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The Late Miocene ‘ovibovin’ bovids in Eurasia

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Abstract During the Late Miocene, numerous medium to large-sized herbivores, that resemble the living *Ovibos* in skeletal morphology, dispersed throughout the Holarctic realm and comprised eleven genera: *Lantiantragus*, *Shaanxispira*, *Tsaidamotherium*, *Criotherium*, *Mesembriacerus*, *Hezhengia*, *Urmiatherium*, *Parurmiatherium*, *Plesiaddax*, *Sinotragus*, and *Prosinotragus*. These genera are primarily found in eastern Asia, in which nine genera are found in northern China, as well as in countries in eastern Europe and western Asia. They are distinguished by unique characteristics, including a perpendicular braincase, specialized horn cores, and a robust basioccipital. Previous studies have often classified these ‘ovibovin’ bovids as part of the conventional subfamily/tribe Ovibovinae/Ovibovini, along with extant *Ovibos*. Nevertheless, an increasing number of studies do not support the monophyly of the subfamily/tribe Ovibovinae/Ovibovini, nor is a close relationship likely between these Late Miocene ‘ovibovin’ bovids and extant *Ovibos*. Among the eleven genera of ‘ovibovin’ bovids, *Plesiaddax*, *Hezhengia*, and *Urmiatherium* are often considered to have a very close relationship and conventionally form the tribe Urmiatheriini. However, previous phylogenetic analyses do not support the monophyly of Urmiatheriini. This paper presents a summary of the transmutation of the terms Ovibovidae/Ovibovinae/Ovibovini/Ovibovina, the temporal and spatial distribution of the Late Miocene ‘ovibovin’ bovids in Eurasia, the principal characteristics of these taxa, and the previous phylogenetic analyses.

Key words Eurasia, Late Miocene, ‘ovibovin’ bovids, Bovidae, temporal and spatial distribution

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1 Introduction

Bovids are ruminant artiodactyls that were the dominant mammalian herbivores in Old World terrestrial communities with diverse extant and extinct species in Africa, Eurasia, and North America (Simpson, 1945). The extant bovids include approximately 45 genera and

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140 species (Vrba, 1985; Kingdon, 1989; Grubb, 1993; Bibi et al., 2009) in two subfamilies and approximately 13 tribes (Bibi and Tyler, 2022). Of all the living bovids, the North American muskox (*Ovibos moschatus*) is a particularly unique animal due to its distinctive cranial features and high adaptability to the harsh environment of the Arctic tundra (Lent, 1988). Traditionally, the muskox was believed to be closely related to the takin (*Budorcas*) from southern China (Simpson, 1945). Gray (1872) proposed the family Ovibovidae for *Ovibos* and *Budorcas*. In the same year, Gill (1872) proposed the subfamily Ovibovinae, which included both living *Ovibos* and extinct *Bootherium* (Table 1). Lydekker (1913) and Bohlin (1935a) also used the subfamily Ovibovinae. Sickenberg (1933) established the subfamily Urmiatheriinae, which included two extinct genera: *Parurmiatherium* and *Urmiatherium*. Bohlin (1935a) subsequently merged the Urmiatheriinae into the Ovibovinae. Bohlin (1935a) even placed four additional extinct genera, *Parurmiatherium*, *Plesiaddax*, *Pseudobos*, and *Urmiatherium*, in the subfamily Ovibovinae. Bohlin (1937) reevaluated his earlier classification and agreed that the subfamily Urmiatheriinae could be legitimate due to the unique horn core growth processes between *Urmiatherium* and modern *Ovibos*. Simpson (1945) concurred with the close relationship between *Ovibos* and *Budorcas* and grouped them together with nine extinct genera, namely *Boopsis*, *Bootherium*, *Criotherium*, *Euceratherium*, *Parurmiatherium*, *Plesiaddax*, *Symbos*, *Tsaidamotherium*, and *Urmiatherium*, in the tribe Ovibovini under the subfamily Caprinae. These genera span a temporal range from the Late Miocene to the Pleistocene. Simpson's classification has been widely accepted for a long time. McKenna and Bell (1997) adopted Simpson's (1945) framework but expanded the Ovibovini tribe to include additional extinct genera such as *Damalavus*, *Lyrocerus*, *Makapania*, *Megalovis*, *Palaeoreas*, *Praeovibos*, and *Soergelia*. Grubb (2001) classified the two genera, *Ovibos* and *Budorcas*, within the tribe Ovibovini, which is part of the subfamily Caprinae. Chen and Zhang (2004) resurrected the subfamily Urmiatheriinae, proposed by Sickenberg (1933), for some Late Miocene bovids in northern China. Their subfamily includes *Turcocerus*, *Urmiatherium*, *Plesiaddax*, *Hezhengia*, and *Shaanxispira*. Chen and Zhang (2009) divided the subfamily Urmiatheriinae into two tribes: Turcocerini and Urmiatheriini. The latter tribe includes *Lantiantragus*, *Urmiatherium*, *Plesiaddax*, *Hezhengia*, *Tsaidamotherium*, *Shaanxispira*, *Sinotragus*, and *Prosinotragus*. Nevertheless, a recent phylogenetic analysis did not corroborate the monophyly of the tribe Urmiatheriini (Shi and Deng, 2021). In the Handbook of Hoofed Mammals, Groves and Leslie (2011) classified *Ovibos* and *Budorcas* in the tribe Caprini under the subfamily Antilopinae, along with several other living genera, including *Ammotragus*, *Arabitragus*, *Capra*, *Carpricornis*, *Hemitragus*, *Naemorhedus*, *Nilgiritragus*, *Oreamnos*, *Ovis*, *Pantholops*, *Pseudois*, and *Rupicapra*. However, molecular evidence, particularly mitochondrial DNA analysis, indicates that *Ovibos* is more closely related to

Table 1 Various concepts of scientists about the groups of fossil ‘ovibovin’ bovids

Gray (1872)	Gill (1872)	Lydekker (1913)	Bohlin (1935a)	Simpson (1945)	McKenna and Bell (1997)	Grubb (2001)	Groves and Leslie (2011)	Hassanin et al. (2012)
Family Ovibovidae	Family Bovidae Subfamily Ovibovinae	Family Bovidae Subfamily Ovibovinae	Subfamily Ovibovinae	Superfamily Bovoidea Family Bovidae Subfamily Caprinae Tribe Ovibovini	Superfamily Bovoidea Family Bovidae Subfamily Caprinae Tribe Ovibovini	Family Bovidae Subfamily Caprinae Tribe Ovibovini	Family Bovidae Subfamily Caprinae Tribe Caprini	Family Bovidae Subfamily Antilopinae Tribe Caprini Subtribe Ovibovina
Ovibos *Budorcas*	*Ovibos* †*Bootherium*	*Ovibos*	†*Parurmiatherium* †*Plesiaddax* †*Pseudobos* †*Urmiatherium*	*Ovibos* *Budorcas* †*Boopsis* †*Bootherium* †*Criotherium* †*Euceratherium* †*Parurmiatherium* †*Plesiaddax* †*Symbos* †*Tsaidamotherium* †*Urmiatherium*	*Ovibos* *Budorcas* †*Boopsis* †*Bootherium* †*Criotherium* †*Damalavus* †*Euceratherium* †*Lyrocerus* †*Makapania* †*Megalovis* †*Palaeoreas* †*Parurmiatherium* (including †*Plesiaddax*) †*Praeovibos* †*Soergelia* †*Symbos* †*Tsaidamotherium* †*Urmiatherium*	*Ovibos* *Budorcas*	*Ovibos* *Carpricornis* *Naemorhedus* *Pantholops* *Oreamnos* *Budorcas* *Ammotragus* *Arabitragus* *Hemitragus* *Pseudois* *Capra* *Nilgiritragus* *Ovis* *Rupicapra*	*Ovibos* *Capricornis* *Naemorhedus*

Capricornis and *Naemorhedus* than to *Budorcas* (Lalueza-Fox et al., 2005; Ropiquet and Hassanin, 2005; Bibi et al., 2012; Hassanin et al., 2012). Hassanin et al. (2012) proposed the subtribe Ovibovina, which belongs to the tribe Caprini and includes only the living *Ovibos*, *Capricornis*, and *Naemorhedus*. For the fossil bovids that are similar to *Ovibos*, Lazaridis et al. (2017) used a general term, “ovibovine-like taxa”. In this text, it is proposed to use the term ‘ovibovin’ bovids to refer all fossil taxa that are not closely related to *Ovibos*, following Kostopoulos et al. (2023), as the conventional Ovibovinae/Ovibovini is no longer applicable to the living *Ovibos* and the “urmiatherines” are not monophyly. It is also worth noting that the positions of these ‘ovibovin’ fossil bovids remain unsolved.

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover, Germany; BMNH, Natural History Museum, London, UK; BSPM, Bayerische Staatssammlung für Paläontologie und Geologie, Paläontologisches Museum, Munich, Germany; ÇO, Çankırı Museum, Turkey; DOE, Department of the Environment, Maragheh, Iran; HMV, Hezheng Paleozoological Museum, Gansu, China; HUW, Howard University, Laboratory of Evolutionary Biology, Washington, DC, USA; IGPM, Institute für Geologie und Paläontologie, Universität Münster, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LGPUT, Laboratory of Geology and Palaeontology, Aristotle University of Thessaloniki, Thessaloniki, Greece; MMTT, fossils from Maragheh localities of LRE deposited either in Tehran or in Washington, DC, USA; MNHN, Muséum national d’Histoire Naturelle, Paris, France; MTA, Maden Tetkik ve Arama Museum, Ankara, Turkey; MYŞE PV, Natural History Museum of Ege University, Izmir, Turkey; NHML, Natural History Museum, London, UK; NHMUK, Natural History Museum, London, UK; NHMW, Naturhistorisches Museum, Vienna, Austria; NLB, Niedersächsisches Landesamt für Bodenforschung, Hannover, Germany; NMNH, National Museum of Natural History, Sofia, Bulgaria; PGMA, Palaeontology and Geology Museum, University of Athens, Athens, Greece; PMU, Museum of Evolution in Uppsala University, Uppsala, Sweden.

