

# New *Olonbulukia* material and its related assemblage reveal an early radiation of stem Caprini along the north of the Tibetan Plateau

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**Abstract.**—Living Caprini are dominant bovids in the pan-Tibetan area that are strongly adapted to dry steppe and high-mountain meadow habitats. Some taxa with Holarctic distributions, e.g., *Ovis* Linnaeus, 1758, were thought to originate on the Tibetan Plateau and subsequently dispersed elsewhere, which was depicted as an ‘out of Tibet’ story. However, except for some information on a stem caprine assemblage from the Qaidam Basin, the early evolution of Caprini around the Tibetan Plateau is poorly known. Here, we report new material of *Olonbulukia tsaidamensis* Bohlin, 1937, which was a member of this stem caprine assemblage, from the Wuzhong region, northern China, confirming the similarity of the Wuzhong Fauna and ‘Qaidam Fauna.’ Based on a biometric study of horncores from the ‘Qaidam’ and Wuzhong faunas, we recognize six taxa from this stem caprine assemblage: *O. tsaidamensis*, *O. sp.*, *Qurlignoria cheni* Bohlin, 1937, *Tossunnoria pseudibex* Bohlin, 1937, *?Protoryx cf. P. enanus* Köhler, 1987, and cf. *Pachytragus sp.* Among these taxa, *Q. cheni* and *T. pseudibex* are probably related to some extant Tibetan endemic species, e.g., the Tibetan antelope, *Pantholops hodgsonii* (Abel, 1826), and the Himalayan tahr, *Hemitragus jemlahicus* (Smith, 1826). Others might be ancestral to the Turolian caprine assemblages and even possibly gave rise to the extant Caprina. This work reveals an early radiation of stem caprines along the northern side of the rising Tibetan Plateau and indicates a mixed pattern of pan-Tibetan stem caprine evolution prior to their dispersal out of the Tibetan Plateau.

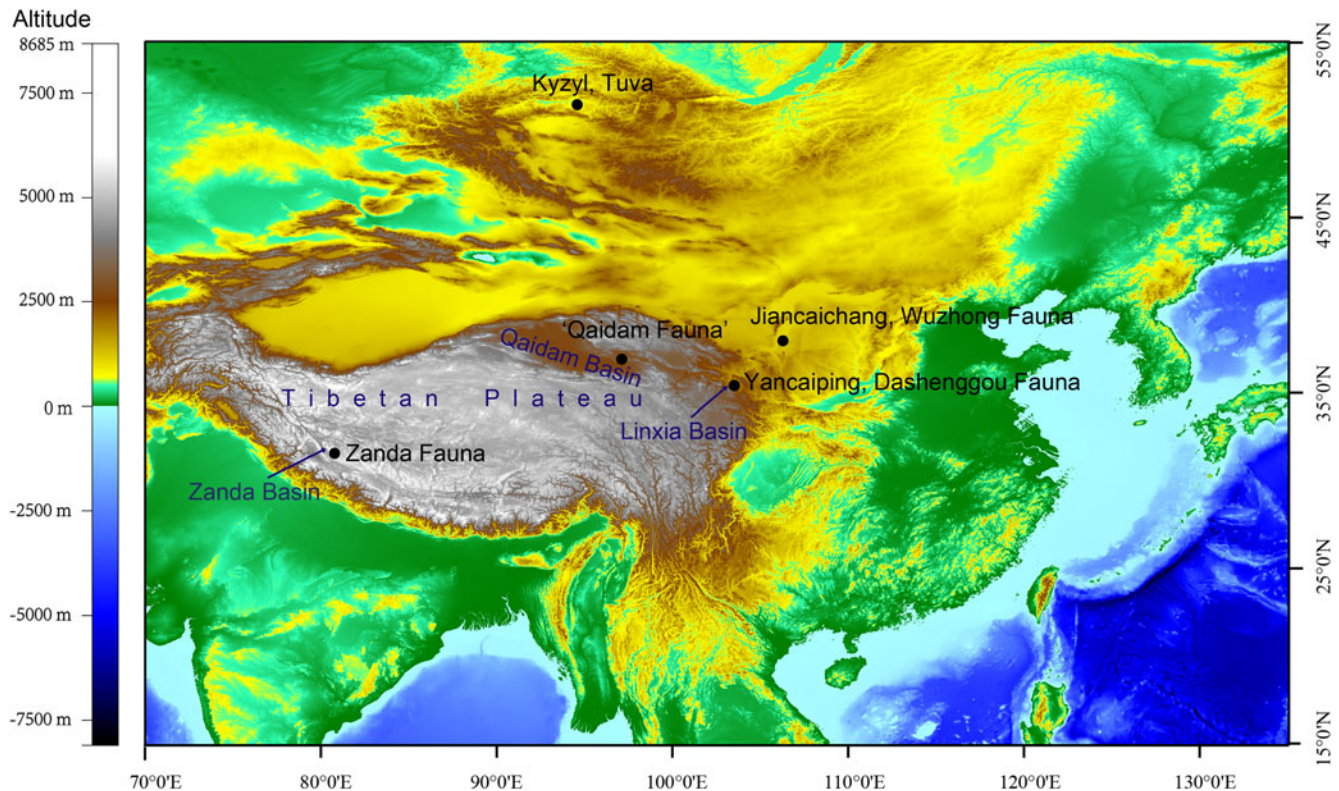
## Introduction

Bohlin (1937) reported the ‘Qaidam (= Tsaidam) Fauna’ from the Qaidam Basin (Fig. 1) in the northern part of the Tibetan Plateau. Among the fossil assemblages in the early paleontological history of China, this fauna is distinctive in the occurrence of various specialized bovids that are seldom recovered elsewhere (i.e., *Olonbulukia* Bohlin, 1937, *Qurlignoria* Bohlin, 1937, *Tossunnoria* Bohlin, 1937, and *Tsaidamotherium* Bohlin, 1935a). The most specialized bovid, *Tsaidamotherium*, which has a very odd horncores (Bohlin, 1935a; Shi, 2014), was attributed to Ovibovinae or Urmitheriinae, and its phylogenetic position has been substantially debated (Köhler, 1987; Gentry, 1992; Bibi et al., 2009; Chen and Zhang, 2009). Other taxa were grouped as presumed with Caprinae (Gentry, 2000), and were recently changed to Caprini based on both morphological and molecular evidence (Bibi et al., 2009; Hassanin et al., 2012). *Qurlignoria* is hypothesized to be the ancestor of the extant Tibetan antelope or chiru, *Pantholops hodgsonii* (Abel, 1826) (Gentry, 1968, 2000; Deng et al., 2011). *Tossunnoria pseudibex* Bohlin, 1937 seems to be related to the extant Himalayan tahr, *Hemitragus jemlahicus* (Smith, 1826), or goats (*Capra* spp.) (Bohlin, 1937; Gentry, 1971, 2000). Therefore, ‘Qaidam Fauna’ bovids could represent an early radiation of endemic

stem Caprini on the Tibetan Plateau. Except for the above-named taxa, there are still several types of horncores with relatively unspecialized morphology, which Bohlin (1937) referred to as ‘Antelope gen. et sp. indet.’ I–IV. However, these unnamed taxa have been inadequately noticed by subsequent researchers (but see Bibi and Güleç, 2008).

The ‘Qaidam Fauna’ was considered the earliest *Hipparion* fauna in northern China, because of the occurrence of early hipparions, early tetralophodont gomphotheres, an early *Acerorhinus*, and some primitive cervids (i.e., *Lagomeryx* Roger, 1904 and *Dicrocerus* Lartet, 1837) that were thought to be middle Miocene relicts (Qiu et al., 1987). Recently, Wang et al. (2011) studied Bohlin’s field records and investigated the stratigraphy of the fossiliferous region; consequently, they recognized two fossil assemblages in the ‘Qaidam Fauna,’ the late middle Miocene Olongbuluk Fauna (ca. 15–12.5 Myr) and early late Miocene Tuosu Fauna (ca. 12–10.5 Myr). Therefore, the ‘Qaidam Fauna’ was a fossil assemblage complex, and we refer to the ‘Qaidam Fauna’ using quotation marks.

Recently, we discovered a horncore of *Olonbulukia tsaidamensis* Bohlin, 1937 and possibly stem Caprini dental material from the Wuzhong Building Material Plant (Jiancaichang locality, Wuzhong), Ningxia Province, China (Fig. 1) from the early late Miocene Ganhegou Formation. This is



**Figure 1.** Topology of eastern Asia with related fossil localities in the present article, emphasizing the Tibetan Plateau. The map was downloaded from the public source, General Bathymetric Chart of the Oceans (<https://www.gebco.net/>).

the first report of *Olonbulukia* outside of the Qaidam Basin. This locality was previously reported by Qiu et al. (1987), with the discovery of *Qurliqnorina cheni* Bohlin, 1937. The occurrence of *O. tsaidamensis* and *Q. cheni*, with recent palaeomagnetic data of the Ganhegou Formation (ca. 10 Ma, see Shen et al., 2001), proves that the fossil assemblage from the Jiancaichang locality (denoted herein as the Wuzhong Fauna) is comparable to the classic Tuosu Fauna. In the same period, fossils were rarely discovered from northern China. Therefore, an in-depth study of the bovid assemblages of these two faunas is helpful in understanding the radiation of caprines, which are very important members of today's dry and cold Holarctic habitats (Geist, 1987).

