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Primitive Tibetan antelope, *Qurlignoria hundesiensis* (Lydekker, 1881) (Bovidae, Artiodactyla), from Pliocene Zanda and Kunlun Pass basins and paleoenvironmental implications

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Abstract

Well adapted to extremely cold winters (hypothermia) and low oxygen (hypoxia), the Tibetan antelope (or chiru), *Pantholops hodgsonii* Abel, is an iconic species in the Tibetan Plateau. Its extinct relative, *Qurlignoria* Bohlin, represents the earliest endemic Tibetan mammal going back to the late Miocene, suggesting a long process of adaptations within Tibetan Plateau for ~ 10 million years. We reexamine holotype materials of *Q. hundesiensis* (Lydekker) from the British Museum, originally discovered by British explorers in the Himalayas in the early 1800s, and new materials recently discovered in the Pliocene strata of Zanda Basin, southwestern Tibet. We refer additional horncore and dental materials from the Kunlun Pass Basin at 4,700–4,900 m asl, and leverage these new data to place *Q. hundesiensis* within modern biostratigraphic and paleoenvironmental frameworks. Although *Qurlignoria* remains the best candidate of a distant sister-group of living *Pantholops*, the Pliocene representatives offer no sign of transitions to living chiru. We infer that the *Qurlignoria* lineage has persisted throughout late Miocene and Pliocene of the Tibetan Plateau in a chronospecies succession, i.e., *Q. cheni* to *Q. hundesiensis*. The Pliocene *Qurlignoria* probably did not directly give rise to *Pantholops*, suggesting that a direct ancestor of *Pantholops* is yet to be found. We discuss the paleoenvironmental and paleoelevation implications of the new *Qurlignoria* materials and analysis for Tibetan Plateau faunal evolution.

Keywords *Qurlignoria* · Bovidae · Zanda Basin · Tibetan Plateau · Elevation · Paleoenvironment

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Introduction

The Tibetan antelope (or chiru, Tibetan language for antelope), *Pantholops hodgsonii* (Abel, 1826), is an iconic species in the Tibetan Plateau. Known for its adaptations to the harsh environments in the high plateau, such as cold winters (hypothermia), low oxygen (hypoxia), and high UV radiation, *Pantholops* is the only endemic genus of large mammals on the Tibetan Plateau (Wang et al. 2014b). This endemism at the generic level is also consistent with its oldest fossil records, going back to *Qurlignoria cheni* in the late Miocene, a taxon with the longest history within the plateau (Tseng et al. 2022).

Despite living at very high altitudes, where atmospheric oxygen drops to about half that of the sea level, the chiru is capable of a sustained speed of 80 km/hour and a top speed of 100–120 km/hour (Zhang et al. 2003) maintained for over 800 m (Schaller 1996). This is remarkable because the chiru is one of a few medium-sized mammals in the high Tibet that is not dependent on the ability to scale steep cliffs for

escape from predators. Instead, it is adapted to cold deserts and alpine steppes of the Tibetan Plateau, relying on speed and endurance to escape over open-terrain from Tibetan grey wolves, its principal predator. In addition, chirus must endure Arctic-style snowstorms, which are the main cause of mortality in their populations (Schaller 1996, 1998; Smith and Xie, 2013). Such a feat in surviving extreme hypothermia and hypoxia conditions is aided by phenotypic adaptations, such as an enlarged air sac in the nasal passage (Hodgson 1833; Schaller 1998; Leslie and Schaller 2008) and dense under furs (Rollins and Hall 1999) for superb thermal insulation, and at molecular and developmental levels, for enhanced oxygen transport in the blood (Ge et al. 2013; Ma et al. 2014; Signore and Storz 2020).

Perhaps as a result of such extraordinary adaptations, the chirus are among the most successful large mammals in high Tibet, and along with the Tibetan yak, have come to symbolize the mammal fauna in Tibetan Plateau. Early explorers often remarked about great flocks of Tibetan chirus roaming across the plains of Qiangtang region (Hedin 1922:130, 237) and “there could not have been less than 15,000 or 20,000 visible ...”, “as far as the eye could reach” (Rawling 1905:85). Massive female herds are known to migrate great distances to give birth (Schaller 1996, 1998), a behavior that renders populations vulnerable to habitat fragmentation and human developments in the plateau (Buho et al. 2011). Chiru populations were greatly reduced in numbers due to illegal poaching in last century and was listed as seriously endangered by the International Union for Conservation of Nature (IUCN). In recent years under more strict protective measures, the chiru is recovering and has been downgraded to “near threatened” by IUCN in 2017.