2 Geographic and stratigraphic distribution of Late Miocene ‘ovibovin’ bovids in Eurasia

The Late Miocene ‘ovibovin’ bovids include *Criotherium*, *Hezhengia*, *Lantiantragus*, *Mesembriacerus*, *Parurmiatherium*, *Plesiaddax*, *Shaanxispira*, *Sinotragus*, *Prosinotragus*, *Tsaidamotherium*, and *Urmiatherium*. They are concentrated in eastern Europe and northern China (Fig. 1). *Plesiaddax*, *Sinotragus*, and *Urmiatherium* are widely distributed in both northern China and eastern Europe (Shi and Deng, 2021). In contrast, *Criotherium* and *Mesembriacerus* are restricted to eastern Europe. *Criotherium* is distributed to the Late Miocene of Greece, Bulgaria, and Turkey (Forsyth-Major, 1891; Solounias, 1981; Bouvrain, 1994; Geraads and Spassov, 2008; Kostopoulos et al., 2023), while *Mesembriacerus* is only found in Greece (Bouvrain and Bonis, 1984; Spassov et al., 2018). *Parurmiatherium* has been discovered in Greece, Iraq, and southwestern Turkey (Sickenberg, 1932, 1933; Bouvrain et al., 1995; Kostopoulos and Karakütük, 2013). Nine genera occur in northern China; five of them are endemic, including *Hezhengia*, *Lantiantragus*, *Shaanxispira*, *Prosinotragus*, and *Tsaidamotherium*. *Hezhengia* is primarily discovered in the poorly defined "Liushu Formation" (see Qiu et al., 2023) in the Linxia Basin located at the northeastern edge of the Tibetan Plateau (Qiu et al., 2000; Deng et al., 2013; Shi and Deng, 2021). *Lantiantragus* is limited to the Bahe Formation in the Lantian Basin, Shaanxi Province (Chen and Zhang, 2004, 2009). *Shaanxispira* is found in the Bahe and Liushu formations in northwestern China (Liu et al., 1978; Zhang, 2003; Shi et al., 2014). *Tsaidamotherium* was discovered in the Shangyoushashan Formation in the Qaidam Basin, Qinghai, and the Liushu Formation in the Linxia Basin, Gansu, northwestern China (Bohlin, 1935b; Shi, 2014; Wang and Ye, 2023). *Prosinotragus* is only discovered in Qingyang, Gansu Province (Bohlin, 1935a).

Fig. 1 Map showing the geographic distribution of fossil 'ovibovin' bovids in Eurasia

Red dots represent the localities of the Late Miocene 'ovibovin' bovids. Localities 1–8 are in China, 9 in Iran, 10 in Iraq, 11–14 in Turkey, 15–17 in Greece, 18 in Bulgaria. *Plesiaddax* (1 Siziwangqi, 2 Hequ, 4 Baode; 12 Kayadibi, 13 Garkin), *Hezhengia* (3 Fugu, 7 Linxia), *Urmiatherium* (4 Baode, 6 Qingyang, 9 Maragheh, 14 Muğla [Salihpaşalar and Şerefköy-2], 15 Samos, 16 Fourka), *Parurmiatherium* (10 Injana, 14 Muğla, 15 Samos), *Sinotragus* (4 Baode, 14 Muğla), *Prosinotragus* (6 Qingyang), *Shaanxispira* (5 Lantian; 7 Linxia), *Lantiantragus* (5 Lantian), *Tsaidamotherium* (7 Linxia, 8 Qaidam), *Criotherium* (11 Çorakyerler, 15 Samos, 18 Kalimantsi), and *Mesembriacerus* (17 Ravin de la Pluie, N Macedonia).

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The majority of the ‘ovibovin’ bovids in Eurasia from the Late Miocene are from the early Late Miocene, except for *Urmiatherium intermedium*, *U. rugosifrons*, *Sinotragus wimani*, and *Prosinotragus tenuicornis*, which appear in the late Late Miocene (Fig. 2). *Tsaidamotherium* is the earliest member among all the Late Miocene ‘ovibovin’ bovids abovementioned, appearing at the boundary between the Middle and the Late Miocene. This genus is endemic to northwestern China and comprises two species, the number of specimens of which is limited. *T. hedini* was primarily discovered in the Shangyoushashan Formation in the Quanshuiliang area of the eastern Qaidam Basin (Wang et al., 2011), while *T. brevirostrum* was found in the “Liushu Formation” in the Linxia Basin (Shi, 2014). Both species of *Tsaidamotherium* belong to the Bahean Age of the Chinese Land Mammal Age. *Lantiantragus* is a monotypic genus that includes only the type species *L. longirostralis*, which was discovered in loc. 12 of the lower part of the Bahe Formation in the Lantian Basin, Shaanxi. This species is in the Bahean Age, with a magnetic dating of approximately 9.95 Ma (Chen and Zhang, 2004; Zhang et al., 2013). *Hezhengia* consists of two species, *H. bohlini* and *H. minor*. The holotype of *H. bohlini* was discovered in the greyish-yellow silts in the Linxia Basin. Qiu et al. (2000) considered that the fossils from this layer can be correlated with the *Hipparion* faunas in the Hezheng and Baode area, which are believed to date to the late Late Miocene. *H. minor* was originally referred to the genus *Plesiaddax* by Bohlin (1935a) with some reservation and then was transferred to the genus *Hezhengia* by Shi and Deng (2021). This species was discovered in Fugu, Shanxi, and its age is approximately 8.0 Ma, according to palaeomagnetic data (Bohlin, 1935a; Xue et al., 1995). *Urmiatherium* has a wide distribution throughout Eurasia with three known species. The type species, *U. polaki*, was discovered in the Maragheh Formation of Karaj Abad, Maragheh, Iran, with an estimated age of ~8.7–7.5 Ma (Rodler, 1889; de Mecquenem, 1925; Kostopoulos and Bernor, 2011). *U. intermedium* was discovered in the red clays of Baode, Shanxi, and Qingyang, Gansu, as well as in the “Liushu Formation” in the Linxia Basin, Gansu, northwestern China. Its age is within the Baodean Age (late Late Miocene). *U. kassandriensis* is a recently established species based on the material from the Antonios Formation in Fourka, Chalkidili, Greece, and its age is about 9.0–8.0 Ma (Lazaridis et al., 2017). *Parurmiatherium* is a monotypic genus that includes only the type species *P. rugosifrons*. The species was discovered in the Mytilinii Formation of Samos, eastern Greece, the Bakhtiari Formation of Injana, Iraq, and the Salihpaşalar and Şerefköy-2 localities in the Yatağan Formation of southwestern Turkey (Sickenberg, 1932, 1933, Bouvrain et al., 1995, Kostopoulos and Karakütük, 2013). *Plesiaddax* is distributed from northern China to Turkey, with three species. Its type species is *P. depereti*, which was discovered from the Baode Formation in Shanxi, China. The latter two species, *P. inundates* and *P. simplex*, have recently been described as *Hezhengia* with some

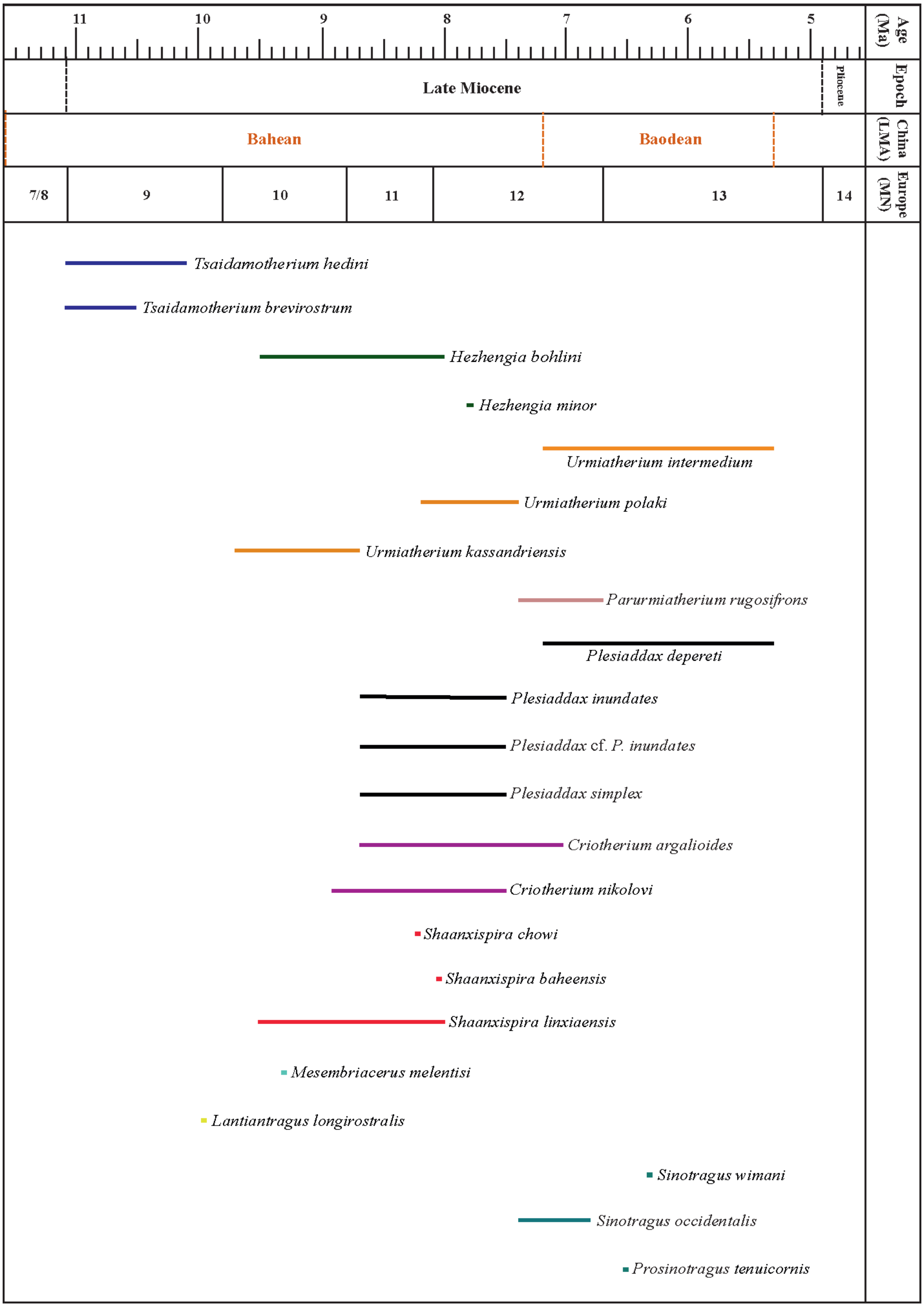

Fig. 2 Biochronological distribution of the Late Miocene 'ovibovin' bovids in Eurasia