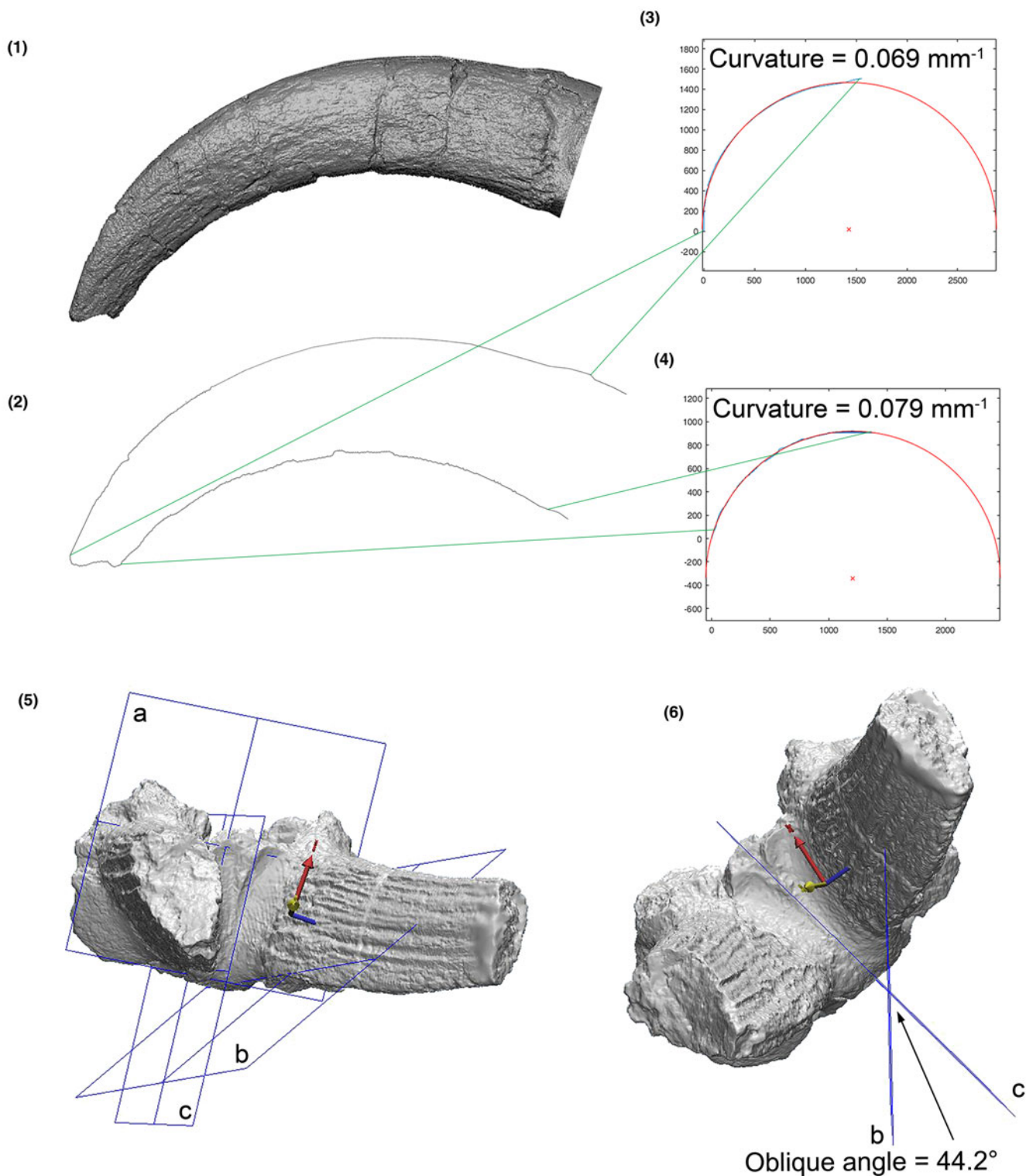
## Materials and methods

**Horncore biometric study and 3D models.**—We used three biometric parameters to characterize horncore morphology. (1) Mediolateral compression was inferred by basal anteroposterior diameter (DAP)/transverse diameter (DT); data were measured using calipers. (2) Curvature (unit / mm) was represented by the mean curvature of horncore anterior and posterior edges; to obtain these data, we took photographs of the direct lateral view of the horncore (Fig. 2.1) and extracted the outlines of the anterior and posterior edges (Fig. 2.2); then, we used the least-squares method to fit a circle by the sample points of the outlines, and calculated the curvature of the regressed circle (Fig. 2.3, 2.4). Calculation was performed using a set of

self-programmed MATLAB (MathWorks, Inc.; ver. R2016a) codes. (3) Oblique angle was represented by the angle between the medial sagittal plane and the vertical plane that passes through the long axis of the pedicle; to obtain these data, we acquired the 3D surface digital models of the horncores using an Artec 3D Spider scanner and measured the angle on the 3D models using the Materialise 3-matic program (ver. 9.0) (Fig. 2.5, 2.6). All of the 3D models (see Supplemental data SI 1–17) are available in the public online repository Dryad. Other biometric data were measured using calipers.

**One-way ANOVA.**—Student's t-tests were performed to test the statistical significance of differences in horncore curvature and oblique angle between *Olonbulukia* and *Qurliqnorina*, and mediolateral compression between *O. tsaidamensis* and *Olonbulukia* sp. Equal variance was hypothesized, and differences were considered significant if the double-tailed test was  $< 0.05$ .

**Repositories and institutional abbreviations.**—IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (IVPP RV is the prefix for the specimens that were previously published under informal numbering systems); NGM = Ningxia Geological Museum, Yinchuan, Ningxia, China. All of the specimens examined here are housed in IVPP, except one from NGM. Comparative materials were from previous publications. Ruminant tooth terminology follows that used by Bärmann and Rössner (2011).



**Figure 2.** Horncore biometric data acquisition: (1) photo of a horncore (*Olonbulukia tsaidamensis*, IVPP RV37008, taken from 3D digital model) in lateral view; (2) outlines of the horncore in Figure 2.1; the green lines denote the sections of anterior and posterior edges; (3, 4) circle fitting of the anterior (3) and posterior (4) edges of the horncore; the blue lines denote the horncore outlines and the red lines denote the fitted circles; (5) sectioning plane on the 3D digital horncore model (*Qurliqnorja cheni*, IVPP RV37100); a = horizon plane, b = vertical plane through the pedicle long axis, c = medial sagittal plane; The red, blue, and yellow arrows represent the X, Y, and Z coordinates that were arbitrarily generated by the 3-matic program; (6) oblique angle measurement, or the angle between the b and c planes. The red, blue, and yellow arrows represent the X, Y, and Z coordinates that were arbitrarily generated by the 3-matic program; the arrowhead of the blue arrow is hidden by the 3D model of the horncore body.

## Systematic paleontology

Order Artiodactyla Owen, 1848

Family Bovidae Gray, 1821

Subfamily Antilopinae Gray, 1821 (sensu Kingdon, 1982)

Genus *Olonbulukia* Bohlin, 1937

*Type species.*—*Olonbulukia tsaidamensis* Bohlin, 1937.

*Diagnosis.*—Medium-sized bovid with mediolaterally compressed horncore that possesses an anterior keel. The horncore has a weak spiral structure with strong posterior bending (curvature 0.04–0.10/mm). The oblique angle of the pedicle is small (15–30°). The top of the cranium is vaulted, and the profile of the dorsal cranium is curved dorsally instead of straight, resembling that of *Protoryx* Major, 1891. (Revised from Bohlin, 1937.)

*Occurrence.*—Qaidam Basin and Wuzhong regions, China; middle Miocene and early late Miocene (late Tunggurian and early Bahean, Chinese Land Mammal Age), which were correlated to MN 6–9.

*Olonbulukia tsaidamensis* Bohlin, 1937

Figure 3.1–3.3; Table 1

*Holotype.*—IVPP RV37008 [Bohlin's (1937) field no. 356], a brain case with both horncores; the ventral surface is deeply weathered.

*Diagnosis.*—The horncore is strongly compressed with DAP/DT 1.6–1.9 (at the horncore base). Otherwise as for the genus.

*Occurrence.*—Bohlin Camp (BB, 165), Qaidam Basin, basal red beds (Olongbuluk Fauna), middle Miocene, ca. 15 Ma (Wang et al., 2011).

*Description.*—The right horncore (Fig. 3.1–3.3) is strongly lateromedially compressed. The horncore cross section at the base is a compressed oval. This shape is retained throughout the preserved length, and only becomes slightly smaller distally (Fig. 3.1.1–3.1.3). The long axis of the cross section at the right horncore base is slightly oblique to the midsuture of the frontal bone by an angle of 19.7°, suggesting that the two long axes of horncore cross sections posteriorly diverge by ~40°. No less than 1/3 of the distal part of the horncore is broken. In lateral and medial views, the preserved horncore portion shows a posterior curvature. In anterior and posterior views, the horncore is slightly laterally oblique. The horncore is slightly homonymous. Strong furrows are present along the entire length of the horncore. An anterior keel is present, but is not as sharp as that of the type specimen. The pedicle is moderately long, with the anterior edge longer than the posterior edge. The anterior opening of the supraorbital channel is small and located at the proximal base slightly lateral to the anterior edge of the pedicle, which is relatively close to the midsuture of the frontal bone. No groove surrounds the supraorbital foramen. The postcornual fossa is weak and close to the horncore base.

The remaining frontal bone can be subdivided into three surfaces. (1) The cerebral surface is anterodorsally bordered by the midsuture of the frontal bone and posterodorsally bordered by the frontal-parietal suture; it is triangular and deeply concave with many digital impressions. The midsuture of the frontal bone is half-crescent-shaped. The anterior part is strongly thickened, extends posterodorsally, and thins. The frontal-parietal suture forms a right angle. (2) The orbital surface is located laterally. However, the thin orbital rim was broken. This surface is smoothly concave. The posterior opening of the supraorbital channel is located at the deepest point of the orbital surface and is almost at the same level as the anterior opening. (3) The frontal sinus surface is small; it is located at the anteroventral part of the bone. The frontal sinus is irregular and shallow on the surface. However, we do not know whether the excavation of the frontal sinus in the horncore is present.

