

The first discovery of *Urmiatherium* (Bovidae, Artiodactyla) from Liushu Formation, Linxia Basin postprint

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Abstract

A new skull fossil of *Urmiatherium intermedium* from the Linxia Basin, Gansu Province, is reported and described herein. The specimen was recovered from the upper part of the Liushu Formation and is attributed to the Late Miocene Yangjiashan fauna. *U. intermedium* is a large Late Miocene bovid characterized by specialized horn-cores that are short, plate-like, and closely appressed at their bases. Extensive exostoses develop on the frontal and parietal bones anterior and posterior to the horn-cores; together with the horn-cores, these exostoses constitute the horn apparatus. In the early 20th century, Bohlin reported numerous fossils of *U. intermedium* from the Late Miocene strata of northern China, including over twenty skulls from Baode, Shanxi, and Qingyang, Gansu, as well as many fragmentary dental and postcranial remains. The *Urmiatherium* skull reported herein represents the first record of *Urmiatherium* from the Linxia Basin of Gansu, extending its geographic distribution in northern China westward to the northeastern margin of the Tibetan Plateau. *Urmiatherium* is widely considered to be closely related to other Late Miocene “ovibovine” bovids such as *Plesiaddax*, *Hezhengia*, and *Tsaidamotherium*, although its phylogenetic position remains contentious. Compared to other Late Miocene “ovibovine” bovids, *Urmiatherium* exhibits a relatively broad distribution, ranging from Iran to northern China, yet it rarely co-occurs with other Late Miocene “ovibovine” bovids. In the Linxia Basin, *Sinotragus* is the only bovid taxon documented to co-occur with it to date.

Full Text

Preamble

The First Discovery of *Urmitherium* (Bovidae, Artiodactyla) from the Liushu Formation, Linxia Basin

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Abstract

A new skull of *Urmitherium intermedium* (Bovidae, Artiodactyla) from the Linxia Basin, Gansu Province is described here. *U. intermedium* is a large Late Miocene bovid with an odd-looking horn apparatus, consisting of a pair of degenerate, closely situated horn-cores, and a large area of exostoses on the frontal and parietal bones. Numerous skulls, teeth, and bone fragments of *U. intermedium* have been reported from North China, but the skull described here represents the first discovery from the Linxia Basin, expanding the geographic distribution of *U. intermedium* to the northeastern edge of the Tibetan Plateau. Although *Urmitherium* is generally thought to be closely related to *Plesiaddax*, *Hezhengia*, *Tsaidamotherium*, and other Late Miocene “ovibovines,” its phylogenetic position remains debated. The distribution of *Urmitherium* spans from Iran to North China. In North China, *Urmitherium* is seldom found accompanying other Late Miocene “ovibovines,” but instead co-occurs with other bovids such as *Sinotragus*.

Keywords: Linxia Basin, Late Miocene, Bovidae, *Urmitherium*

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1. Introduction

Urmitherium is a large Late Miocene bovid characterized by its peculiar horn apparatus, shortened cranium, perpendicular cranial roof, and thickened basicranium. The horn apparatus comprises short, posteriorly positioned, and closely inserted horn-cores that are sometimes partially fused at the base, along with elongated horn bases featuring very rough surfaces. Exostoses are well developed on the frontal and/or parietal bones. Two species are recognized: the

type species *U. polaki* from Maragheh and *U. intermedium* from North China. The material of *U. polaki* is rare, consisting of three partial skulls (two posterior parts and one facial portion), several cervical vertebrae, isolated teeth, broken mandibles, and limb bones, most of which are poorly preserved. All specimens were discovered at different localities in Maragheh (Karajabad and Ilkhchi), representing different geological ages (Middle and Upper Maragheh, 8.16–7.9 Ma and 7.9–7.4 Ma respectively). In contrast, *U. intermedium* is represented by abundant material: approximately 20 skulls, numerous lower dentitions, isolated teeth, and bone fragments, primarily from Baode localities (Anderson locs. 30, 43, 44, 49, 108), with only one skull and some fragments from Qingyang (Anderson locs. 115, 116). The age of *U. intermedium* in Baode ranges from approximately 7.0 Ma (loc. 49) to 5.7 Ma (loc. 30) according to Kaakinen et al. (2013).