reservation (Kostopoulos et al., 2023). *Criotherium* has two species. The type species *C. argalioides* is known from the Mytilinii Formation in Samos, Greece, the Sinap Formation of Kemiklitepe-D, and the Tüğlu Formation of Çorakyerler in Turkey (Forsyth-Major, 1891; Solounias, 1981; Bouvrain, 1994; Geraads and Spassov, 2008; Kostopoulos et al., 2023). *C. nikolovi* was discovered in the Kalimantsi Formation in Kalimantsi-1, Bulgaria. *Shaanxispira* is endemic to northern China, where it is represented by three species. The first two species, *S. chowi* and *S. baheensis*, were discovered from the Bahe Formation in the Lantian Basin, while *S. linxiaensis* was discovered from the "Liushu Formation" in the Linxia Basin (Liu et al., 1978; Zhang, 2003; Shi et al. 2014). *Mesembriacerus melentisi* is the sole representative of its genus found in the Antonios Formation of the Axios Valley in Greece, with an age of approximately 9.3 Ma (Bouvrain and Bonis, 1984; Spassov et al., 2018). *Lantiantragus* is based on an anterior part of the skull from the Bahe Formation in the Lantian Basin, Shaanxi, which comprises only the type species *L. orientalis.* The species is restricted to the Bahe Formation of the Lantian Basin (Chen and Zhang, 2004, 2009). *Sinotragus* was established based on cranial materials with two species. The type species, *S. wimani*, was discovered in the Baode Formation of Baode County, Shanxi, China. The second species *S. occidentalis* was found from an unidentified locality within the Yatağan Formation in Turkey (Geraads et al., 2002). *Prosinotragus* was erected with its type species *P. tenuicornis* in the Liushu Formation of Qingyang area, Gansu with an age of approximately 6.5 Ma (Bohlin, 1935a). *Sinotragus* is considered as synonymous with *Prosinotragus* in few studies (Chen and Zhang, 2009).

3 Systematic paleontology

Artiodactyla Owen, 1848

Bovidae Gray, 1821

***Urmiatherium* Rodler, 1889**

Type species *Urmiatherium polaki* Rodler, 1889.

Distribution China, Iran, Greece.

Included species *Urmiatherium intermedium* Bohlin, 1935a; *U. kassandriensis* Lazaridis et al., 2017.

Ages *Urmiatherium polaki*, ~8.2–7.4 Ma; *U. intermedium*, ~7.2–5.3 Ma; *U. kassandriensis*, 9.7–8.7 Ma (MN 10); see Table 2.

Remarks *Urmiatherium* was named by Rodler (1889) based on the material from Maragheh, Iran, and currently includes three species: *U. polaki*, *U. intermedium*, and *U. kassandriensis*. *Urmiatherium* is a Late Miocene bovid characterized by closely inserted and caudally oriented horn cores (Fig. 3A), a perpendicular cranial roof, a thickened basicranium, and hypsodont cheek teeth (Rodler, 1889; de Mecquenem, 1925; Bohlin, 1935a, Sickenberg, 1932, 1933; Kostopoulos, 2009; Kostopoulos and Bernor, 2011; Jafarzadeh et al., 2012; Kaya et al., 2012; Kostopoulos and Karakütük, 2013; Shi et al., 2016; Lazaridis et al., 2017). Among the Late Miocene 'ovibovin' bovids, *Urmiatherium* has the highest tooth crown. The earliest *Urmiatherium* is *U. kassandriensis*, whose horn cores are short and separated (Fig. 3E). The horn core of *Urmiatherium* became more specialized in the two later lineages in both northern China and western Asia, with the horn bases merging together and extending on the frontal and parietal crania (Fig. 3A, C).

At the tribal level, the assignment of *Urmiatherium* remains a topic of debate. Apart from its conventional classification as the Ovibovinae/Ovibovini (Bohlin, 1935a; Solounias, 1981), Kostopoulos (2009, 2014) referred to it as the Antilopini tribe and the Oiocerina subtribe.

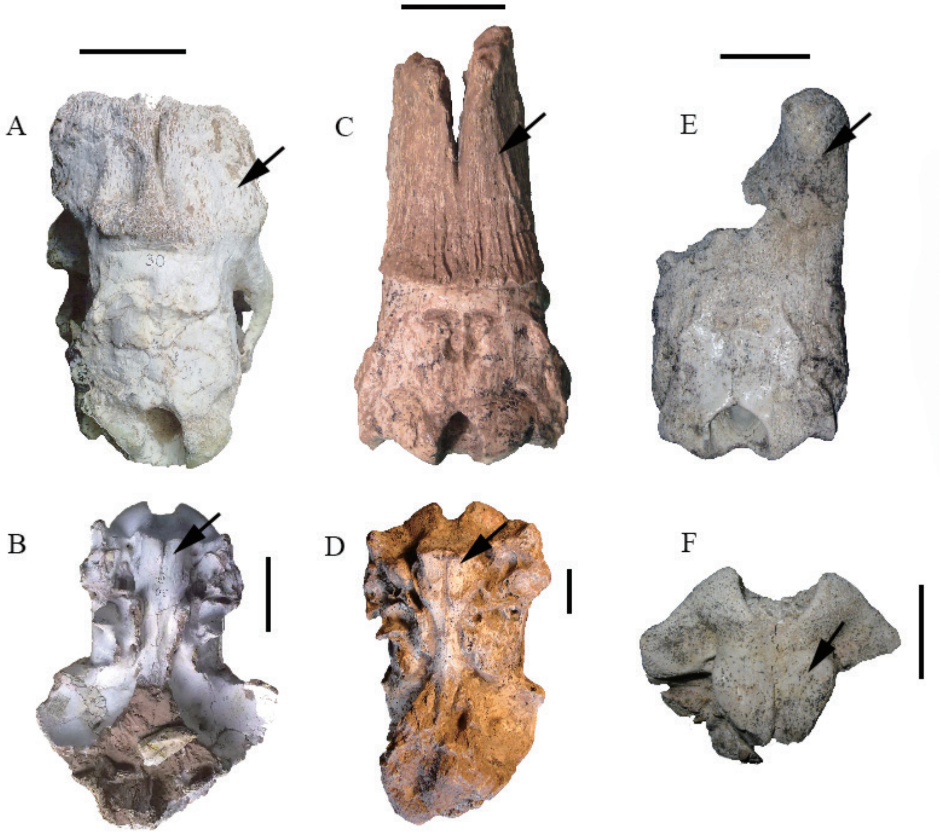

Fig. 3 Selected crania of *Urmiatherium*

A, B. skulls of *Urmiatherium intermedium*, PMU M823 (A), PMU M3620 (B), from Baode, China; C, D. skull of *U. polaki*, MNHN MAR 3215, from Maragheh, Iran; E, F. partial craniums of *U. kassandriensis*, LGPUT FRK19 (E) and LGPUT AMPG-103 (F) from Fourka locality, Greece

The arrows show the specific peculiarity of horn core and basioccipital in each species

A, C, E. posterior views; B, D, F. ventral views

Scale bars = 5 cm. C–F, courtesy of D S Kostopoulos

However, some other researchers followed Sickenberg's (1932) original assignment and referred it to the Urmiatheriini tribe (Chen and Zhang, 2009; Shi et al., 2016; Shi and Deng, 2021).

Criotherium Forsyth-Major, 1891

Type species *Criotherium argalioides* Forsyth-Major, 1891.

Included species *Criotherium nikolovi* Geraads & Spassov, 2008.

Distribution Greece, Bulgaria, and Turkey.

Ages *Criotherium argalioides*, ~8.7–7.5 Ma; *C. nikolovi*, ~8.9–7.5 Ma; see Table 2.