*Materials.*—IVPP V23373, a right horncore with partial frontal bone; the distal part of the horncore is broken.

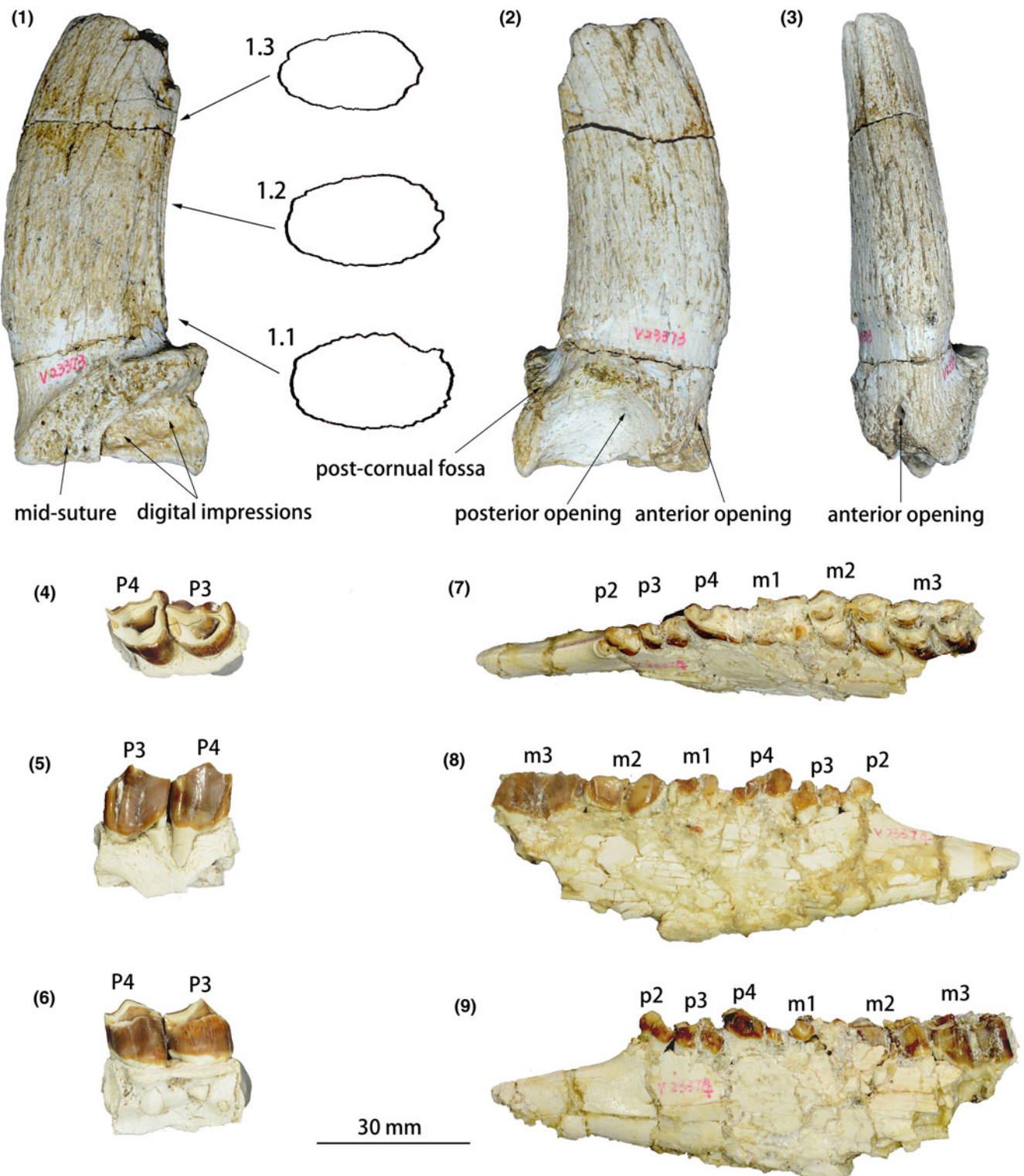
*Locality and age of the new material.*—The Wuzhong Building Material Plant (Jiancaichang locality), Northeast Quarry (IVPP no. NXWZ201502), 37°49'50.46"N, 106°07'12.08"E, 1169.0H (Fig. 1), early late Miocene Ganhegou Formation, Bahean, correlated to ~MN 9.

*Remarks.*—*Olonbulukia tsaidamensis* is a stem caprine species with relatively specialized horncores for its age. The horncore is remarkably laterally compressed with strong posterior curvature. The holotype is from the Bohlin Camp (BB, 165) of the Olongbuluk Fauna, Qaidam Basin, ca. 15 Ma of the middle Miocene (Wang et al., 2011). This age is very early, even for stem caprines. *Olonbulukia tsaidamensis* also occurred in the early late Miocene Tuosu Fauna but was never found outside of the Qaidam Basin prior to this study. The newly discovered horncore from the Wuzhong Fauna displays almost identical morphology with the holotype, except for smaller dimensions, possibly due to a younger ontogenetic stage. The Jiancaichang site of the Wuzhong Fauna is ca. 10 Ma, very close to and probably slightly later than the Tuosu Fauna of the Qaidam Basin. The new horncore is the first report of *O. tsaidamensis* outside of the Qaidam Basin.

Antilopinae gen. indet. sp. indet.

Figure 3.4–3.9; Table 2

*Description.*—The P3 and P4 (Fig. 3.4–3.6) are moderately worn. In occlusal view (Fig. 3.4), the P3 is semicircular with a straight labial wall and a rounded lingual wall. The labial cone is relatively anteriorly positioned. The anterior style is also strong, labially protruded. The posterior style is relatively blunt. The fossa is strongly anteriorly positioned. It is fabaceous with a small central fold on the posterolingual crista. The dentinal area of posterolabial and posterolingual cristae is very large, and a shallow posterior fossa is developed on the posterolingual crista. This fossa is narrow and cuts through the posterior wall of the tooth enamel at the lingual side of the posterior style. In buccal view (Fig. 3.5), the labial cone is high and sharp. The ribs of the labial cone



**Figure 3.** Stem caprines from the Jiancaichang locality, Wuzhong (Wuzhong Buliding Material Plant), China, Bahean age (ca. 10 Ma), late Miocene: (1–3) *Olonbulukia tsaidamensis*, IVPP V23373, right horncore with fragmentary frontal bone remains, in medial (1), lateral (2), and anterior (3) views (anterior at left and lateral at top), with cross sections at 0 (1.1), 37.8 (1.2), and 59.1 (1.3) mm distal to the pedicle; (4–6) *Antilopinae gen. indet. sp. indet.*, NGM WJCCD-10-N-006, right P3 and P4, in occlusal (4), buccal (5), and lingual (6) views; (7–9) *Antilopinae gen. indet. sp. indet.*, IVPP V23374, right hemimandible with p2–m3 tooth row, in occlusal (7), lingual (8), and buccal (9) views. Notes: M/m = upper/lower molar; P/p = upper/lower premolar.

**Table 1.** Information and biometric data of the horncores discussed in this study. \* = type specimen; \*\* = both horncores preserved.

Taxon	Number	Bohlin taxonomy	Bolin field no.	Age (Miocene)	Locus	Anterior curvity (mm <sup>-1</sup> )	Posterior curvity (mm <sup>-1</sup> )	Long axis (mm)	Short axis (mm)	Oblique angle (°)
<i>Olonbulukia tsaidamensis</i>	V23373 (SI 1)	(Wuzhong specimen)	–	late	right	0.0693	0.0543	45.3	26.5	19.7
	RV37008* (SI 4)	<i>O. tsaidamensis</i>	356	middle	right**	0.0691	0.794	55.4	32.3	16.0
	RV37093 (SI 5)	<i>O. tsaidamensis</i>	429	late	left	0.0918	0.0705	48.6	27.1	22.6
	RV37094 (SI 6)	Antilope gen. et sp. indet. III	514	late	left	0.0665	0.0476	46.4	27.7	25.3
<i>Olonbulukia</i> sp.	RV37095 (SI 7)	? <i>Olonbulukia</i> sp.	423	late	right	0.0795	0.0699	54.1	36.8	26.6
	RV37096 (SI 8)	Antilope gen. et sp. indet. II	479	late	left	0.0658	0.0840	38.1	25.7	–
	RV37097 (SI 9)	Antilope gen. et sp. indet. II	486	late	right	0.0751	0.0598	40.2	28.9	27.8
	RV37098 (SI 10)	Antilope gen. et sp. indet. II	499	late	left	0.0424	0.0623	38.1	25.9	27.7
<i>Qurlignoria cheni</i>	RV37100* (SI 11)	<i>Qurlignoria cheni</i>	441	late	right**	0.0336	0.0208	48.4	30.0	44.2
	RV37101 (SI 12)	<i>Qurlignoria cheni</i>	491	late	right	0.0469	0.0217	43.0	31.5	53.8
	RV37102 (SI 13)	<i>Qurlignoria</i> sp.	508	late	left**	0.0362	0.0245	39.1	27.5	56.4
	RV37103	<i>Qurlignoria</i> sp.	531	late	left	0.0227	0.0164	42.0	27.1	–
<i>Tussunnoria pseudibex</i>	RV37086* (SI 14)	<i>Tussunnoria pseudibex</i>	481	late	right	0.1022	0.0643	75.4	43.3	32.0
	RV37087 (SI 15)	<i>Tussunnoria pseudibex</i>	449	late	right	0.0543	0.0602	69.0	36.7	33.8
cf. <i>Pachytragus</i> sp.	RV37104 (SI 16)	Antilope gen. et sp. indet. I	492	late	left**	0.0667	0.0752	37.4	29.0	45.2
? <i>Protoryx</i> cf. <i>P. enanus</i>	RV37099 (SI 17)	Antilope gen. et sp. indet. IV	451	middle	right	0.0987	0.0881	40.9	30.7	19.4

and anterior style are strong and columnar-like, and are close to each other. The rib of the posterior style is weak.

