily Hypsodontinae remains uncertain; however, the primitive dental characteristics suggest a relatively basal position within the subfamily.

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References

Aiglstorfer M, Wang SQ, Cheng J, Xing LD, Fu J, Mennecart B (2023) Miocene Moschidae (Mammalia, Ruminantia) from the Linxia Basin (China) connect Europe and Asia and show an early evolutionary diversity of a today monogeneric family. Palaeogeography, Palaeoclimatology, Palaeoecology 619: 111531. https://doi.org/10.1016/j.palaeo.2023.111531

Bärmann EV, Rössner GE (2011) Dental nomenclature in Ruminantia: towards a standard terminological framework. Mammalian Biology 76: 762–768. https://doi.org/10.1016/j.mambio.2011.07.002

Bibi F, Bukhsianidze M, Gentry AW, Geraads D, Kostopoulos DS, Vrba ES (2009) The fossil Record and Evolution of Bovidae: State of the Field. Palaeontologia Electronica 12(3): 1–11.

Bonis LD, Koufos GD, Sen S (1998) Rumminants (Bovidae and Traguliade) from the middle Miocene (MN 5) of the island of Chios, Aegean sea (Greece). Neues Jahrbuch für Geologic und Paläontologie, Abhandlungen 210(3): 399–420. https://doi.org/10.1127/njgpa/210/1998/399

Chen GF (1988) Remarks on the *Oioceros* species (Bovidae, Artiodactyla, Mammalia) from the Neogene of China. Vertebrata PalAsiatica 26(3): 157–172. [in Chinese]

Chen GF (1990) Discovery of the genus *Kubanotragus* (Bovidae, Artiodactyla) from the Middle Miocene in Lantian District, Shaanxi Province, China. Vertebrata PalAsiatica 28(1): 1–9. [in Chinese]

Chen GF, Wu WY (1976) Miocene mammalian fossils from Jiulongkou, Cixian, Hebei Province. Vertebrata PalAsiatica 14(1): 6–19. [in Chinese]

Chen GF, Zhang ZQ (2004) *Lantiantragus* gen. nov. (Urmiatheriinae, Bovidae, Artiodactyla) from the Bahe formation, Lantian, China. Vertebrata PalAsiatica 42(3): 205–215. [in Chinese]

Chen GF, Zhang ZQ (2009) Taxonomy and evolutionary process of Neogene Bovidae from China. Vertebrata PalAsiatica 47(4): 265–281. [in Chinese]

Cirić A (1960) O hioskoj fauni iz Prebreze. Vesnik Zavoda za geološka i geofizička istraživanja NR Srbije 18/A:1–82. [in Serbian]

Cirić A, Thenius E (1959) Über das Vorkommen von Giraffokeryx (Giraffidae) im europäischen Miozän. Anzieger der Matematisch-naturwissenschaftlische Klasse der Österreichische Akademie der Wissenschaften 9: 153–162. [in Serbian]

Deng T (2006) Chinese Neogene mammal biochronology. Vertebrata PalAsiatica 44(2): 143–163.

Deng T, Fang XM, Li Q, Wang SQ, Wu FX, Hou SK, Ma J, Jiangzuo QG, Sun DH, Zheng Y, Shi QQ, Sun BY, Li L (2024) Neogene integrative stratigraphy, biotas, and paleogeographical evolution of the Qinghai-Tibetan Plateau and its surrounding areas. Science China Earth Sciences 67(4): 1326–1359. [in Chinese] https://doi.org/10.1360/SSTe-2022-0412

Dmitrieva EL (2007) Caprinae (Bovidae, Artiodactyla, Mammalia) from the Neogene of Mogolia. Paleontological Journal 41(6): 671–682. https://doi.org/10.1134/S0031030107060111

Gabunia LK (1973) Belomechetskaya fauna of the fossil vertebrates. "Metsniereba", Tbilisi, 137 pp. [in Russian]

Gentry AW (1970) The Bovidae (Mammalia) of the Fort Tenan Fossil Fauna. In: Leakey LSB, Savage RJG (Eds) Fossil Vertebrates of Africa. Academic Press, New York, 243–323.

Gentry AW (1990) Evolution and dispersal of African Bovidae. In: Bubenik GA, Bubenik AB (Eds) Horns, pronghorns and antlers. Springer, New York, 195–227. https://doi.org/10.1007/978-1-4613-8966-8_6

Gentry AW (1992) The subfamilies and tribes of the family Bovidae. Mammal Review 22(1): 1–32. https://doi.org/10.1111/j.1365-2907.1992.tb00116.x

Gentry AW (2003) Ruminantia (Artiodactyla). In: Fortelius M, Kappelman J, Sen S (Eds) Geology and paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York, 332–379.

Gentry AW (2010) Bovidae. In: Werdelin L, Sanders W (Eds) Cenozoic Mammals of Africa. University of California Press, Berkeley, 747–803. https://doi.org/10.1525/california/9780520257214.003.0038

Geraads D, Güleç E, Saraç G (1995) Middle Miocene Ruminants from Inönü, Central Turkey. Neues Jahrbuch für Geologie und

Paläontologie 1995(8): 462–474. https://doi.org/10.1127/njgpm/1995/1995/462

Geraads D, McCrossin M, Benefit B (2023) Bovidae (Mammalia) from the early Middle Miocene of Maboko, Kenya. Historical Biology 36(3): 619–630. https://doi.org/10.1080/08912963.2023.2179397

Hou SK, Li Q, Wang SQ, Sun BY, Lu XK, Shi QQ, Wu FX, Jiangzuo QG, Deng T (2021) Lithostratigraphic subdivision and correlation of the Neogene in China. Journal of Stratigraphy 45(3): 426–439. [in Chinese]

Jiangzuo QG, Jiang H, Wang SQ (2023) Evolution, succession and paleoecology of the Late Cenozoic order Carnivora in China. Quaternary Sciences 43(3): 673–691.