Remarks *Criotherium* is the only 'ovibovin' bovid with heteronymously twisted horn cores. As such, *Criotherium* is unlikely to be closely related to the other genera of 'ovibovin' bovids, assuming the direction of twists evolved separately. Its cranium morphologies, such as a short and broad braincase, low and broad occipital, strong posterior tuberosities, and supplementary articulations medial to the paroccipital processes, are similar to other 'ovibovin' bovids. *Criotherium* is common in Samos (Greece), but it is quite rare in Kemiklitepe-D (Western Turkey), Kalimantsi-1 (Bulgaria), and Çorakyerler (Turkey) (Solounias, 1981; Bouvrain, 1994; Geraads and Spassov, 2008; Kostopoulos et al., 2023). *C. nikolovi* differs from the type species, *C. argalioides*, in its smaller size, less upright horn cores (Fig. 4D, H), and less lengthened and broader muzzle (Fig. 4A, E), which are probably primitive (Geraads

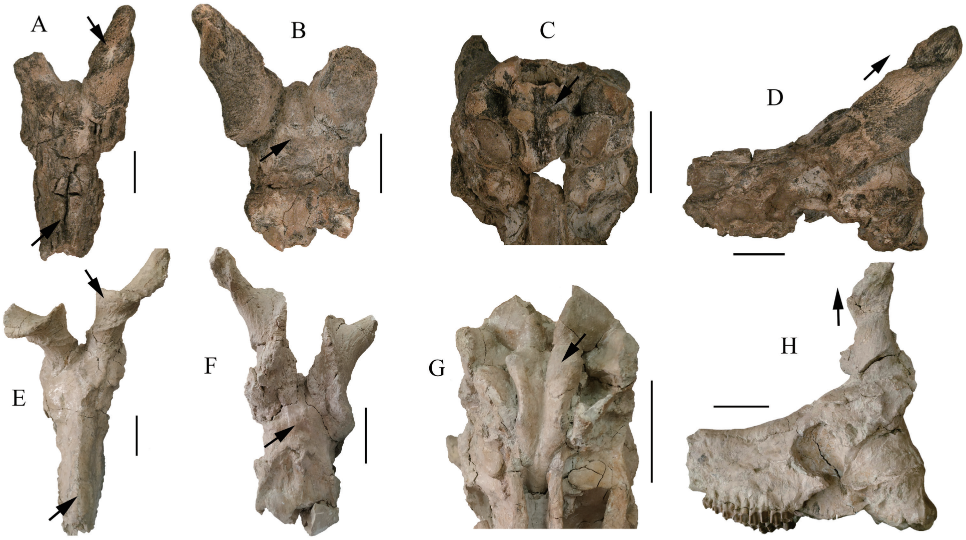

Fig. 4 Selected crania of *Criotherium*

A–D. *Criotherium nikolovi*, NMNH FM-1740 (holotype) from Kalimantsi-1, Bulgaria;
E–H. *C. argalioides*, ÇO 1045 from Çorakyerler, Turkey. The arrows show the specific peculiarity of parietal, nasal, basioccipital and horn core twist and direction in each species
A, E. dorsal views; B, F. posterior views; C, G. ventral views; D, H. left lateral views
Scale bars = 5 cm. A–D, courtesy of D Geraads; E–H, courtesy of D S Kostopoulos

and Spassov, 2008). According to Gentry (1971), *Criotherium* was a large antilopine closely related to *Palaeoreas*, evolving in parallel with *Urmiatherium* and sharing many similar traits. Morphologically, *Criotherium* is the most similar to Garkin's ?*Plesiaddax inundates*, although it cannot be included in *Plesiaddax* due to the weak homonymous torsion of ?*P. inundates* (Bosscha-Erdbrink, 1978; Geraads and Spassov, 2008; Kostopoulos et al., 2023).

Plesiaddax **Schlosser, 1903**

(Fig. 5)

Type species *Plesiaddax depereti* Schlosser, 1903.

Included species *Plesiaddax inundates* Bosscha-Erdbrink, 1978; *P. simplex* Köhler, 1987.

Distribution Western Turkey, northern China.

Ages *Plesiaddax depereti*, ~7.2–5.3 Ma; *P. inundates*, ~8.7–7.5 Ma (MN 11) and *P. simplex*, ~8.7–7.5 Ma (MN 11); see Table 2.

Remarks *Plesiaddax* was established by Schlosser (1903) based on the material

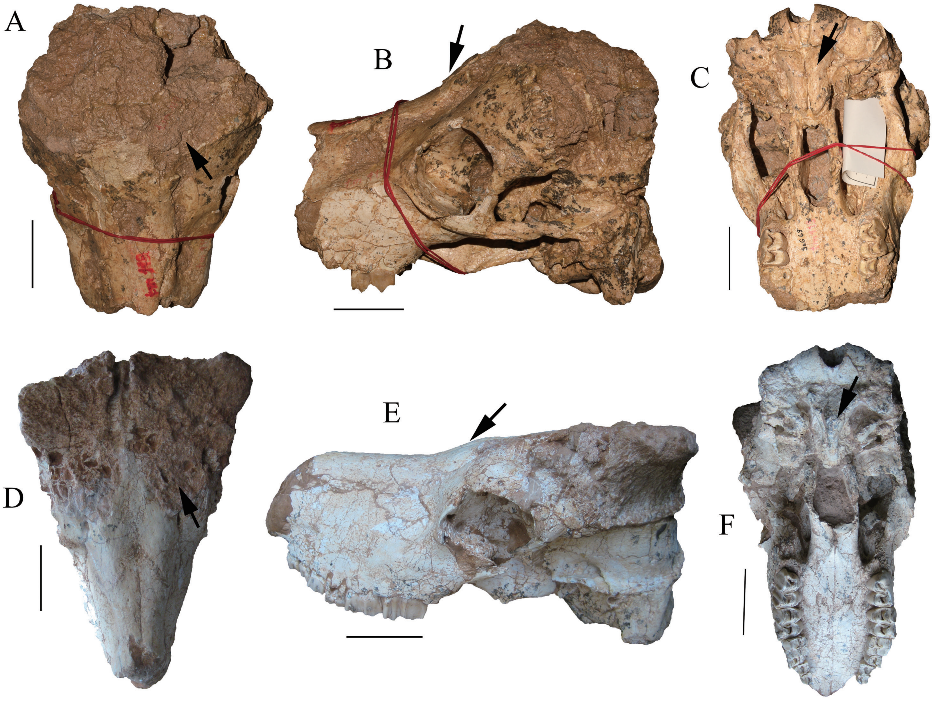

Fig. 5 Selected crania of *Plesiaddax*
A, B, C. *Plesiaddax inundates*, NLB SaG 69 from Garkin, Turkey;
D, E, F. *P. depereti*, PMU M1258 from Hequ, China
The arrows show the specific peculiarity of frontal, frontal sinuses and basioccipital in each species
A, D. dorsal views; B, E. lateral views; C, F. ventral views
Scale bars = 5 cm. A–C, courtesy of D S Kostopoulos

from Hequ, Shanxi, China. It is an 'ovibovin' bovid with extremely short and laterally extended horn cores, similar to *Hezhengia* but much shorter. Solounias (1981) suggested that *Plesiaddax* is synonymous with *Parurmiatherium*, but Shi et al. (2016) treated them as two independent genera. *Plesiaddax* shares similarities with *Hezhengia* in terms of skull and horn core morphology. They may have a closer relationship than other Late Miocene 'ovibovin' bovids, such as *Urmiatherium*, *Tsaidamotherium*, and *Criotherium*, as pointed out by Qiu et al. (2000). Shi and Deng (2021) also suggested a close relationship among *Plesiaddax*, *Hezhengia*, and *Urmiatherium*. The type species of *Plesiaddax* is *P. depereti*, which is characterized by several beautifully preserved skulls and mandibles. The two included species, namely *P. simplex* and *P. inundates*, have inadequate material. In contrast to *P. depereti*, the horn bases in *P. simplex* are not enlarged anteriorly by buttresses. Additionally, *P. inundates* is more similar to *Criotherium* or *Hezhengia* than *P. depereti* (Bouvrain et al., 1995; Geraads and Spassov, 2008; Kostopoulos et al., 2023). Kostopoulos et al. (2023) have questioned the generic attribution of these two species and suggested that they should be transferred to the genus *Hezhengia*. (Fig. 5)

***Parurmiatherium* Sickenberg, 1932**

(Fig. 6)

Type species *Parurmiatherium rugosifrons* Sickenberg, 1932.

Distribution Greece, southwestern Turkey, and Iraq.

Age ~7.4–6.7 Ma; see Table 2.

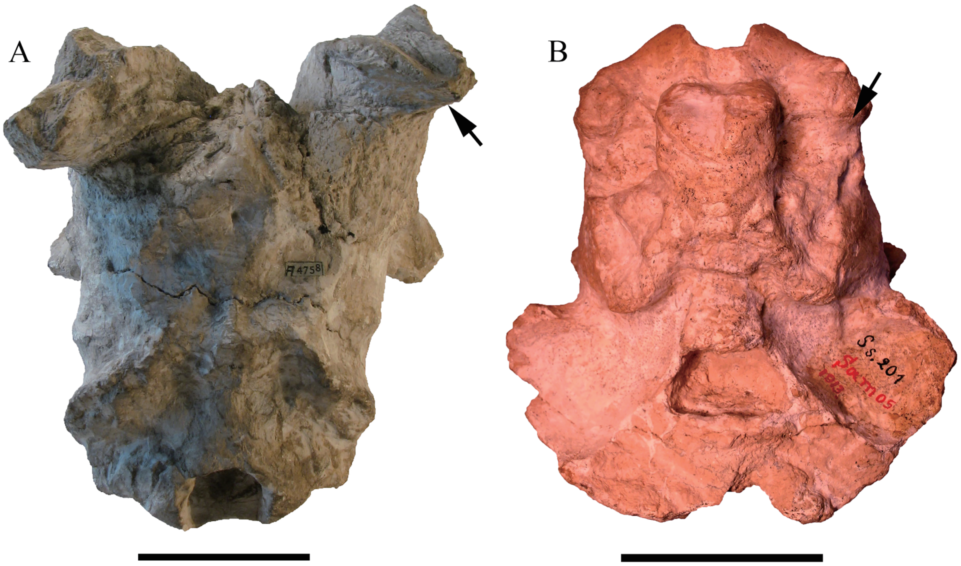

Fig. 6 Cranium of *Parurmiatherium rugosifrons*, NHMW A4758 (lectotype), from Samos, Greece
The arrows show the characteristics of basioccipital and horn core direction
A. posterior view; B. ventral view. Scale bars = 5 cm. A and B, courtesy of D S Kostopoulos

Remarks *Parurmiatherium* was named by Sickenberg (1932) based on material from Samos, E Greece. It includes only the species *P. rugosifrons*. This genus is characterized by its diminutive size and the presence of a horn core that is very short, robust, medially unfused, strongly homonymously twisted, and grooved. It is also distinguished by the presence of low buttresses that extend anteriorly from the frontals (Sickenberg, 1932; Gentry et al., 1999; Kostopoulos, 2009; 2014). Gentry et al. (1999) considered this genus a synonym of *Urmiatherium*. This classification was followed by Kostopoulos (2009, 2014) and Kostopoulos et al. (2023). Solounias (1981) synonymized *Plesiaddax* with *Parurmiatherium*, whereas Shi et al. (2016) treated *Parurmiatherium* as an independent genus. These debates reflect that *Parurmiatherium* exhibits mixed characteristics of both *Urmiatherium* and *Plesiaddax*. For instance, the backwards extending horn cores and the extremely strong posterior tuberosity are similar to *Urmiatherium*. In contrast, the wide opisthocranium and the separate horn bases are similar to *Plesiaddax* (Fig. 6A, B).