Recently, a skull of *Urmitherium intermedium* (IVPP V 18955) was discovered in the Linxia Basin, Gansu Province, Northwest China, at locality LX0029 near Huaigou village, approximately 10 km southeast of Hezheng County [Figure 1: see original paper]. The specimen was excavated from the upper Liushu Formation and belongs to the Late Miocene Yangjiashan Fauna of the late Bahean age, spanning approximately 8.7 to 7.2 Ma. Thus, the stratigraphic age of this new skull from the Linxia Basin is slightly earlier than those from Baode and nearly contemporaneous with *P. polaki* from Maragheh. Although numerous Late Miocene bovids are known from the Linxia Basin, this represents the first discovery of *Urmitherium* there, extending the distribution of *U. intermedium* to the northeastern edge of the Tibetan Plateau.

Institutional abbreviations: DOE, Department of Environment, Iran; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PIUU, Paleontological Institute, University of Uppsala, Sweden.

2. Systematics

Artiodactyla Owen, 1848

Bovidae Gray, 1821

Urmitherium Rodler, 1889

Urmitherium intermedium (Schlosser, 1903)

Pseudobos intermedium Schlosser, 1903

Pseudobos sinensis Schlosser, 1903

Chilinothierium tingi Wiman, 1922

Lectotype: PIUU M 3943 (Bohlin, 1935a: Ex. 1, loc. 30; textfig. 1, pl. 1, figs. 1–3).

Described specimen: IVPP V 18955, a male adult skull (Figs. 2–4).

Description: The new skull IVPP V 18955 is severely compressed from side to side and split into two parts along a plane extending from the posterior portion of the nasal to the pterygoid, but has been well restored with plaster. Although the cranium is heavily damaged (particularly the occiput), the horn apparatus is preserved in relatively good condition. The cheek tooth rows are nearly intact, except that the P2s are missing on both sides. The muzzle anterior to the cheek teeth is missing.

The basioccipital is thick, short, and rectangular [Figure 2: see original paper]A, C: Bo. The posterior tuberosities protrude ventrally and fuse together, leaving only a narrow groove in ventral view [Figure 2: see original paper]C: PosT. The posterior facets of the posterior tuberosities are nearly square with a shallow central depression. In lateral view, these facets form an angle of approximately 120° with the ventral border of the basioccipital [Figure 2: see original paper]A. The anterior tuberosities are slender and ridge-like. The condyles and paroccipital processes are broken on both sides. A small portion of the left accessory articular surface is observable, indicating a shallow depression between the condyle and paroccipital process [Figure 2: see original paper]C, AAS. Both auditory bullae are missing. The oval foramina are moderately large, facing laterally and anteriorly [Figure 2: see original paper]C: VF. The pterygoid crests are sharp and protruding [Figure 2: see original paper]A, C: PtC. At the root of the pterygoid crests lie the orbito-rotundum foramina, which are barely visible in lateral view. The distance from the oval foramen to the orbito-rotundum foramen is nearly equal to that from the orbito-rotundum foramen to the optic foramen [Figure 2: see original paper]A: OpF. The ethmoidal foramen is small, positioned in the center of the orbit [Figure 2: see original paper]A: EmF.

The occiput is heavily damaged. The broken foramen magnum extends to the upper part of the occipital, exposing part of the brain cavity [Figure 3: see original paper]: broken FM. Above the broken foramen lies a large external occipital protuberance flanked bilaterally by two deep depressions for nuchal ligament attachment [Figure 3: see original paper]: EOP. A small portion of the right mastoid is also preserved [Figure 3: see original paper]: Mas. The nuchal crest is sharp and protruding [Figure 3: see original paper]: NC. Above the external occipital protuberance is the small supra-occipital [Figure 3: see original paper]: SpO. The suture between the supra-occipital and parietal is zigzag near the temporal fossa but indistinguishable in the center [Figure 2: see original paper]A: suture . The parieto-temporal suture is simple and relatively straight, whereas the parieto-frontal suture is barely distinguishable [Figure 2: see original paper]A: suture . The left temporal fossa is broken, exposing the lateral wall of the cranium approximately 1 cm thick [Figure 2: see original paper]C.