In occlusal view (Fig. 3.4), the P4 is shorter and wider than the P3, and its width is greater than the length. The labial cone is medially positioned. The anterior and posterior styles are equally developed, and both labially protrude. The fossa is also anteriorly positioned like that of P3, and the shape of the fossa is inverted trapezoid. The lingual cone is relatively anteriorly positioned and displays a strong posterolingual crista. A small, shallow posterior fossa that cuts through the posterior enamel wall is also present, but this fossa is much smaller than that of the P3. In buccal view (Fig. 3.5), the buccal cone is also high and sharp, as is the posterior style (the top of the anterior style is broken). The ribs of the anterior and posterior styles are strong and columnar-like. The rib of the labial cone is also columnar-like, but it is relatively weak.

The left hemimandible is deeply weathered (Fig. 3.7–3.9). The tooth row is almost complete except regarding the third lobe of the m3. However, the tooth row is deeply worn. The premolar row is moderately long relative to the molar row (Table 2). The p2 is small. The anterolabial cristid is hook-like and extends from the mesolabial conid. The mesolingual conid is juxtaposed with the mesolabial conid, and a thin posterolingual cristid extends from the mesolingual conid. The posterolabial and posterolingual conids are interconnected.

The p3 is longer than the p2. The anterior conid and anterior stylid are fork-like, and link to the mesolabial conid by the anterolabial cristid. The transverse cristid is posteriorly oblique and connected to a slightly inflated mesolingual conid. A thin posterolingual cristid is also present. There is a groove between the mesolabial and posterolabial conids. The posterolabial and posterolingual conids are deeply worn and interconnected.

The p4 is much larger than the p3. However, morphology of the two teeth is very similar, except for the stronger mesolingual and posterolingual conids of the p4.

The m1 is so deeply worn that nearly all of the enamel is worn down. The shape is relatively quadrate, which is the only character that can be observed.

The two m2 lobes are of equal dimensions. The metaconid is more lingually prominent than the entoconid. The mesostylid and metastylid are weak, but this feature might be due to the deep wear. The entoconid protrudes posteriorly. The protoconid and hypoconid show rounded labial walls. A small ectostylid is present. The anterior cingulid (goat fold) is absent. No ribs can be seen on the lingual wall.

The third m3 lobe is broken. The anterior two lobes are narrower than the two lobes of the m2. Both metaconid and entoconid are slightly inflated. The mesostylid and metastylid are slightly protruded. The protoconid and hypoconid also have rounded labial walls, and a very small ectostylid occurs between

**Table 2.** Tooth measurements of Antilopinae gen. indet. sp. indet. from the Jiangcaichang locality. Measured at: \* = lingual cone; \*\* = mesolabial cone; \*\*\* = mesolingual cone; \*\*\*\* = anterior cone; \*\*\*\*\* = metaconid cone.

Number	Locus	Length (mm)	Width (mm)	Height (mm)
NGM WJCCD-10-N-006 (SI 1)	P3	12.72	11.33	13.50*
	P4	11.58	13.75	13.13*
IVPP V23373 (SI 3)	p2	7.7	4.55	5.33+**
	p3	9.95	10.64	6.34+***
	p4	12.33	6.62	5.90+****
	m1	11.99	9.24	4.43+*****
	m2	16.13	10.54	7.33+*****
	m3	~20	10.03	9.37+*****
	Premolar length (mm)	27.56	–	–
	Molar length (mm)	~45	–	–
	Tooth row length (mm)	~74.5	–	–
	Premolar/molar length ratio	0.612	–	–

the two conids. The anterior cingulid cannot be observed. As in the m2, no lingual ribs can be observed.

**Materials.**—IVPP V23374, a left cheek tooth row (p2–m3) with broken hemimandible, from the Jiancaichang locality, Northeast Quarry (IVPP no. NXWZ201502, coordinates as above); NGM WJCCD-10-N-006, right P3 and P4 with partial bone of the upper jaw, also from the Jiancaichang locality, coordinates not recorded.

**Remarks.**—The teeth remains from the Jancaicheng site, Wuzhong Fauna, coincide in morphology with Miocene stem caprines (Bohlin, 1935b). At this site, two stem caprines have been reported, *Olonbulukia tsaidamensis* and *Qurlignoria cheni* (Qiu et al., 1987). However, teeth of these two species are yet unknown to us. The new material might belong to either of the two species, or another uncovered one. Here we refer these teeth to Antilopinae gen. indet. sp. indet.

## Results

**Comparisons.**—The newly discovered horncore from the Jiancaichang locality (Wuzhong Fauna) shows great similarity to that of the type specimen of *Olonbulukia tsaidamensis* from the Qaidam Basin (Bohlin, 1937). Previous studies showed that horncore growth generates at the tip (Dove, 1935; Janis and Scott, 1987). It seems that a constant development velocity is retained and maintains a constant horncore curvature. The horncore body is vertically erect, and the vertical plane that passes through the long axis of the pedicle is close to the medial sagittal plane with an angle between the two planes (oblique angle of the pedicle) of 19.7° (16.0° in the type specimen) (Fig. 4.2). The pedicle is moderately long, and the supraorbital foramen is close to the elongation line of the anterior edge of the horncore body. These features are distinct from those of other stem caprine genera. For example, in *Qurlignoria*, the DAP/DT ranges 1.364–1.616, curvature ranges 0.020–0.034/mm, and the oblique angle of the pedicle ranges 44.2–56.4° (Table 1). These biometrics are greatly distinct from *Olonbulukia*. Furthermore, in *Qurlignoria*, the pedicle is relatively low, and the supraorbital foramen is more laterally remote to the horncore elongation line. In *Tossunnoria*, the horncore is very short and thick, and the two horncores greatly diverge, which substantially differs from that of *Olonbulukia*.

One difference between the Wuzhong specimen and the type specimen is that the Wuzhong specimen is smaller. All of the biometric differences are proportional, which is easily interpreted as a result of ontogeny. The Wuzhong specimen is comparable in size to some referred specimens from the ‘Qaidam Fauna,’ as described below. Furthermore, the postcornual fossa in the Wuzhong specimen is smaller and less clear than that of the Qaidam specimens. As a result, we are confident that the Wuzhong specimen belongs to *Olonbulukia tsaidamensis*.

**Biometric study of horncores from the ‘Qaidam Fauna’.**—Stem caprine remains from the ‘Qaidam Fauna’ reported by Bohlin (1937) (Fig. 5) represent the most abundant material from this group during the middle and early late Miocene of northern

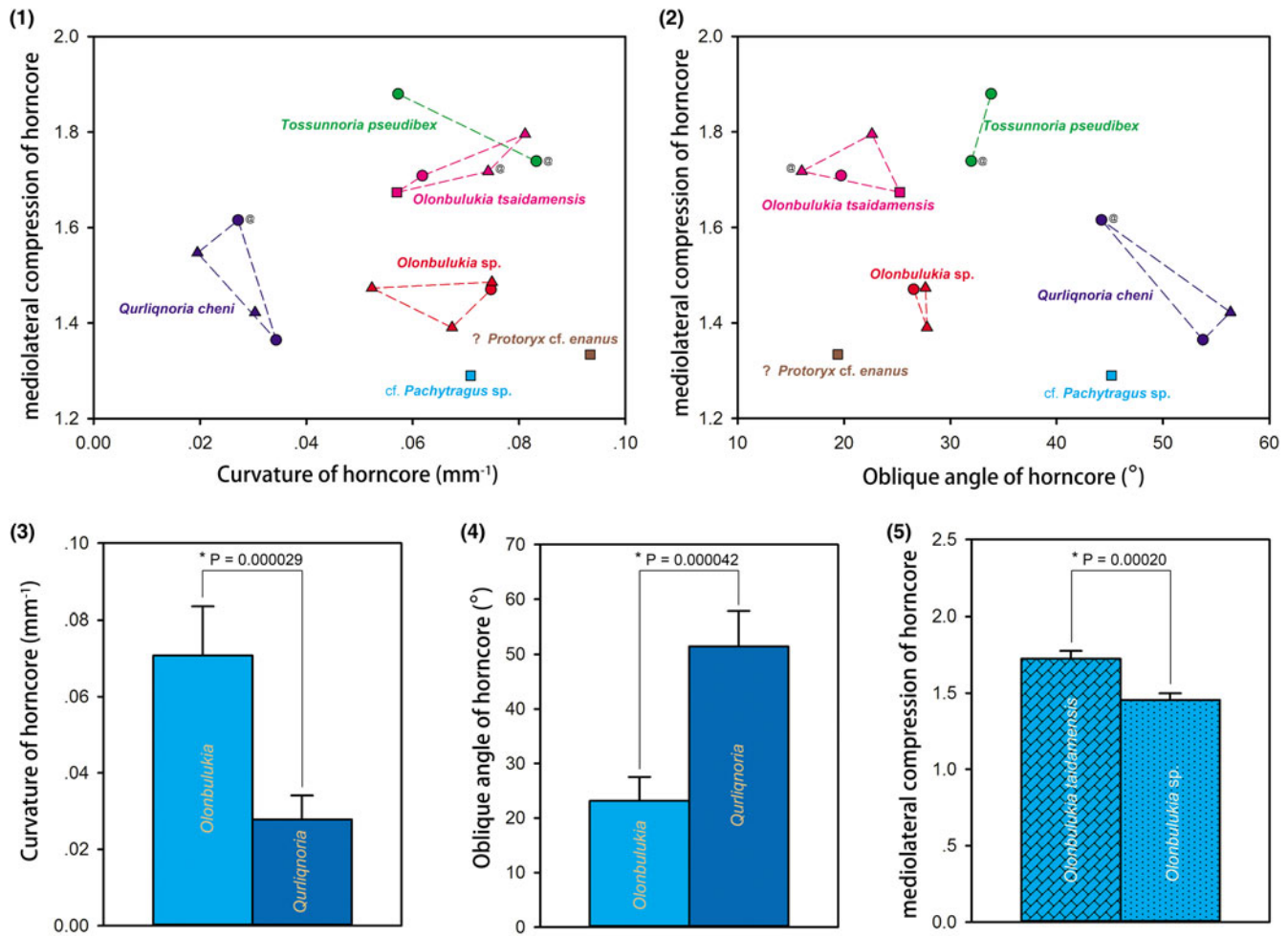
China. Bohlin (1937) reported a total of nine taxa based on the horncores. Except for the named *Olonbulukia tsaidamensis* (Fig. 5.1, 5.2, 5.13), *?Olonbulukia* sp. (Fig. 5.14), *Qurlignoria cheni* (Fig. 5.3, 5.4, 5.18), *Qurlignoria* sp. (Fig. 5.5, 5.6), and *Tossunnoria pseudibex* (Fig. 5.19–5.22) with relatively specialized horncore morphology, other unnamed taxa (i.e., ‘Antilope gen. et sp. indet.’ I [Fig. 5.9–5.11], II [Fig. 5.15–5.17], III [Fig. 5.12], and IV [Fig. 5.7, 5.8]) have relatively unspecialized horncores. This rigorous classification seems to inadequately account for individual variation, especially for elucidating ontogeny. Qiu et al. (1987) considered *Qurlignoria cheni*, and *Qurlignoria* sp. to be the same species.