Sinotragus Bohlin, 1935a

(Fig. 7)

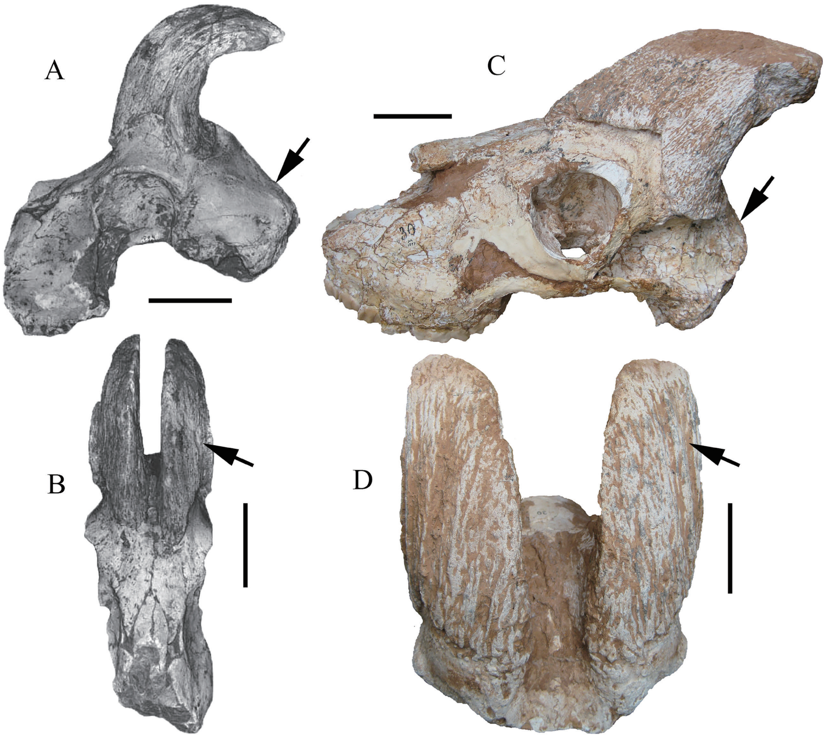

Fig. 7 Selected crania of *Sinotragus*
A, B. *Sinotragus occidentalis*, MTA 1894 (holotype, Geraads et al., 2002: fig 2), from Yatağan Formation, Muğla, SW Turkey; C, D. *S. wimani*, PMU M1297 (C) and PMU M3930 (D), from Baode, China
The arrows show the parietal and horn core characters in each species
A, C. lateral views; B, D. latero-dorsal views. Scale bars = 5 cm. A and B, courtesy of D Geraads

Type species *Sinotragus wimani* Bohlin, 1935a.

Included species *S. occidentalis* Geraads et al., 2002.

Distribution China and Turkey.

Ages *Sinotragus wimani*, ~5.7 Ma; *S. occidentalis* 7.4–6.8 Ma (MN 12); see Table 2.

Remarks *Sinotragus* and its type species *S. wimani* were named by Bohlin (1935a) based on cranial materials from Baode, Shanxi. The genus is characterized by prominent horn cores and a relatively short skull. The horn cores are long, slightly homonymously twisted, and closely inserted with each other. Geraads et al. (2002) erected a new species of *Sinotragus*, *S. occidentalis*, based on the material from the Late Miocene of Muğla, Turkey. However, Chen and Zhang (2009) noted that *S. occidentalis* differs from *Sinotragus* in China in several cranial features, such as the position of the cranial curve not being located at the frontal bone anterior to the base of the horn core, the long length of the braincase (Fig. 7A, C), and the untwisted horn cores. They suggested that *S. occidentalis* may not belong to *Sinotragus*. For a long time, *Sinotragus* has been considered a representative of *Protoryx* in the East Asia. This group was first included in the subfamily Hippotraginae but was later referred to as the tribe Caprini (Bohlin, 1935a; Gentry, 1971, 2000). However, previous works have often classified *Sinotragus* in the tribe Urmiatheriini due to its homonymously twisted horn cores, short braincase, wide and flat occiput, and strongly developed basioccipital tuberosities (Zhang, 2003; Chen and Zhang, 2009).

***Prosinotragus* Bohlin, 1935a**

(Fig. 8)

Type species *Prosinotragus tenuicornis* Bohlin, 1935a.

Distribution China.

Age *P. Tenuicornis*, ~6.5 Ma; see Table 2.

Fig. 8 Skull of *Prosinotragus tenuicornis*, PMU M3942 from Qingyang, China
The arrows show the parietal and horn core characters. A. lateral view; B. latero-dorsal view
Scale bars = 5 cm

Remarks *Prosinotragus* was also named by Bohlin (1935a) based on cranial materials from Qingyang, Gansu. The genus is characterized by its slender, distinctive anterior keels and weakly twisted horn cores. *P. tenuicornis* was originally the type species of the *Prosinotragus*, but its cranial morphology is identical to that of *Sinotragus wimani*. Chen and Zhang (2009) proposed that *Prosinotragus* is synonymous with *Sinotragus* because of its cranial morphology. However, *P. tenuicornis* can be distinguished from *S. wimani* by its slender, distinctive anterior keels and weakly twisted horn cores (Fig. 8A, B). Further research will elucidate and unveil the characteristics of this genus and species.

Tsaidamotherium **Bohlin, 1935b**

(Fig. 9)

Type species *Tsaidamotherium hedini* Bohlin, 1935b.

Included species *Tsaidamotherium brevirostrum* Shi, 2014.

Distribution Northwestern China.

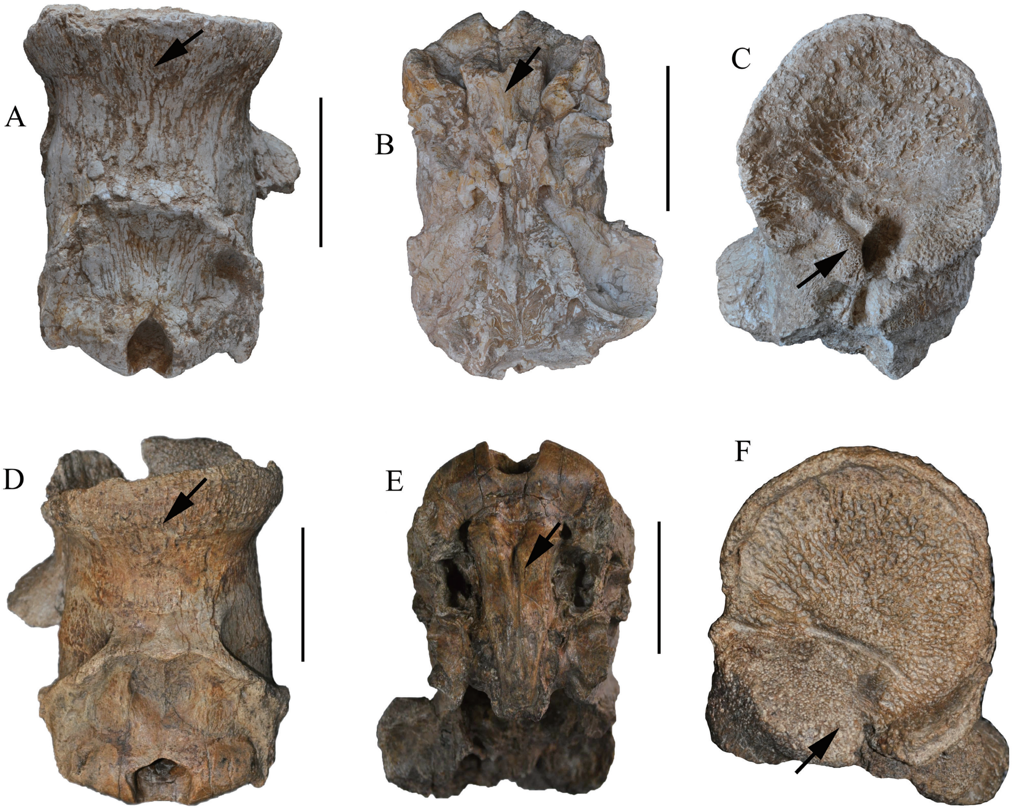

Fig. 9 Selected crania of *Tsaidamotherium*
A, B, C. *Tsaidamotherium brevirostrum*, IVPP V17925 (holotype), from Linxia Basin, China;
D, E, F. *T. hedini*, IVPP RV35052, from Qaidam Basin, China
The arrows show the specific peculiarity of horn core and basioccipital in each species
A, D. posterior views; B, E. ventral views; C, F. dorsal views. Scale bars = 5 cm

Ages *Tsaidamotherium hedini*, ~11.1–10.1 Ma (Tuosu Fauna); *T. brevirostrum*, ~11.1–10.5 Ma (Guonigou Fauna; equivalent to MN 9); see Table 2.