The horn apparatus is large and complex, forming a prominent bulge above the cranium and covering surfaces from the foremost point of the frontal to the rearmost point of the parietal, but lacks horn-cores in the proper sense [Figure 2: see original paper]A, B. Bohlin' s (1935a) division of the horn apparatus into

four sections (I, II, III, and IV) is readily applicable to this specimen [Figure 2: see original paper], [Figure 3: see original paper]. Section I represents the horn-cores proper, described as “low and sharp ridges, on which in most male individuals the vertex is recognizable” (Bohlin, 1935a:21). In the new specimen, the horn-cores proper are low and laterally compressed, with clearly defined vertices pointing upwards and backwards. In dorsal view, the horn-cores proper converge posteriorly but remain separated at the rearmost point by a narrow deep fissure [Figure 2: see original paper]B. Medial to the horn-cores proper are two deep grooves separating them from the bulging horn bases at the center [Figure 2: see original paper]B, double-headed arrows. The horn bases between the horn-cores proper are very high, partially due to skull compression and deformation. Clear depressions anterior to the horn-cores proper separate them from the frontal exostoses, whereas posterior separation is vague. Anterior to the horn-cores proper, the horn bases rise high above the orbit, comprising the main portion of the horn apparatus and corresponding to Bohlin’s sections II and III. These sections represent exostoses expansion on the frontal with highly cancellous surfaces. Due to severe deformation, the border between sections II and III is difficult to distinguish in the new specimen. Sections I, II, and III vary considerably among individuals. Posterior to the horn-cores proper, the exostosis expansion on the parietal is well developed, extending to the rearmost point of the parietal and defined as section IV. In some individuals the left and right exostoses fuse, but in most specimens, including the new one, they are separated by a deep narrow fissure along the sagittal line [Figure 3: see original paper]: fissure. In the new specimen, this fissure is long and the exostoses surface is very rough, indicating that section IV is better developed than in most skulls from Baode and Qingyang (Bohlin, 1935a).

The frontals are partially damaged, exposing porous inner structures [Figure 2: see original paper]A: FS. On the right side, the surface bone lamina above the orbit is nearly absent, revealing that the frontal sinuses are so well developed that the frontals are filled with large air cavities and thin supporting bone laminae. The supra-orbital foramina are small, deeply sunken in the frontals and facing forwards [Figure 2: see original paper]A: SoF. The supra-orbital grooves are distinct and long [Figure 2: see original paper]A: SoG. The internal openings of the supra-orbital foramina are also small, facing mostly downwards. The canal between external and internal openings of the supra-orbital foramen is long (approximately 4 cm). The anterior border of the orbital rim lies posterior to the back of M3.

The lachrymals are rectangular and large [Figure 2: see original paper]A: L. The fronto-lachrymal [Figure 2: see original paper]A: suture and lachrymo-jugal sutures [Figure 2: see original paper]A: suture are complex, especially near the orbital rim. On the orbital surface of the lachrymal is a large lachrymal bulla [Figure 2: see original paper]A, LB. The jugals are relatively small with two clear lobes [Figure 2: see original paper]A: J. Most of the nasals and anterior parts of the maxillae are missing. The infra-orbital foramina are small, opening at the level between P3 and P4 [Figure 2: see original paper]A: IoF.

In ventral view, the maxillo-palatine suture is difficult to determine. The palatine foramina are small, situated at the level of the posterior lobe of M2 [Figure 2: see original paper]C: PF. The anterior edge of the choanae is V-shaped, with its anterior point positioned posterior to the tooth rows and lateral indentations.

The cheek teeth are hypsodont. The premolar rows are short, with a premolar to molar length ratio of approximately 55.8%. The P2s are missing on both sides, though the root of the right P2 is preserved. The paracone of P3 is anteriorly positioned, separated from the sharp parastyle by a narrow groove. The metastyle of P3 is large. P4 is similar in length to P3 but slightly wider, with a flat lingual border making it nearly square. The buccal border of P4 is almost symmetrical with a weak paracone rib. The central fossettes of P3 and P4 are deep and narrow. M1 is slightly longer than wide, with weak buccal ribs, an unrecognizable metastyle, and a flat lingual wall. Two enamel islands are present in M1: a larger oval lingual island and a much smaller buccal one. M2 is longer than M1, with well-developed parastyle and mesostyle (though the latter is thinner). The metastyle and metacone rib are weak, while the paracone rib is moderately developed. Only one enamel island is present in M2. M3 is almost as long as M2, but its occlusal surface is slightly narrower, particularly in the posterior lobe. The ribs and styles are well developed except for the metacone rib. In both M2 and M3, the lingual wall of the fossettes protrudes medially and posteriorly. All molars have shallow lingual valleys and lack basal pillars.