We further studied the taxonomy of all groups in this fauna based on biometric analyses. In curvature vs. mediolateral compression plane (Fig. 4.1), the sample points are distributed in three regions. *Qurlignoria* samples cluster at the left half of the plane, which indicates straighter horncores in *Qurlignoria* than in other taxa. In the upper right part of the plane are the *Olonbulukia tsaidamensis* samples, which include the Wuzhong specimen and Antilope gen. et sp. indet. III., and the *Tossunnoria pseudibex* samples, indicating that these taxa have curved and strongly compressed horncores. In the lower right part of the plane are samples of the other taxa. It is noticeable that Antilope gen. et sp. indet. I and IV are located at the lowest right part of the plane, which indicates relatively rounded horncores with strong curvatures.

In oblique angle vs. mediolateral compression plane (Fig. 4.2), the *Qurlignoria* samples cluster in the right half with Antilope gen. et sp. indet. I, which indicates strongly oblique horncores. *Tossunnoria pseudibex* samples are located at the middle-upper part of the plane, indicating that the horncore oblique angle of *Tossunnoria* is intermediate between those of *Qurlignoria* and *Olonbulukia*. Other samples are in the right part of the plane and are separated into the upper *O. tsaidamensis* and Antilope gen. et sp. indet. III, and lower *O. sp.* and Antilope gen. et sp. indet. II, which is like curvature vs. mediolateral compression plane. Also as in curvature vs. mediolateral compression plane, Antilope gen. et sp. indet. IV is in the lower left corner of the plane and is relatively distant from the *Olonbulukia* sp. and Antilope gen. et sp. indet. II samples.

Based on the biometric analysis and morphological comparison of stem caprine horncores from the ‘Qaidam’ and Wuzhong faunas, we recognize the following groups:

- (1) *Tossunnoria pseudibex* (Fig. 5.19–5.23; SI 14, 15) shows the most specialized horncore morphology. The horncore is very short and thick (this feature is not reflected in our biometric analysis) with strong mediolateral compression.
- (2) All *Qurlignoria* specimens (Fig. 5.3–5.6, 5.18; SI 11–13) had straight horncores that are very oblique to the middle sagittal plane, which differs substantially from the other groups. We agree with the assertion of Qiu et al. (1987) that Bohlin’s *Q. cheni* and *Q. sp.* represent ontogenetic or individual variation and belong to one species.
- (3) Bohlin’s Antilope gen. et sp. indet. III, a complete left horncore (Fig. 5.12; SI 6), can be grouped with *Olonbulukia tsaidamensis* (Fig. 5.1, 5.2, 5.13; SI 4, 5). Bohlin (1937) also stated that this horncore is very similar to that of *Olonbulukia*, and might be a young individual. This horncore



legends:

*Olonbulukia tsaidamensis* (pink color): ●, Wuzhong specimen; ▲, Bohlin's *O. tsaidamensis*; ■, Bohlin's Antelope indet. III;

*Olonbulukia sp.* (red color): ●, Bohlin's ? *Olonbulukia sp.*; ▲, Bohlin's Antelope indet. II;

*Qurliqnorina cheni* (purple color): ●, Bohlin's *Q. cheni*; ▲, Bohlin's *Qurliqnorina sp.*; ●, *Tossonnorina pseudibex* (green color);

■, ? *Protoryx cf. enanus* (brown color) = Bohlin's Antelope indet. IV; ■, *Pachytragus sp.* (cyan color) = Bohlin's Antelope indet. I.

"@" denotes the type specimen and "\*" indicates statistical significance (significance level = 0.05)

**Figure 4.** Biometric data and statistics of stem caprine horncores from Wuzhong and Qaidam Basin: (1) bivariate plot of curvature (average curvature of the anterior and posterior edges of horncore) vs. mediolateral compression (DAP/DT); (2) bivariate plot of oblique angle (angle between the medial sagittal plane and the vertical plane passing through the long axis of the pedicle) vs. mediolateral compression; (3–5) arithmetic mean (bars) and standard deviation (errors) of curvature (3), oblique angle (4), and mediolateral compression (5) between two groups; in addition, student's t-tests were performed on each pair.

differs from the type specimen based on the more rapid tapering and shorter pedicle. As we discussed above, the horncore elongates from the bone tissue at the tip. In this process, curvature is maintained. The shorter pedicle can also be interpreted as a younger ontogenetic stage.

- (4) Bohlin's ?*Olonbulukia sp.* (Fig. 5.14; SI 7) and Antelope gen. et sp. indet. II (Fig. 5.15–5.17; SI 8–10) are similar based on biometric analysis. This group has similarly curved but less laterally compressed horncores than *Olonbulukia tsaidamensis*. The anterior keel of these horncores is relatively blunt relative to *O. tsaidamensis*. Bohlin's ? *Olonbulukia sp.* is larger than Antelope gen. et sp. indet. II. However, this difference can be interpreted as a result

of ontogeny. In the present paper, we refer to this group as *Olonbulukia sp.*

- (5) Bohlin's Antelope gen. et sp. indet. I (Fig. 5.9–5.11; SI 16) shows clearly distinct morphology from *Olonbulukia* and *Qurliqnorina*. The horncore oblique angle is large, close to that of *Q. cheni*, and the horncore curvature is strong and like that of *Olonbulukia*. The cross section displays an approximate round-cornered triangle (Fig. 5.11.1). A deep groove runs longitudinally along the posterior surface of the horncore. The morphology seems consistent with the diagnosis of *Pachytragus* Schlosser, 1904 from Samos, Greece (Schlosser, 1904) and is very similar to that of *P. crassicornis* Schlosser, 1904 (Schlosser,





**Figure 5.** Stem caprines published by Bohlin (1937), from the Qaidam Basin (photos taken on 3D digital models): (1, 2) *Olonbulukia tsaidamensis*, IVPP RV37008 (type specimen), brain case with both horncores, Bohlin's field no. 356 (also below), middle Miocene Olongbuluk Fauna (MMOF), in anterior (1) and lateral views (2); (3, 4) *Qurlignoria cheni*, IVPP RV37100 (type specimen), both horncores with frontal remains, no. 441, late Miocene Tuosu Fauna (LMTF), in anterior (3) and lateral views (4) (the distal part of both horncores has been lost, but were figured by Bohlin, 1937, pl. 3, figs. 6, 7); (5, 6) *Q. cheni*, IVPP RV37102, both horncores with frontal remains, no. 508, LMTF, in anterior (5) and lateral (6) views; (7, 8) *?Protoryx* cf. *P. enanus*, IVPP RV37099, right horncore with frontal remains, no. 451, MMOF, in lateral (7) and anterior (8) views, with cross section at the base (8.1) (anterior at top, lateral at right); (9–11) cf. *Pachytragus* sp., IVPP RV37104, both horncores with frontal remains, no. 492, LMTF, in anterior (9), lateral (10), and dorsal (11) views, with cross section at the base (11.1) (anterior at top, lateral at left); (12) *O. tsaidamensis*, IVPP RV37094, left horncore with frontal remains, no. 514, in lateral view, LMTF; (13) *O. tsaidamensis*, IVPP RV37093, left horncore with frontal remains, no. 429, in lateral view, LMTF; (14) *O. sp.*, IVPP RV37095, right horncore with frontal remains, no. 423, in lateral view, LMTF; (15) *O. sp.*, IVPP RV37096, right horncore, no. 479, in lateral view, LMTF; (16) *O. sp.*, IVPP RV37097, right horncore with frontal remains, no. 486, in lateral view, LMTF; (17) *O. sp.*, IVPP RV37098, left horncore with frontal remains, no. 499, in lateral view, LMTF; (18) *Q. cheni*, IVPP RV37101, right horncore with frontal remains, no. 491, in lateral view, LMTF; (19–22) *Tossunnoria pseudibex*, IVPP RV37086 (type specimen), brain case with both horncores, no. 481, in dorsal (19), lateroventral (20), ventral (21), and anterior (22) views, LMTF; (23) *T. pseudibex*, IVPP RV37087, fragmentary brain case with both horncores, no. 449, in anterior view, LMTF.