Remarks Bohlin (1935b) named *Tsaidamotherium* and its type species *T. hedini* based on three incomplete skulls from the south limb of the Oulongbuluk Anticline in the Quanshuiliang, eastern Qaidam Basin (See Wang et al., 2011: locality 447 and 457). Despite the lack of evidence for the anterior skull parts (Bohlin, 1935a, b), *T. hedini* was placed in the subfamily Ovibovinae by Bohlin (1935b) due to its cranial resemblance to *Plesiaddax*, *Ovibos*, and *Urmiatherium*. The second species of the genus *T. brevirostrum* was established by Shi (2014) based on an almost complete skull (HMV 1865) from the Linxia Basin in Gansu. This genus is an endemic bovid found only in northwestern China and is characterized by its unique plate-like and asymmetric horn core apparatus (Fig. 9C). *T. hedini* and *T. brevirostrum* are similar in size and have similar posterior horn core plate morphology (Fig. 9A, D). However, the proportion of the real horn cores relative to the skull is smaller in *T. brevirostrum* than in *T. hedini* (Fig. 9C, F). Wang and Ye (2023) reported the upper and lower dentitions of *T. hedini* from the Tuosu Lake area in the eastern Qaidam Basin. These dentitions are comparable to those of *T. brevirostrum*, exhibiting an elongated M3, a flat labial wall, and a well-developed mesostyle in the upper molars.

The phylogenetic position of *Tsaidamotherium* is a topic of debate. According to conventional views, this genus was classified as either Ovibovinae/Ovibovini (Bohlin, 1935b; Shi, 2014) or Urmiatheriini (Köhler, 1987). Chen and Zhang (2009) placed this genus in the tribe Urmiatheriini under the subfamily Urmiatherinae, along with other Late Miocene “ovibovines”. Shi and Deng (2021) considered it a distantly related bovid to urmiatherins. The argument presented by Wang et al. (2003a, b) and Wang and Ye (2023) is that *Tsaidamotherium* belongs to the stem taxon Discokerycinae and is a giraffoid rather than a bovid, due to differences in the median parietal headgear and bony labyrinth. However, Hou et al. (2023) commented that *Tsaidamotherium* has mesodont teeth, a short premolar row, fully fused cones in molars, and flat labial walls on the upper molars, which suggests that it belongs to the Bovidae rather than the Giraffidae.

Mesembriacerus Bouvrain, 1975

Type species *Mesembriacerus melentisi* Bouvrain, 1975.

Distribution Northern Macedonia, Greece.

Age ~9.3 Ma; see Table 2.

Remarks Bouvrain (1975) named *Mesembriacerus* based on material from Macedonia, Greece. This genus comprises only its type species, *M. melentisi*, which is characterized by long, straight, and strongly inclined horn cores. The horn cores of *Mesembriacerus* are inserted far behind the orbit and an accessory articular surface between the paroccipital process and the occipital condyle. These characteristics are similar to those of *Ovibos*, which classifies

Mesembriacerus as a member of Ovibovini according to conventional views (Bouvrain and Bonis, 1984). Additionally, the relatively small body size, slender horn cores, and primitive braincase suggest a primitive evolutionary stage for 'ovibovin' bovids. *Mesembriacerus* is considered the most primitive member of the lineage that gave rise to *Plesiaddax*, *Tsaidamotherium*, and *Urmiatherium* (Bouvrain and Bonis, 1984). It possibly originated in Asia and arrived in the southern Balkans during the late Vallesian period (Lazaridis et al., 2017). However, its small parieto-occipital angle and postero-ventrally faced occiput (Fig. 10C) are distinct from all other Late Miocene 'ovibovin' bovids, implying a different evolutionary lineage.

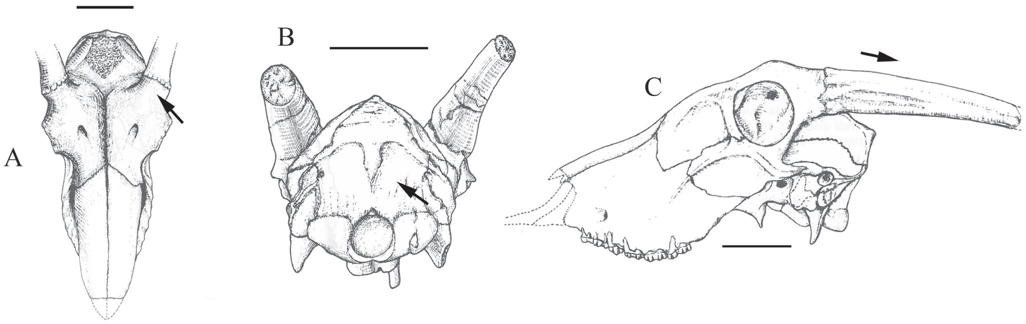

Fig. 10 Cranium with horn cores of *Mesembriacerus melentisi*, LGPUT RP l43 (holotype) from Ravin de la Pluie, Macédoine, Greece

Modified from Bouvrain and Bonis, 1984. The arrows show the frontal, occipital and horn core direction

A. dorsal view; B. posterior view; C. lateral view. Scale bars = 5 cm

Shaanxispira Liu et al., 1978

Type species *Shaanxispira chowi* Liu et al., 1978.

Included species *Shaanxispira baheensis* Zhang, 2003; *S. linxiaensis* Shi et al., 2014.

Distribution Northern China.

Ages *Shaanxispira chowi*, 8.21 Ma; *S. baheensis*, 8.07 Ma; *S. linxiaensis*, ~9.5–8 Ma; see Table 2.

Remarks *Shaanxispira* is an endemic genus found only in northern China. It is characterized by long, straight, and strongly homonymously twisted horn cores. Although the horn core of *Shaanxispira* is not similar to that of *Ovibos*, its cranium is short and strong, making this genus also a phylogenetically close relative of urmiatherins (Chen and Zhang, 2009). All three known species of *Shaanxispira* are contemporaneous and of similar size. The most notable difference between them lies in the morphology of their horn cores (Shi et al., 2014). The type species, *S. chowi*, has an extra postero-lateral keel on the horn core (Fig. 11E, F), distinguishing it from the other two species. *S. baheensis* (Fig. 11C, D), on the other hand, has more inclined horn cores and weaker keels than *S. linxiaensis* (Fig. 11A, B) (Zhang, 2003; Shi et al., 2014).

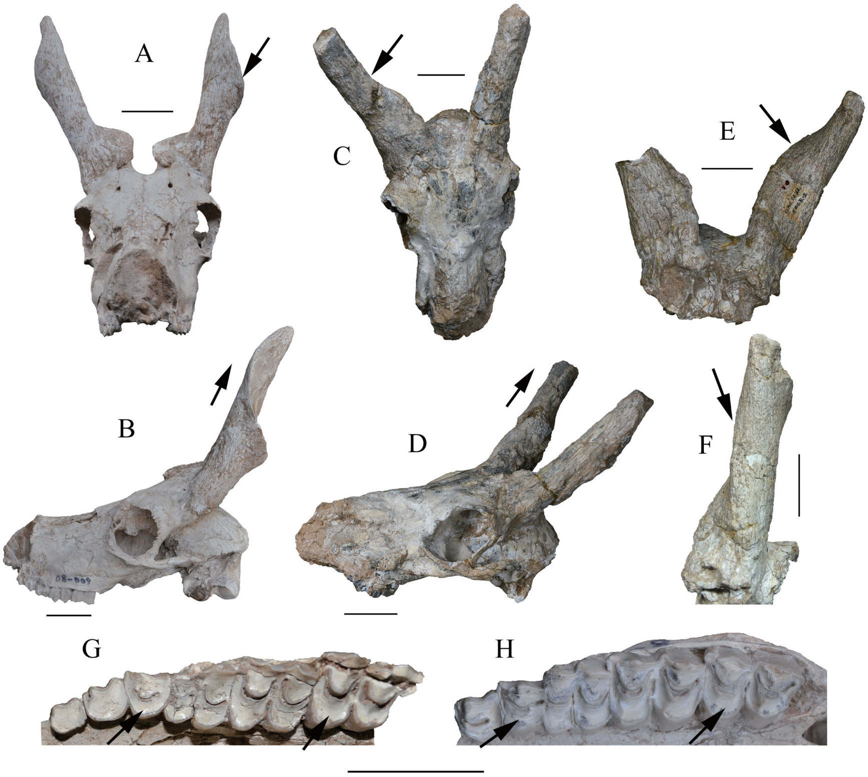

Fig. 11 Selected crania with horn cores of *Shaanxispira* and upper dentition of *Lantiantragus longirostralis* and *Shaanxispira linxiaensis*
A, B, H. skull (A, B) and upper dentition (H) of *Shaanxispira linxiaensis*, HMV 1922 (holotype), from Linxia Basin, China; C, D. skull of *S. baheensis*, IVPP V13626 (holotype), from Lantian County, Shaanxi Province, China; E, F. horn cores of *S. chowi*, IVPP V3124 (holotype) from Lantian County, China; G. upper dentition of *Lantiantragus longirostralis*, IVPP V13908 (holotype), from Lantian County, China
The arrows show the peculiarity of the horn core twist and direction in each species, as well as the teeth similarities between *Shaanxispira* and *Lantiantragus*
A. anterodorsal view; C, E. dorsal views; B, D, F. lateral views. G, H. occlusal views. Scale bars = 5 cm

Hezhengia **Qiu et al., 2000**

Type species *Hezhengia bohlini* Qiu et al., 2000.