Recently, Tseng et al. (2022) documented additional late Miocene records of *Qurlignoria* from the Qaidam Basin, placing the earliest and most primitive species, *Qurlignoria cheni*, in a modern phylogenetic context of possibly in a direct ancestral relationship to the living chiru. In this paper, we describe Pliocene materials from the Kunlun Pass and Zanda basins discovered during the past 20 years by our field expeditions on the Tibetan Plateau (Figs. 1 and 2). We also synthesize historical records from the Zanda Basin, going back almost 200 years, and suggest potential associations of horncores and dental materials. With these critical records, we are in a better position to evaluate the evolution of this iconic lineage, as well as its historical importance in the debates on paleoelevations and environments of the Tibetan Plateau.

Institutional and site abbreviations

BMNH, Natural History Museum (formerly British Museum of Natural History), London; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing; **KIZ**, Kunming Institute of Zoology,

Chinese Academy of Sciences, Kunming; **KL**, Kunlun Pass Basin; **MNHN**, Muséum national d'Histoire naturelle, Paris; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **ZD**, Zanda Basin.

A brief history of studies in Zanda Basin

Due to the combination of intense interests during the “Great Game” geopolitical rivalry between imperial Russia and the newly industrialized British Empire, the lofty height of the Himalaya and vertebrate fossils from such an exotic locale, the events that led to the discoveries of Hundes (also known as Tsaprang, or Tsaparang, in literatures of early explorers) were documented in early scientific literatures and popular accounts in the English language. Perhaps fittingly, fossils of the *Qurlignoria-Pantholops* lineage became the very first scientific discoveries in Tibetan vertebrate paleontology (Wang et al. 2020a), dating to as early as 1830s (Traill 1832; Royle 1839), substantially earlier than scientific documentation of the “dragon bones” in China (e.g., Owen 1870). The following is a brief summary related to the holotype of *Qurlignoria hundesiensis*, and for a more in depth narrative, see Wang et al. (2020a).

Moorcroft (1816) was often credited for being an early pioneer of Zanda Basin exploration who produced accurate topographic map of the “Hundes Plains”. Although Moorcroft did not personally find vertebrate fossils, within a few years of his expedition, Reverend Buckland (1823:122) reported “bones of horses and deer” brought to Royal College of Surgeons in London by Captain W. S. Webb, who “procured them from the Chinese Tartars of Daba.” Traill (1832), Commissioner of the Affairs of Kumaon (of then British India), remarked that native traders near the Niti Pass were known to sell fossils ‘Bijli Hár’, or lightning bones, and had acquired a collection that were presented to the Geological Society of London via Henry Colebrooke. Included in this collection were fragments of a partial cranium of a goat or deer-like mammal (Herbert 1831). Furthermore, Herbert (1831:270) personally visited the fossil sites where Traill’s collection was presumably produced, “not far from the town of Dumpu [Dongba in modern spelling]... several days journey beyond the line of snowy peaks forming the zone of greatest elevation”. Webb and Traill’s specimens were illustrated by Royle (1839:xxix, pl. III), which later became the basis of a new species, *Pantholops hundesiensis* (Lydekker, 1881, 1901). The fossils fueled a controversy over paleoenvironments of Zanda Basin and formed the basis for the first attempt to bring vertebrate fossils to bear on paleoelevation (Falconer 1868; Lydekker 1881, 1901), predating an independent but similar argument inspired by *Hipparion* fossils from Gyirong Basin more than a century later (Huang and Ji 1979; Huang et al. 1980; Ji et al. 1980).