3.1 Comparison with Specimens from Baode and Qingyang

The new skull possesses a large horn apparatus extending from nearly the foremost point of the frontal to the rearmost point of the parietal, forming a substantial bulge atop the cranium consistent with *Urmiatherium intermedium*. Skull features including the short cranium, perpendicular cranial roof, thickened basicranium, enlarged posterior facets of the posterior basioccipital tuberosities, small supraorbital foramen, and distinct supraorbital groove demonstrate close affinity with *U. intermedium*. The teeth resemble those of *U. intermedium* in having short premolar rows, hypsodont crowns, and simple central cavities. Therefore, the new specimen is unequivocally assignable to *U. intermedium*.

However, the new skull is larger than most *U. intermedium* skulls from North China. Both skull length (Table 1 : measurement 7) and horn apparatus length (Table 1: measurement 1) approximate those of the largest individuals from Baode (loc. 30), while exceeding the only skull from Qingyang (Table 1: measurement 7). The dentition (Table 2 , P+M) is the largest among all known *U. intermedium*, with length comparable to the largest specimens from Qingyang (loc. 115) and Baode (loc. 30). Individual variation in *U. intermedium* is substantial; at the locality with the most skulls (loc. 30), the largest skull is 15% longer than the smallest, with dentition length variation reaching up to 19%. The new skull does not exceed the known variation range of *U. intermedium*.

Horn apparatus morphology, particularly the parietal exostoses, varies considerably among individuals as noted by Bohlin (1935a). In the new specimen, the section IV exostoses are very well developed, similar to PIUU M 3934 (Ex. 7, loc. 108; Bohlin, 1935a: textfig. 12 [Figure 12: see original paper] & 13), whereas in most Baode and Qingyang specimens, section IV is smaller and smoother. However, sections I and II of the new skull differ from M 3934 but more closely resemble Ex. 15 from loc. 30 (Bohlin, 1935a: textfig. 14 [Figure 14: see original paper]), featuring flatter anterior surfaces, a clear sagittal furrow between the posterior part of section I, and thin bone plates along the horn-cores proper that converge backward.

Given the extensive individual variation in *U. intermedium*, Bohlin (1935a) distinguished three possible types based primarily on size, development of section IV of the horn apparatus, and p4 shape (Type I: loc. 30; Type II: loc. 108 and ?49; Type III: loc. 115; other localities uncertain). Here we group specimens by location and stratigraphic layer (following Kaakinen et al., 2013) and compare skull and dentition measurements (Tables 1, 2). The results show no distinct differences among materials from different layers or locations. Although specimens from loc. ?49 are relatively small, others from the same stratigraphic layer (e.g., loc. 43) are larger, suggesting that observed variations likely stem from inadequate sampling rather than representing distinct types.

3.2 Comparison with *Urmiatherium polaki* and *Parurmiatherium*

The type species *U. polaki* resembles *U. intermedium* in possessing closely inserted horn-cores proper, frontal exostoses, perpendicular cranial roof, stout occipital condyles, and thickened basicranium. However, significant differences exist, which Bohlin considered possibly of generic significance (Bohlin, 1935a:37). The skull of *U. polaki* is longer and much wider than that of *U. intermedium* (Table 1, measurements 3-5, 8-10), with longer dentition and a similar premolar to molar ratio (Table 2). The horn-cores of *U. polaki* are longer, while the exostoses are less developed and do not extend onto the parietal. The basicranium of *U. polaki* is thicker with larger oval posterior facets on the posterior tuberosities.

Two posterior partial skulls of *U. polaki* were previously considered ontogenetically distinct based on horn-core differences (Mecquenem, 1925; Kostopoulos and Bernor, 2011). However, the fully developed basicrania of both skulls indicate they are fully adult, and horn-cores in adult bovids typically do not grow continuously with age. Furthermore, although the holotype's horn-cores are smaller, its frontal surface is coarser, and frontal exostoses generally become larger and rougher with age. Thus, if these two Maragheh skulls belong to the same species, they likely represent individual variation rather than different ontogenetic stages.