Kaya T, Geraads D, Tuna V (2003) A new Middle Miocene mammalian fauna from Mordoğan (Western Turkey). Paläontologische Zeitschrift 77(2): 293–302. https://doi.org/10.1007/BF03006943

Köhler VM (1987) Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei. 28). Paleontologia i Evolució 21: 133–246.

Kostopoulos DS (2014) Taxonomic re-assessment and phylogenetic relationships of Miocene homonymously spiral-horned antelopes. Acta Palaeontologica Polonica 59(1): 9–29. https://doi.org/10.4202/app.2011.0013

Li YK, Li Q, Ni XJ, Wang SQ, Aiglstorfer M, Deng T (2020) The oldest known bovid from China and reappraisal of the Chinese '*Eotragus*'. Papers In Palaeontology 7: 913–929. https://doi.org/10.1002/spp2.1319

Liu LP, Eronen JT, Fortelius M (2009) Significant mid-latitude aridity in the middle Miocene of East Asia. Palaeogeography, Palaeoclimatology, Palaeoecology 279: 201–206. https://doi.org/10.1016/j.palaeo.2009.05.014

Matthee CA, Davis SK (2001) Molecular Insights into the Evolution of the Family Bovidae: A Nuclear DNA Perspective. Molecular Biology and Evolution 18(7): 1220–1230. https://doi.org/10.1093/oxfordjournals.molbev.a003908

Pavlović MB (1969) Mioyän-Saugetiere des Toplica-Beckens palaeontologisch-stratigraphische Studie. Geološki anali Balkanskoga poluostrva 44: 269–394.

Pavlović MB, Thenius E (1959) Gobycion macrognatus aus dem Miocän Jugoslaviens. Anzeiger der mathematis-chnaturwissenschatliche Klasse der Österreichische Akademie der Wissenschaften 11: 214–222.

Pickford M, Gabunia L, Mein P, Morales J, Azanza B (2000) The Middle Miocene mammalian site of Belomechetskaya, north Caucasus: an important biostratigraphic link between Europe and China. Geobios 33(2): 257–267. https://doi.org/10.1016/S0016-6995(00)80023-6

Pilgrim GE (1934) Two new species of sheep-like antelope from the Miocene of Mongolia. American Museum Novitiates 716: 1–29.

Qiu ZD, Wang BY, Li L (2023) Middle Cenozoic micromammals from Linxia Basin, Gansu Province, China, and their implications for biostratigraphy and Palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 616: 111467. https://doi.org/10.1016/j.palaeo.2023.111467

Rögl VF (1998) Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums in Wien 99A: 279–310.

Sokolov II (1949) On Fossil of Bovids (Bovidae, Mammalia) from the Middle Miocene of northern Caucasus. Doklady Akademii Nauk SSSR, 67(6): 1101–1104. [in Russian]

Sokolov II (1952) On the Presence of Bovids (Bovidae, Mammalia) in the Lower Miocene Beds of the Western Gobi. Trudy Paleontologicheskogo Instituta, Akademiya Nauk SSSR 41:155–158 [in Russian].

Solounias N (2007) Family Bovidae. In: Prothero DR, Foss SE (Eds) The Evolution of Artiodactyls. The Johns Hopkins University Press, Maryland, 278–291.

Solounias N, Barry JC, Bernor RL, Lindsay EH, Raza SM (1995) The oldest bovid from the Siwaliks, Pakistan. Journal of Vertebrate Paleontology 15(4): 804–814. https://doi.org/10.1080/02724634.1995.10011263

Stefanovic I, Mijovic D (2004) The Middle Miocene fossil site prebreza in southern Serbia. In: Ber A, Alexandrowicz Z, Balabanis P (Eds) Geological heritage concept, conservation and protection policy in Central Europe, October 2003. Polish Geological Institute Special Papers, Warszawa, 13: 209–212.

Thomas H (1984) Les bovidae (Artiodactyla: Mammalia) du miocène du sous-continent indien, de la péninsule arabique et de l'afrique: Biostratigraphie, biogéographie et écologie. Palaeogeography, Palaeoclimatology, Palaeoecology 45: 251–299. https://doi.org/10.1016/0031-0182(84)90009-9

Wang SQ (2023) Large herbivorous mammals in the Neogene of China and their biostratigraphy. Quaternary Sciences 43(3): 637–672. [in Chinese]

Wang SQ, Li CX, Li Y, Zhang XX (2023) Gomphotheres from Linxia Basin, China, and their significance in biostratigraphy, biochronology, and paleozoogeography. Palaeogeography, Palaeoclimatology, Palaeoecology 613: 111405. https://doi.org/10.1016/j.palaeo.2023.111405

Ye J (1989) Middle Miocene artiodactyls from the northern Junggar Basin. Vertebrata PalAsiatica 27(1): 37–52. [in Chinese]

Ye J, Wu WY, Bi SD, Zhang Y, Meng J (1999) A new species of *Turcocerus* from the Middle Miocene of the Northern Junggar Basin. In: Wang YQ, Deng T (Eds) Seventh Annual Meeting of the Chinese Society of Vertebrata Paleontology, April 1999. China Ocean Press, Beijing, 149–156. [in Chinese]

Zheng Y, Qiu ZX, Qiu ZD, Li L, Wei XH, Zhang R, Yue LP, Deng T (2023) Revised magnetostratigraphy of the Linxia Basin in the northeast Tibetan Plateau, constrained by micromammalian fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 623: 111620. https://doi.org/10.1016/j.palaeo.2023.111620