1904; Kostopoulos, 2005), but the specimen is smaller. Bibi and Güleç (2008) suggested that this specimen might belong to *Caprotragoides* Thenius, 1979 or *Tethytragus* Azanza and Morales, 1994. In our opinion, although the dimensions of the cross section fall into the range of the *Caprotragoides-Tethytragus-Gentrytragus* group (Bibi and Güleç, 2008, fig. 8), the subtriangular shape of the cross section and strong obliquity of horn pedicle differ from those in *Caprotragoides* and its affinities with an oval cross section and less obliquity (Köhler, 1987; Azanza and Morales, 1994; Bibi and Güleç, 2008). Because of the incompleteness of the specimen, we prefer to assign this specimen to cf. *Pachytragus* sp. rather than to *Caprotragoides* or *Tethytragus*.

- (6) Bohlin's Antelope gen. et sp. indet. IV (Fig. 5.7, 5.8; SI 17), an incomplete right horncore, also displays morphology distinct from *Olonbulukia* and *Qurliqnorina*. The horncore cross section is oval (Fig. 5.8.1) and more rounded than any *Olonbulukia* and *Qurliqnorina* specimen and have more backward bending. It is also anteriorly positioned relative to the orbit. This specimen occurred in the middle Miocene Olongbuluk Fauna, which is geologically older than most of the other *Olonbulukia* samples, except for the type specimen (Fig. 6). The horncore morphology is like that of the middle Miocene *Protoryx enanus* Köhler, 1987 from western Turk (Köhler, 1987), although the generic attribution of the *P. enanus* sample has been questioned (Gentry, 2000). The cross-sectional dimensions of Bohlin's Antelope gen. et sp. indet. IV also fall into the ranges for *P. enanus* (see Köhler, 1987). Alternatively, this specimen is also like *Caprotragoides* and *Tethytragus*, but is larger. Nevertheless, Köhler (1987) considered that *T. langai* Azanza and Morales, 1994 = *C. potwaricus* (Köhler, 1987), *P. enanus*, and *P. solignaci* (Robinson, 1972) belong to the same lineage. Here, we refer this specimen to ?*P. cf. P. enanus* because of the sample limitations.

We performed one-way ANOVAs to test if there are statistically significant differences in the biometric data between *Olonbulukia* and *Qurliqnorina*, and species within *Olonbulukia*. The results showed that the horncore curvature and the pedicle oblique angle differed strongly and significantly between the two genera ( $p < 0.05$  for both traits; Fig. 4.3, 4.4). Therefore, these two characters efficiently discriminate these two genera. Horncore mediolateral compression also strongly significantly differed between *O. tsaidamensis* and *O. sp.* ( $p < 0.05$ ; Fig. 4.5).

## Discussion

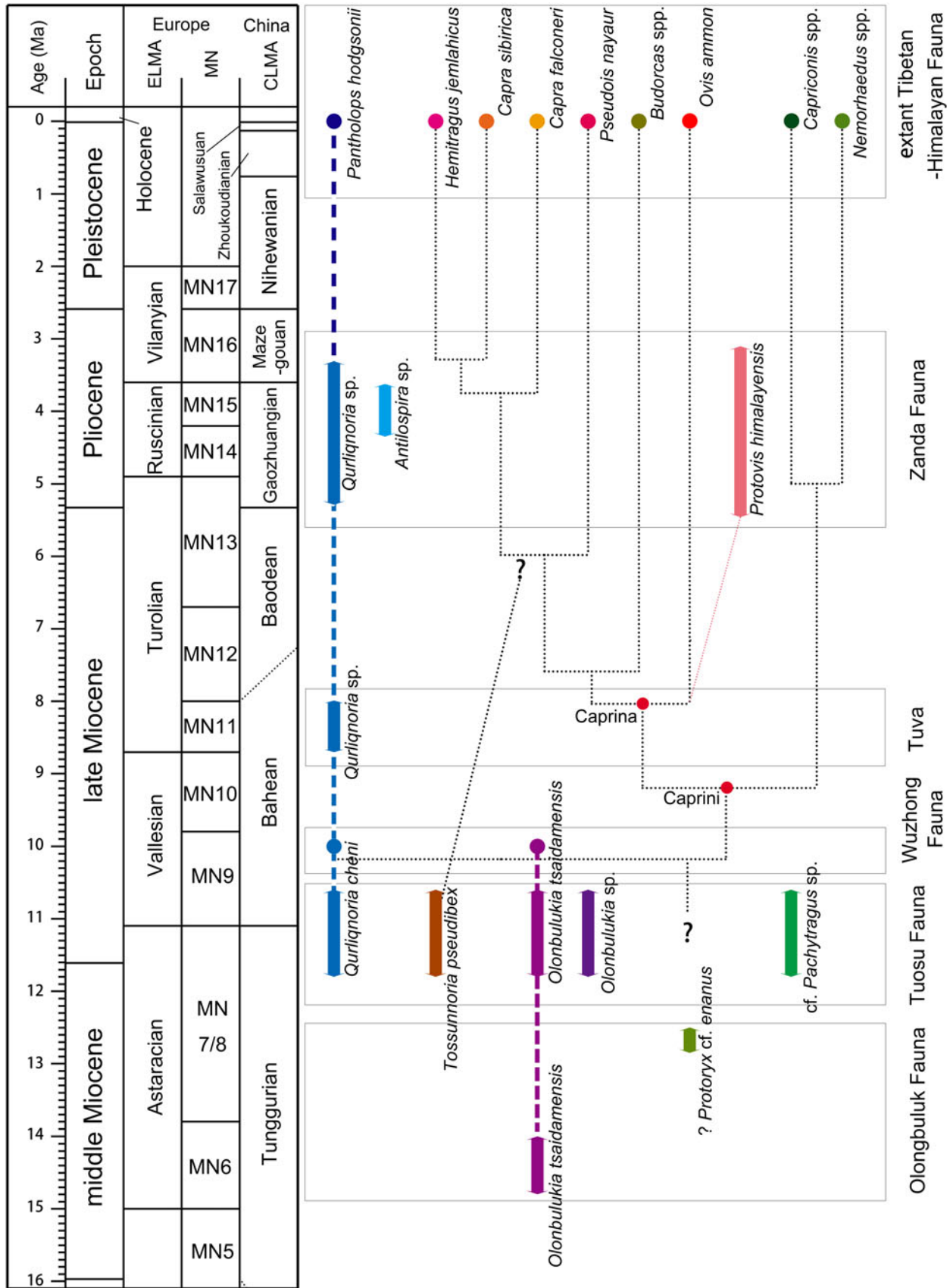
The Wuzhong specimen is the only *Olonbulukia* record aside from specimens from the type locality, the Qaidam Basin (Fig. 1). In the Qaidam Basin, the type specimen is from the middle Miocene Olongbuluk Fauna (ca. 15–12.5 Myr, see Wang et al., 2011; Fig. 6); whereas most of the other specimens are from the early late Miocene Tuosu Fauna (ca. 11–10 Myr, see Wang et al., 2011). The age of the Wuzhong Fauna is ca. 10 Ma, which corresponds to the beginning of the Ganhegou Formation (Shen et al., 2001; S.Q. Wang et al., 2016) (Fig. 6). Therefore, *O. tsaidamensis* is probably one of the earliest stem

caprines (if both the attribution and dating are correct) and crossed the middle/late Miocene boundary. Another stem caprine, *Qurliqnorina cheni*, was also reported in the Wuzhong Fauna (Qiu et al., 1987). However, we did not see this specimen. The sympatry of *Olonbulukia tsaidamensis* and *Qurliqnorina cheni* indicates a close relationship of the Tuosu and Wuzhong faunas, and the age of the two faunas should be very similar. Nevertheless, mammalian fauna from ca. 10 Ma is rare in northern China (Qiu et al., 1987). Another very specialized genus from the Tuosu Fauna, *Tsaidamotherium*, was also reported from the Yangcaiping locality, Linxia Basin (Shi, 2014) (Fig. 1). This locality was attributed to the Dashenggou Fauna. Therefore, further studies should be carried out to examine whether *Olonbulukia* and/or other stem caprine genera also existed in the Wuzhong and Dashenggou faunas.

The stem caprine assemblage from the 'Qaidam' and Wuzhong faunas displays a mixed appearance. Although *Olonbulukia* seems to have no modern descendants, Gentry (2000) proposed that *Olonbulukia* could be related to *Protoryx carolinae* Major, 1891 from the Pikemi fauna (Turolian) of Greece. *Protoryx* is an unspecialized Turolian caprine that is widely distributed across eastern Europe, northern Africa, western and central Asia, and even China (Bohlin, 1935b; Gentry, 1971, 2000; Köhler, 1987; Dmitrieva and Serdyuk, 2011). Two other taxa—cf. *Pachytragus* sp. and ?*Protoryx cf. P. enanus*—display strong morphological similarity to the western analogues *Pachytragus crassicornis* and *Protoryx enanus* from the late and middle Miocene of the Mediterranean region (Schlosser, 1904; Köhler, 1987), which also indicates an exchange of caprine related groups between the Mediterranean and eastern Asian regions during this period. ?*Protoryx cf. P. enanus* might be very closely related to the ancestor of the Caprini-Hippotragini-Alcelaphini clade, because it is very similar to *Tetrytragus* and *Caprotragoides*, as discussed by Gentry (2000) and Bibi et al. (2009).