Parurmiatherium shows great similarities to *Urmiatherium* in cranial and ba-

sicranial morphology and has been considered a junior synonym by some researchers (Gentry, 2010; Kostopoulos, 2009, 2014). Given the poor preservation of *Parurmiatherium* specimens (all skulls from Samos and Iraq are broken), it is difficult to determine whether generic distinction is warranted. Nevertheless, horn differences are obvious: *Parurmiatherium* has horn bases that approach each other anteriorly with homonymously spiraled, widely spaced horn-cores, whereas in *Urmiatherium* the horn bases approach each other posteriorly and the horn-cores are straight and sometimes fused at the base. Frontal exostoses are well developed in *Urmiatherium*, forming a single rough surface present even in females, whereas in *Parurmiatherium* the horn-cores are clearly separated. Therefore, *Parurmiatherium* might be retained as a separate genus pending discovery of more complete specimens.

4.1 Phylogeny

The phylogeny of *Urmiatherium* (and *Parurmiatherium*) remains debated due to its peculiar horn apparatus and skull morphology. Sickenberg (1933) established a new subfamily Urmiatheriinae for *Urmiatherium* and *Parurmiatherium*, whereas Bohlin (1935a) assigned *Urmiatherium* to subfamily Ovibovinae together with *Plesiaddax* and *Tsaidamotherium*, citing similarities to the extant *Ovibos*. Bohlin's opinion was widely followed, with *Urmiatherium* described as a Late Miocene "ovibovine" by many researchers (Qiu et al., 2000). In 1987, Köhler established the tribe Urmiatheriini, including *Urmiatherium*, *Tsaidamotherium*, *Criotherium*, *Parurmiatherium*, and *Plesiaddax* (Köhler, 1987). Later, Chen and Zhang (2004, 2009) assigned additional Late Miocene bovids to Urmiatheriini and reestablished subfamily Urmiatheriinae. The revised Urmiatheriini shares similar members with Late Miocene "ovibovines," with the main difference concerning their relationship to extant *Ovibos*. Kostopoulos (2014) assigned *Urmiatherium* to Oiocerini based primarily on the homonymously twisted horn-cores of *Parurmiatherium*. In this paper, we provisionally use the term Late Miocene "ovibovines" following traditional usage.

When Bohlin assigned Late Miocene "ovibovines" to Ovibovinae, basicranial morphology was considered important, a view we consider reasonable. Although thickened basicranium and enlarged posterior tuberosities may be highly related to male fighting and competitive behavior, other characters such as the shallow depression between the occipital condyle and paraoccipital process and the developed accessory articular surface at the depression's base are less common and potentially phylogenetically significant. The basicrania of Late Miocene "ovibovines" are very short, differing from other Late Miocene bovids such as caprines and boselaphines. Exostoses development is also a common trait of Late Miocene "ovibovines" and *Ovibos*, rarely observed in other bovids. Additional similarities include short braincase, short and stout condyles, mesodont or hypsodont teeth, and simple molar fossettes. Whether Late Miocene "ovibovines" and *Ovibos* form a monophyletic clade remains uncertain, but they

share more similarities with each other than with any other bovids.

4.2 Distribution

Urmitherium exhibits a wide distribution spanning from Iran to North China, whereas most other Late Miocene “ovibovines” are more localized. *Tsaidamotherium*, *Shaanxiplina*, *Lantiantragus*, and *Hezhengia* are known only from North China, while *Parurmiatherium* occurs in Greece and West Asia. *Plesiaddax* is another widespread Late Miocene “ovibovine,” distributed from western Turkey to North China. However, the Turkish *Plesiaddax* specimens are problematic: those from Kayadibi are very few and fragmentary, lacking crucial characters, while the abundant specimens from Garkin probably do not represent *Plesiaddax* either. Thus, *Urmitherium* has a wider distribution than most other Late Miocene “ovibovines.”

Although several Late Miocene “ovibovine” species have been discovered in the Linxia Basin (*Urmitherium*, *Tsaidamotherium*, *Hezhengia*, two *Shaanxiplina* species, and an unpublished new genus), none co-occur with *Urmitherium*. One *Shaanxiplina* species occurs in the same stratigraphic layer but at non-overlapping localities (Deng et al., 2013). Another contemporaneous Late Miocene “ovibovine” in North China is *Plesiaddax*, but most specimens of *Urmitherium* and *Plesiaddax* come from different localities. In the Linxia Basin, the only other bovid found at the same locality as *Urmitherium* is *Sinotragus*, a caprine reported from both Turkey and China. In North China, *Sinotragus* and its possible synonym *Prosinotragus* also occur in Baode and Qingyang, where they accompany *Urmitherium*.

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Note: Figure translations are in progress. See original paper for figures.

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