Included species *Hezhengia minor* (Bohlin, 1935a).

Distribution Northwestern China.

Ages *Hezhengia bohlini*, ~9.5–8 Ma (Dashengou Fauna); *H. minor*, ~7.8 Ma (Lamagou Fauna); see Table 2.

Remarks *Hezhengia* is a medium-sized 'ovibovin' bovid that is endemic to northern China. It is characterized by short and robust horn cores that insert well behind the orbit and extend mainly laterally (Fig. 12A) (Qiu et al., 2000; Shi and Deng, 2021). Qiu et al. (2000)

established the genus *Hezhengia* and its type species, *H. bohlini*, based on hundreds of well-preserved skulls from the Linxia Basin. Shi and Deng (2021) acknowledged that the two upper jaws from Fugu County, Shaanxi, originally identified as *Plesiaddax minor*, share similar tooth morphology, particularly that of the P3, with *H. bohlini.* They reclassified *P. minor* as *H. minor. H. minor* coexisted with *Miotragocerus gregarius*, *Gazella gaudryi*, *Dorcadoryx* sp., and *Urmiatherium* sp., forming the Lamagou Fauna with an estimated age of ~7.8 Ma (Xue et al., 2006). *H. bohlini* is part of the Dashengou Fauna, estimated from an earlier age of ~9.5–9.0 Ma (Deng et al., 2019). However, Shi (2023) correlated the Dashengou Fauna with the Lamagou Fauna due to the high similarity of the bovid taxa, suggesting that these two faunas may be contemporaneous.

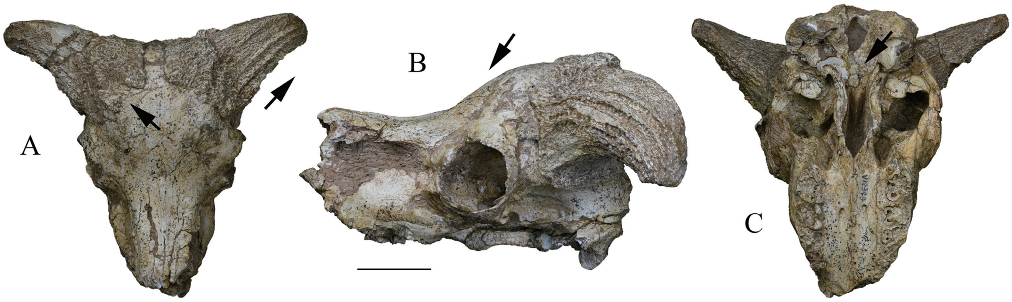

Fig. 12 Skull of *Hezhengia bohlini*, IVPP V12349, from Linxia Basin, China
The arrows show the characters of basioccipital, frontal and horn core direction
A. dorsal view; B. lateral view; C. ventral view. Scale bar = 5 cm

Lantiantragus Chen & Zhang, 2004

Type species *Lantiantragus longirostralis* Chen & Zhang, 2004.

Distribution Northern China.

Age 9.95 Ma, the Bahean Age; see Table 2.

Remarks *Lantiantragus* was named by Chen and Zhang (2004) based on a skull from the Bahe Formation in the Lantian Basin, Shaanxi. It includes only its type species, *L. longirostralis*. *Lantiantragus* is the only genus established on the material without horn cores among all the ‘ovibovin’ bovids from northern China. This large bovid genus has an extremely long muzzle (Chen and Zhang, 2004). Chen and Zhang (2009) classified *Lantiantragus* in the tribe Urmiatheriini and suggested a close relationship among *Lantiantragus*, *Urmiatherium*, and *Plesiaddax*. Our observation indicates that the dentition of *Lantiantragus* is similar to that of *Shaanxispira*, suggesting a close relationship between these two genera. However, *Lantiantragus* differs from *Ovibos*, which has an extremely short and high muzzle.

Table 2 List of fossil ‘ovibovin’ bovids in the Late Miocene with age and localities described (modified from Shi, 2012)

Species	Material	Locality	Country	Housed	Age (Ma)	Reference
Urmiatherium polaki	A snout and partial cranium along with horn cores	Karaj Abad site, Maragheh	Iran	DOE MNHN NHML	~8.2–7.4	Rodler, 1889; de Mecquenem, 1925; Kostopoulos and Bernor, 2011
U. intermedium	Plenty of skulls, teeth, and bone fragments	Baode (Locs. 30, 43, 44, 49 and 108) and Qingyang (Locs. 115, 116)	China	IVPP	7.2–5.3	Schlosser, 1903; Bohlin, 1925, 1935a, Shi et al., 2016
U. kassandriensis	A partial cranium and an opisthocranium with horn cores	Fourka locality, Chalkidiki	Greece	LGPUT PGMA	9.7–8.7	Lazaridis et al., 2017
Parurmiatherium rugosifrons	A partial opisthocranium, frontlets, axis, and cervical vertebra	Samos [unknown levels], Injana, Salihpaşalar and Şerefköy-2	E Greece, Iraq and SW Turkey	MYŞE NHMW BSPM	~7.4–6.7	Sickenberg, 1932, 1933; Bouvrain et al., 1995; Kostopoulos and Karakütük, 2013
Tsaidamotherium hedini	Two broken posterior parts of the skull and two cervical vertebrae	Qaidam Basin	China	IVPP	Tuosu Fauna: ~11.1–10.1	Bohlin, 1935b; Xue et al., 2006
T. brevirostrum	A complete skull, cranial part of skull with horn core apparatus, and an upper jaw	Yancaiping	China	HMV IVPP	Guonigou Fauna: ~11.1–10.5	Shi, 2014
Hezhengia bohlini	More than 100 skulls and few mandibles	Guanghe County	China	HMV IVPP	Dashenggou Fauna: ~ 9.5–8	Qiu et al., 2000; Shi and Deng, 2021
H. minor	Two fragmentary skulls and upper jaws	Fugu County	China	IVPP PMU	Lamagou Fauna: 7.8	Bohlin, 1935a
Plesiaddax depereti	Plenty of skulls, few snouts, mandibles, and isolated teeth	Baode, Hequ and Siziwang Banner	China	IVPP PMU	~7.2–5.3	Schlosser, 1903; Bohlin, 1935a; Deng et al., 2011
P. inundates	Skulls, mandibles, upper jaws and post-cranials	Garkin	Turkey	NLB BGR	~8.7–7.5	Bosscha-Erdbrink, 1978
Plesiaddax cf. *P. inundates*	Isolated teeth	Mahmutgazi	Turkey	BGR	~8.7–7.5	Köhler, 1987
P. simplex	Partial cranium, few mandibles and an upper jaw	Kayadibi	Turkey	BGR	~8.7–7.5	Köhler, 1987
Criotherium argalioides	Plenty of skulls, jaws and mandibles	Samos, Mytilinii Basin (precise locality unknown) and Kemiklitepe-D, Çorakyerler	Greece and Turkey	ÇO, NHMW, NHML, BSPM, IGPM AMNH	~8.7–7.5	Solounias, 1981; Bouvrain, 1994; Kostopoulos et al., 2023
C. nikolovi	Cranium	Kalimantsi-1	Bulgaria	NMNH, Sofia	8.9–7.5	Geraads and Spassov, 2008
Shaanxispira chowi	A fractured skull with horn cores, jaw, and mandible	Lantian	China	IVPP	8.21	Liu et al., 1978
S. baheensis	A partial skull, frontlet with horn cores, and mandible	Lantian	China	IVPP	8.07	Zhang, 2003
S. linxiaensis	An almost complete and undeformed skull	Panyang, Linxia	China	IVPP	~9.5–8	Shi et al., 2014
Mesembriacerus melentisi	Cranium	Axios valley	Greece	LGPUT	~9.3	Bouvrain and Bonis, 1984 Spassov et al., 2018
Lantiantragus longirostralis	A snout and mandible	Loc. 12 , Lantian	China	IVPP	9.95	Chen and Zhang, 2004
Sinotragus wimani	Three skulls, a frontlet, and three upper jaws	Loc.30, Baode	China	PMU	~5.7	Bohlin, 1935a
S. occidentalis	A relatively complete skull without muzzle and a frontlet with cranial base	Precise locality is unknown Akgedik-Bayir, Muğla (Salihpaşalar [Kemikalan], Örucebağ [Ankara])	Turkey	MTA Museum, Ankara Izmir Museum	~7.4–6.8	Geraads et al., 2002
Prosinotragus tenuicornis	A broken cranium with horn cores	Qingyang locs. 116, 115	China	PMU	~6.5	Bohlin, 1935a