Alternatively, *Qurliqnorina* survived longer, as was reported from Kyzyl, Tuva (MN 11, 12; Dmitrieva and Serdyuk, 2011) and the Zanda Basin (MN 13–15; Deng et al., 2011; Wang et al., 2013) (Fig. 1). This genus was considered the ancestor of the extant Tibetan antelope (*Pantholops hodgsonii*) (Gentry, 1968, 2000; Deng et al., 2011). *Tossunnoria pseudibex* was also thought to be related to the extant Himalayan tahr (*Hemitragus jemlahicus*) or goats (*Capra* spp.) (Bohlin, 1937; Gentry, 2000). *Qurliqnorina* and *Tossunnoria* records are restricted to eastern Asia and the Tibetan Plateau. Therefore, the presence of *Qurliqnorina* and *Tossunnoria* from the Tuosu Fauna might indicate an early endemic radiation of stem caprines that eventually adapted the cold and dry habitats induced by the rising Tibetan Plateau.

Deng et al. (2011) demonstrated a scenario in which the Pliocene Zanda fauna on the Tibetan Plateau (Zanda Basin, Figs. 1, 6) had pre-emptively adapted to cold weather, and then expanded to the northern tundra during the Pleistocene Ice Ages. In this fauna, one taxon—*Protovis himalayensis* Wang, Xie, and Takeuchi, 2016 (5.24–3.10 Myr)—was shown to be a direct ancestor of worldwide species of *Ovis* Linnaeus, 1758 (X.M. Wang et al., 2016) (Fig. 6). Based on a calibrated molecular phylogeny, *Ovis* is the most basal taxon in the clade Caprina, which consists of at least *Ovis*, *Ammotragus* Blyth, 1840, *Pseudois* Hodgson, 1846, *Hemitragus* Hodgson, 1841, and *Capra* Linnaeus, 1758. The occurrence age of Caprina is



**Figure 6.** Stem and crown Caprini succession in the pan-Tibetan region and their possible phylogenetic relationship. Extant Tibetan-Himalayan caprines after Castelló (2016). Phylogeny and differential ages after Bibi (2013) and X.M. Wang et al. (2016). CLMA = Chinese Land Mammal Age; ELMA = European Land Mammal Age; MN = European Mammal Neogene System.

ca. 8 Ma (Bibi, 2013). Ropiquet and Hassanin (2004) demonstrated that caprines might have originated in the isolated mountains of the Mediterranean mega-archipelago; however, this is somewhat debatable. In our opinion, the Tibetan Plateau, with the formation of isolated mountainous terrains, is a more likely area for caprine origin than the Mediterranean mega-archipelago. Based on the occurrence of *Protovis* Wang, Xie, and Takeuchi, 2016 on the Tibetan Plateau, the common ancestor of *Caprina* could have evolved ca. 8 Ma on and/or around the rising Tibetan Plateau (except for the Indian subcontinent). The stem caprines in the Tuosu and Wuzhong faunas ca. 10 Ma provide ideal precursors of *Caprina*, because there are both small temporal and spatial gaps (Fig. 6). *Olonbulukia tsaidamensis* seems a bit too specialized to be the ancestor of *Caprina* because of the substantially compressed horncore. Although *Tossunoria* was thought to be related to *Hemitragus* and/or *Capra*, it also displayed a specialized horncore, which weakened its potential as an ancestor of *Caprina*. Alternatively, nonspecialized horncores (e.g., *?Protoryx* cf. *P. enanus*, cf. *Pachytragus* sp., and *Olonbulukia* sp. in the present study) are ideal candidates for elucidating the origin of *Caprina*.

According to Deng and Ding (2015), the Tibetan Plateau reached a relatively high elevation during the middle Miocene, which hindered megamammalian faunal exchange between southern and northern sides along the Tibetan Plateau. Simultaneously, a stem caprine assemblage (as we see in the ‘Qaidam’ and Wuzhong faunas) was shaped along the northern Tibetan Plateau and lasted until at least the early late Miocene. This stem caprine assemblage shows a composite appearance of two groups. One relatively specialized group includes at least *Qurlignoria cheni* and *Tossunoria pseudibex*, which are related to some endemic Tibetan taxa; the other even group perhaps includes *?Protoryx* cf. *P. enanus* and cf. *Pachytragus* sp., possibly with *Olonbulukia* sp., pertaining to the common caprines that spread across Eurasia and Mediterranean regions in the Turolian. In particular, certain members might have given rise to the extant *Caprina*, which is an interesting issue and should be studied further.

## Conclusions

- (1) The new horncore from Jiancaichang locality, Wuzhong, northern China is similar to *Olonbulukia tsaidamensis* that also occurred in the ‘Qaidam Fauna.’ With the occurrence of *Qurlignoria cheni*, the Wuzhong Fauna shows high similarity to the Tuosu Fauna and is similar in age.
- (2) The stem caprine horncores from the ‘Qaidam Fauna’ can be divided into the following groups based on biometric analyses. *Tossunoria pseudibex* is the same as Bohlin’s definition; *Qurlignoria cheni* includes Bohlin’s *Q. cheni* and *Q. sp.*; *Olonbulukia tsaidamensis* consists of Bohlin’s *O. tsaidamensis* and Antelope gen. et sp. indet. III; *Olonbulukia* sp. includes Bohlin’s *?O. sp.* and Antelope gen. et sp. indet. II; Bohlin’s Antelope gen. et sp. indet. IV can be attributed to *?Protoryx* cf. *P. enanus*; and Bohlin’s Antelope gen. et sp. indet. I can be attributed to cf. *Pachytragus* sp.
- (3) The stem caprine assemblages from the ‘Qaidam Fauna’ show a combined appearance. *Qurlignoria* and *Tossunoria* are probably related to some extant Tibetan endemic caprine species. Other taxa belong to other Turolian caprine species

and might have given rise to the extant *Caprina*. These results indicate a pan-Tibetan origin of *Caprina* and indicate a pan-Tibetan evolutionary pattern of some megafaunas prior to dispersal from Tibet.

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## Accessibility of supplemental data

Data available from the Dryad Digital Repository: <http://doi.org/10.5061/dryad.736cj0j>.

- SI 1. *Olonbulukia tsaidamensis*, IVPP V23373, right horncore with fragmentary frontal bone remains.
- SI 2. Antilopinae gen. indet. sp. indet., NGM WJCCD-10-N-006, right P3 and P4.
- SI 3. Antilopinae gen. indet. sp. indet., IVPP V23374, right hemimandible with p2–m3 tooth row.
- SI 4. *Olonbulukia tsaidamensis*, IVPP RV37008 (type specimen, Bolin’s field number [same below], no. 356), brain case with both horncores.
- SI 5. *Olonbulukia tsaidamensis*, IVPP RV37093 (no. 429), left horncore with frontal remains.
- SI 6. *Olonbulukia tsaidamensis*, IVPP RV37094 (no. 514), left horncore.
- SI 7. *Olonbulukia* sp., IVPP RV37095 (no. 423), right horncore with frontal remains.
- SI 8. *Olonbulukia* sp., IVPP RV37096 (no. 479), right horncore.
- SI 9. *Olonbulukia* sp., IVPP RV37097 (no. 486), right horncore with frontal remains.
- SI 10. *Olonbulukia* sp., IVPP RV37098 (no. 499), left horncore with frontal remains.
- SI 11. *Qurlignoria cheni*, IVPP RV37100 (type specimen, no. 441), both horncores with frontal remains.
- SI 12. *Qurlignoria cheni*, IVPP RV37101 (no. 491), right horncore with frontal remains.
- SI 13. *Qurlignoria cheni*, IVPP RV37102 (no. 508), both horncores with frontal remains.
- SI 14. *Tossunoria pseudibex*, IVPP RV37086 (type specimen, no. 481), brain case with both horncores.
- SI 15. *Tossunoria pseudibex*, IVPP RV37087 (no. 449), fragmentary brain case with both horncores.
- SI 16. cf. *Pachytragus* sp., IVPP RV37099 (no. 492), right horncore with frontal remains.

SI 17. ?*Protoryx* cf. *P. enanus*, IVPP RV37104 (no. 451), both horncores with frontal remains.