4 Classification and phylogeny of the Late Miocene ‘ovibovin’ bovids

The high-ranking classification of Late Miocene ‘ovibovin’ bovids in Eurasia remains unclear. Bohlin (1935a) classified the ‘ovibovin’ bovids into three groups based on horn core morphology: 1) the *Ovibos*-group, which includes *Plesiaddax* and *Ovibos*, whose horn cores extend laterally and horn bases enlarge forwards, backwards, and medially directed, 2) the *Urmiatherium*-group, which includes *Urmiatherium*, *Parurmiatherium* and *Criotherium*, whose horn cores are medially and posteriorly inserted, the cranial roof is raised, and the horn bases are enlarged mainly forwards, and 3) the *Tsaidamotherium*-group, which includes only the *Tsaidamotherium*, whose real horn cores are inserted above the orbit primitively, and the horn base extends backward and occupies the whole cranial roof. Chen and Zhang (2004, 2009) grouped all the Late Miocene ‘ovibovin’ bovids in China, including *Lantiantragus*, *Urmiatherium*, *Plesiaddax*, *Hezhengia*, *Tsaidamotherium*, *Shaanxispira*, *Sinotragus*, and *Prosinotragus*, into the tribe Urmiatheriini, because of the large body size, short braincase, long face, specialized horn cores, and short premolar tooth row. Recently, based on the phylogenetic analysis, Shi and Deng (2021) suggested narrowing down the Urmiatheriini tribe and considering it paraphyletic. The Late Miocene ‘ovibovin’ bovids in China (see Shi and Deng, 2021) have been classified into three groups: the *Hezhengia*-*Plesiaddax*-*Urmiatherium* group, the *Shaanxispira*-*Lantiantragus* group, and the more distant clade of *Tsaidamotherium* group. *Plesiaddax* and *Hezhengia* share similarities in the postero-laterally inserted horn cores. *Urmiatherium* are also similar in having short horn cores, short braincase, robust occipital condyle, and accessory articular surface medial to the paroccipital process (de Mecquenem, 1925; Bohlin, 1935a; Qiu et al., 2000; Jafarzadeh et al., 2012; Shi and Deng, 2021). *Lantiantragus* and *Shaanxispira* have similar dentition and are likely to have a close relationship. In *Lantiantragus*, the basal pillars are particularly pronounced in the lower molars, which serves to distinguish it from the *Hezhengia*-*Plesiaddax*-*Urmiatherium* group (Shi and Deng, 2021). The homonymously twisted horn core of *Shaanxispira* is comparable to that of *Oioceros*, but the link between *Shaanxispira* and *Oioceros* cannot be determined (Shi and Deng, 2021). The *Tsaidamotherium* group consists of only one genus, *Tsaidamotherium*. This genus is the smallest and most distinctive among all known Late Miocene ‘ovibovin’ bovids in Eurasia (Shi, 2014). A study on the second species of *Tsaidamotherium* from the Linxia Basin, *T. brevirostrum*, revealed significant facial and dental characters, such as a strongly shortened nasal, short and high muzzle, small premaxilla, very short premolar row, and elongated M3, suggesting that this genus may be a distantly related bovid clade (Shi and Deng, 2021).

The phylogenetic relationships of these 'ovibovin' bovids are highly debated in different phylogenetic cladograms using different taxa and characters (Fig. 13) (Bohlin, 1935a, 1937; Bouvrain and Bonis, 1984; Köhler, 1987; Chen and Zhang, 2004, 2009; Lalueza-Fox et al., 2005; Ropiquet and Hassanin, 2005; Geraads and Spassov, 2008; Bibi et al., 2012; Hassanin et al., 2009, 2012; Kostopoulos, 2014; Shi and Deng, 2021; Hou et al., 2023, Wang et al., 2023a, b; Wang and Ye, 2023). The conventional classifications of Ovibovinae/Ovibovini and Urmiatheriini have failed to form a monophyletic group. Most of the Late Miocene 'ovibovin' bovids are probably not very closely related to the extant *Ovibos*, but rather belong to different fossil bovid clades without extant descendants.

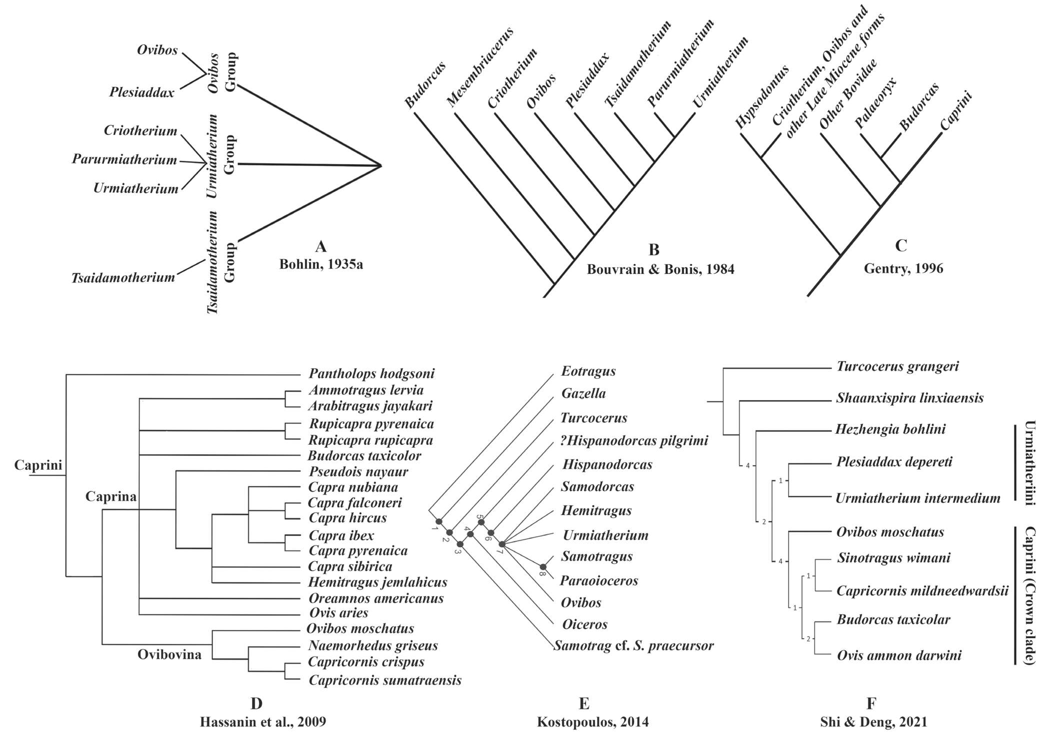

Fig. 13 Different author's concepts about the lineage of 'ovibovin' bovids based on morphological and molecular analysis

5 Discussion

The phylogenetic relationships of the 'ovibovin' bovids are difficult to solve because of their highly specialized horn core and skull morphology as well as their relatively simple and similar tooth structure, which might have evolved convergently. Transitional fossil taxa are also absent to help to bridge the large morphological gaps. In some monotypic genera, the horn core is sometimes so distinct that it is difficult to find any close relatives.

For example, as in *Tsaidamotherium*, the classification was highly controversial at the family/superfamily level because of its strange plate-like horn apparatus. In genera with more species, such as *Plesiaddax*, the main problem is the attribution of the species, which is partially due to the lack of key characters of the genus. The attribution could be highly debatable when the materials are poorly preserved, such as in *P. simplex.* There are also debates about synonymy, such as the validity of *Parurmiatherium*, which is similar to both *Urmiatherium* and *Plesiaddax* in cranium morphology. The swelling frontal above the orbit in *Parurmiatherium* is similar to *Urmiatherium*, and the former is considered a synonym of the latter in some studies (Gentry et al., 1999; Kostopoulos, 2009, 2014; Kostopoulos et al., 2023).

The most important issue regarding these 'ovibovin' bovids is the phylogenetic relationships among the most common Late Miocene 'ovibovin' bovids: *Urmiatherium*, *Plesiaddax*, *Shaanxispira*, and *Hezhengia*. All these genera have plenty of skulls that provide enough morphological information for further research. Most importantly, they are closely related and compose one of China's main evolutionary lineages of bovids. Three questions about this group remain to be solved. First, is *Plesiaddax* more closely related to *Urmiatherium* or *Hezhengia*? In Shi and Deng's (2021) cladogram, the Baodean *Urmiatherium* and *Plesiaddax* are sister groups and are later members of the tribe Urmiatheriini. However, in the traditional view, *Plesiaddax* is more closely related to *Hezhengia* because of its similar horn core position and direction (Qiu et al., 2000). The second question is whether or not *Shaanxispira* is an early branch of Urmiatheriini or related to *Oioceros*. The long and strongly twisted horn core of *Shaanxispira* is different from all the urmiatherins, but it is similar to that of the small bovid *Oioceros*. However, their skulls have many differences, and more studies are needed to confirm their relationships. Third, what is the relationship between urmiatherins and caprins? All the urmiatherins became extinct, and previous studies inferred that their closest extant relatives might be the caprins. However, a recent study proposed that the stem Caprini, *Pantholops*, might have evolved from an early ancestor more than 11 million years ago (Tseng et al., 2022), which means that urmiatherins and caprins have been separated for a very long time and are probably not very closely related.

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欧亚大陆晚中新世 “麝牛类” 牛科动物

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摘要：晚中新世时期出现了许多骨骼形态类似于现生麝牛(*Ovibos*)的中到大型食草动物，它们广泛分布于全北界，包括11个属：*Lantiantragus*, *Shaanxispira*, *Tsaidamotherium*, *Criotherium*, *Mesembriacerus*, *Hezhengia*, *Urmiatherium*, *Parurmiatherium*, *Plesiaddax*, *Sinotragus*和*Prosinotragus*。这些属主要发现于东亚、东欧和西亚地区，其中9个属在中国北方有分布。它们具有独特的特征，包括垂直的脑颅、特化的角心、粗壮的基枕骨。以前的研究经常将这些 “麝牛类” 牛科动物与现生的麝牛一起归入传统的麝牛亚科/麝牛族(Ovibovinae/Ovibovini)。然而，越来越多的研究表明麝牛亚科/麝牛族不是单系的，同时也不支持“麝牛类”动物与现生麝牛存在近的亲缘关系。通常认为在 “麝牛类” 牛科动物的11个属中，近旋角羊(*Plesiaddax*)、和政羊(*Hezhengia*)和乌米兽(*Urmiatherium*)三属具有更密切的关系，三者构成乌米兽族(Urmiatheriini)。然而，先前的系统发育分析并不支持乌米兽族的单系性。总结了Ovibovidae, Ovibovinae, Ovibovini, Ovibovina等术语的嬗变、欧亚大陆晚中新世 “麝牛类” 牛科动物的时空分布、各类群的主要特征及前人的系统发育分析结果。

关键词：欧亚大陆，晚中新世，牛科，“麝牛类” 动物，时空分布

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