## References

- Abel, C., 1826, On the supposed unicorn of the Himalayas: *Philosophical Magazine and Journal*, v. 68, p. 232–234.
- Azanza, B., and Morales, J., 1994, *Tethyragus* nov. gen. et *Gentryragus* nov. gen.: deux nouveaux bovidés (Artiodactyla, Mammalia) du Miocène moyen, relations phylogénétiques des bovidés anté-vallésiens: *Proceedings of the Koninklijke Akademie van Wetenschappen*, v. 97, p. 249–282.
- Bärmann, E.V., and Rössler, G.E., 2011, Dental nomenclature in Ruminantia: towards a standard terminological framework: *Mammalian Biology*, v. 76, p. 762–768, doi:10.1016/j.mambio.2011.07.002.
- Bibi, F., 2013, A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics: *BMC Evolutionary Biology*, v. 13, p. 166, doi:10.1186/1471-2148-13-166.
- Bibi, F., and Güleç, E.S., 2008, Bovidae (Mammalia: Artiodactyla) from the late Miocene of Sivas, Turkey: *Journal of Vertebrate Paleontology*, v. 28, p. 501–519, doi:10.1671/0272-4634(2008)28[501:BMAFTL]2.0.CO;2.
- Bibi, F., Bukhsianidze, M., Gentry, A.W., Geraads, D., Kostopoulos, D., and Vrba, E.S., 2009, The fossil record and evolution of Bovidae: state of the field: *Palaeontologia Electronica*, v. 12, p. 1–10.
- Blyth, E., 1840, Letter February 11: 1840 Proceedings of the Zoological Society of London, v. 1, p. 11–19.
- Bohlin, B., 1935a, *Tsaidamotherium hedini*, n. g., n. sp.: *Geografiska Annaler*, v. 71, p. 66–74.
- Bohlin, B., 1935b, Cavicomer der Hipparion-Fauna Nord-Chinas: *Palaeontologia Sinica*, ser. C, v. 9, p. 1–166.
- Bohlin, B., 1937, Eine tertiäre Säugetier-Fauna aus Tsaidam: *Palaeontologia Sinica*, ser. C, v. 14, p. 1–111.
- Castelló, R.J., 2016, Bovids of the World: Antelopes, Gazelles, Cattle, Goats, Sheep, and Relatives: Princeton, New Jersey, Princeton University Press, 664 p.
- Chen, G.F., and Zhang, Z.Q., 2009, Taxonomy and evolutionary process of Neogene Bovidae from China: *Vertebrata Palasiatica*, v. 47, p. 265–281.
- Deng, T., and Ding, L., 2015, Paleo-altimetry reconstructions of the Tibetan Plateau: progress and contradictions: *National Science Review*, v. 93, p. 92–95, doi:10.1093/nsr/nwv062.
- Deng, T., Wang, X.M., Fortelius, M., Li, Q., Wang, Y., Tseng, Z.J., Takeuchi, G.T., Saylor, J.E., Säilä, L.K., and Xie, G.P., 2011, Out of Tibet: Pliocene woolly rhino suggests high-plateau origin of ice age megaherbivores: *Science*, v. 333, p. 1285–1288, doi:10.1126/science.1206594.
- Dmitrieva, E.L., and Serdyuk, N.V., 2011, Hippotraginae (Bovidae, Artiodactyla, Mammalia) from the late Miocene of Tuva: *Paleontological Journal*, v. 45, p. 665–673, doi:10.1134/S0031030111060050.
- Dove, W.F., 1935, The physiology of horn growth: a study of the morphogenesis, interaction of tissues, and the evolutionary processes of a Mendelian recessive character by means of transplantation of tissues: *The Journal of Experimental Zoology*, v. 69, p. 347–405.
- Geist, V., 1987, On the evolution of the Caprinae, in Lovari, S., ed., *The Biology and Management of Mountain Ungulates*: London, Croom Helm, p. 3–40.
- Gentry, A.W., 1968, The extinct bovid genus *Qurlignoria* Bohlin: *Journal of Mammalogy*, v. 49, p. 769.
- Gentry, A.W., 1971, The earliest goats and other antelopes from Samos *Hipparion* Fauna: *Bulletin of the British Museum (Natural History)*, *Geology*, v. 20, p. 229–296.
- Gentry, A.W., 1992, The subfamilies and tribes of the family Bovidae: *Mammal Review*, v. 22, p. 1–32.
- Gentry, A.W., 2000, Caprinae and Hippotragini (Bovidae, Mammalia) in the upper Miocene, in Vrba, E.S., and Schaller, G.B., eds., *Antelopes, Deer and Relatives: Fossil Record, Behavioral Ecology, Systematics and Conservation*: New Haven, Connecticut, Yale University Press, p. 65–83.
- Gray, J.E., 1821, On the natural arrangement of vertebrate animals: *London Medical Repository*, v. 15, p. 296–310.
- Hassanin, A., Delsuc, F., Ropiquet, A., Hammer, C., Jansen van Vuuren, B., Matthee, C., Ruiz-Garcia, M., Catzeffis, F., Areskoug, V., Nguyen, T.T., and Couloux, A., 2012, Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes: *Comptes Rendus Biologies*, v. 335, p. 32–50, doi:10.1016/j.crv.2011.11.002.
- Hodgson, B.H., 1841, Classified catalogue of mammals of Nepal, corrected to end of 1840, first printed in 1832: *Calcutta Journal of Natural History*, v. 2, p. 212–221.
- Hodgson, B.H., 1846, Description of a new species of Tibetan antelope: *Journal of the Asiatic Society of Bengal*, v. 15, p. 334–343.
- Janis, C.M., and Scott, K.M., 1987, The interrelationships of higher ruminant families with special emphasis on the members of the Cervidae: *American Museum Novitates*, v. 2893, p. 1–85.
- Kingdon, J., 1982, *East African Mammals: An Atlas of Evolution in Africa*, IIC: London, Academic Press, 404 p.
- Köhler, M., 1987, Boviden des türkischen Miozäns (Känozoikum und Braunkohlen der Türkei): *Paleontologia i Evolució*, v. 21, p. 133–246.
- Kostopoulos, D.S., 2005, The Bovidae (Mammalia, Artiodactyla) from the late Miocene of Akkaşdağı, Turkey: *Geodiversitas*, v. 27, p. 747–791.
- Lartet, E., 1837, Notice sur les ossements fossiles des terrains tertiaires de Simorre, de Sansan, etc., et sur la découverte récente d'un emâchoire de singe fossile: *Comptes Rendus Hebdomadaires l'Academie de Sciences*, v. 4, p. 1–583.
- Linnaeus, C., 1758, *Systema Naturae per Regna Tria Naturae* (tenth edition), Volume 1, *Regnum Animale*: Stockholm, Laurentii Salvii, 824 p.
- Major, C.I.F., 1891, Considérations nouvelles sur la faune des vertébrés du Miocène supérieur dans l'Île de Samos: *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, Paris, v. 113, p. 608–610.
- Owen, R., 1848, The Archetype and Homologies of the Vertebrate Skeleton: London, J. van Voorst, 203 p.
- Qiu, Z.X., Ye, J., and Jiang, Y.J., 1987, Some mammalian fossils of Bahe Stage from Wuzhong, Ningxia: *Vertebrata Palasiatica*, v. 25, p. 46–56.
- Robinson, P., 1972, *Pachytragus solignaci*, a new species of caprine bovid from the late Miocene Beglia Formation of Tunisia: *Notes du Service Géologique de Tunisie*, v. 37, p. 73–94.
- Roger, O., 1904, Wirbeltierreste aus dem Obermiozän der bayrisch-schwäbischen Hochebene, V: *Bericht des Naturwissenschaftlichen Vereins für Schwaben und Neuburg*, Augsburg, v. 36, p. 1–19.
- Ropiquet, A., and Hassanin, A., 2004, Molecular phylogeny of caprines (Bovidae, Artiodactyla): the question of their origin and diversification during the Miocene: *Journal of Zoological Systematics and Evolutionary Research*, v. 43, p. 49–60, doi:10.1111/j.1439-0469.2004.00290.x.
- Schlosser, M., 1904, Die fossiles Cavicornis von Samos: *Beiträge zur Paläontologie und Geologie Österreich-Ungarn*, v. 17, p. 21–118.
- Shen, X.H., Tian, Q.J., Ding, G.Y., Wei, K.B., Chen, Z.W., and Chai, C.Z., 2001, The late Cenozoic stratigraphic sequence and its implication to tectonic evolution, Hejiakouzi Area, Ningxia Hui Autonomous Region: *Earthquake Research in China*, v. 17, p. 156–166.
- Shi, Q.Q., 2014, New species of *Tsaidamotherium* (Bovidae, Artiodactyla) from China sheds new light on the skull morphology and systematics of the genus: *Science China: Earth Science*, v. 57, p. 258–266, doi:10.1007/s11430-013-4722-2.
- Smith, C.H., 1826–1827, The seventh order of the Mammalia: The Ruminantia, in Griffith, E., Smith, C.H., and Pidgeon, E., eds., *The Animal Kingdom, the Class Mammalia, Arranged by the Baron Cuvier, with Specific Descriptions*: London, William Clowes, Charing Cross, v. 4, p. 1–498.
- Thenius, E., 1979, Zur systematischen Stellung und verbreitung von *Gazella stehlini* aus dem Miozän Europas: *Anzeiger der Österreichische Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse*, v. 116, p. 9–13.
- Wang, S.Q., Zong, L.Y., Yang, Q., Sun, B.Y., Li, Y., Shi, Q.Q., Yang, X.W., Ye, J., and Wu, W.Y., 2016, Biostratigraphic subdividing of the Neogene Dingjia'ergou mammalian fauna, Tongxin County, Ningxia Province, and its background for the uplift of the Tibetan Plateau: *Quaternary Sciences*, v. 36, p. 789–809, doi:10.11928/j.issn.1001-7410.2016.0402.
- Wang, X.M., Xie, G.P., Li, Q., Qiu, Z.D., Tseng, Z.J., Takeuchi, G.T., Wang, B.Y., Fortelius, M., Rosenström, F.A., Wahlquist, H., Downs, W.R., Zhang, C.F., and Wang, Y., 2011, Early explorations of Qaidam Basin (Tibetan Plateau) by Birger Bohlin—reconciling classic vertebrate fossil localities with modern biostratigraphy: *Vertebrata Palasiatica*, v. 49, p. 285–310.
- Wang, X.M., Li, Q., Xie, G.P., Saylor, J.E., Tseng, Z.J., Takeuchi, G.T., Deng, T., Wang, Y., Hou, S.K., Liu, J., Zhang, C.F., Wang, N., and Wu, F.X., 2013, Mio-Pleistocene Zanda Basin biostratigraphy and geochronology, pre-Ice Age fauna, and mammalian evolution in western Himalaya: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 374, p. 81–95, doi:10.1016/j.palaeo.2013.01.007.
- Wang, X.M., Xie, G.P., and Takeuchi, G., 2016, Out of Tibet: an early sheep from the Pliocene of Tibet, *Protovis himalayensis*, gen. et sp. nov. (Bovidae, Caprinae), and origin of Ice Age mountain sheep: *Journal of Vertebrate Paleontology*, v. 5, p. 1–12, doi:10.1018/02724634.2016.1169190.

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