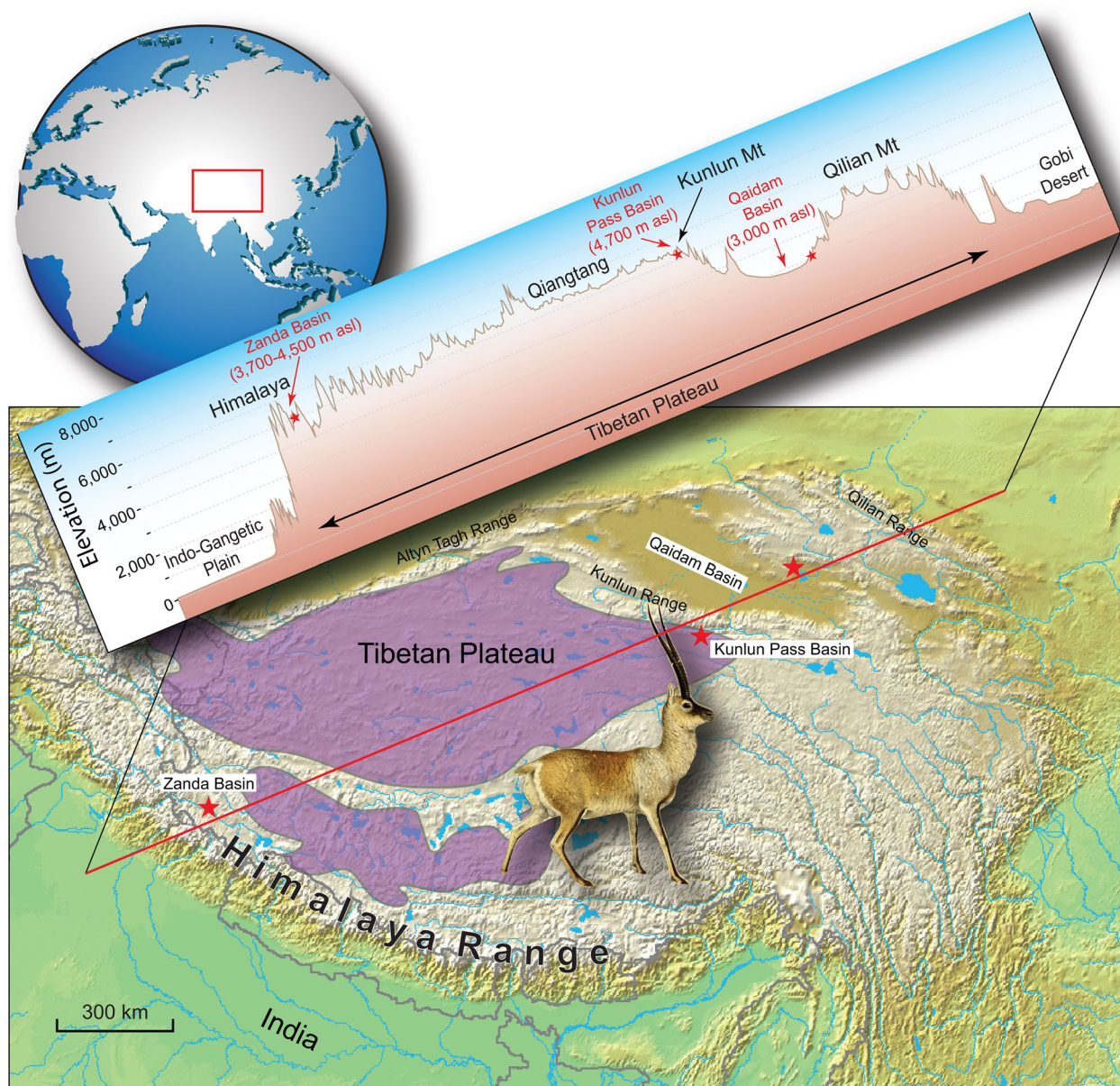


Fig. 1 Map of three major Neogene basins (red stars) in Tibetan Plateau discussed in this paper and an elevation profile passing through these three basins, showing altitudinal relationships. Purple areas are distributions of modern chirus, based on Leslie and Schaller (2008).

After a long hiatus of more than 150 years, scientific explorations resumed by the First Comprehensive Tibetan Plateau Scientific Expedition by the Chinese Academy of Sciences in 1973–1980. Several paleontologic publications resulted from this expedition, describing an extinct giraffe palate, *Palaeotragus microdon* (Zhang et al., 1981), and a new species of three-toed horse, *Hipparion zandaense* (Li and Li, 1990), as well as the first attempt at a paleomagnetic age correlation (Qian 1999). However, due to physical inaccessibility and prohibitive expense, the Chinese Academy

Modern chiru illustration from Sclater and Thomas (1897). Topographic map downloaded from GeoMapApp (Version 2.6.14) (2021) under CC BY license. Elevation profile generated by Google Earth Pro (Version 7.3.3.7786) (2020) and vertical exaggeration is ~57:1

expeditions were limited to small-scale explorations in the Zanda Basin and besides the isolated fossils described, knowledge about the Zanda fauna remained out of reach.

It is not until the 2000s, nearly 200 years after pioneer explorers and scientists set foot in the Zanda Basin, that our teams were finally able to conduct five paleontologic expeditions in Zanda Basin from 2006 to 2012 (Wang et al. 2013b). Much, however, remains to be done but see Faunas and Ages section (under Geological Setting) for a summary of papers related to Zanda faunas. As the latest installment,

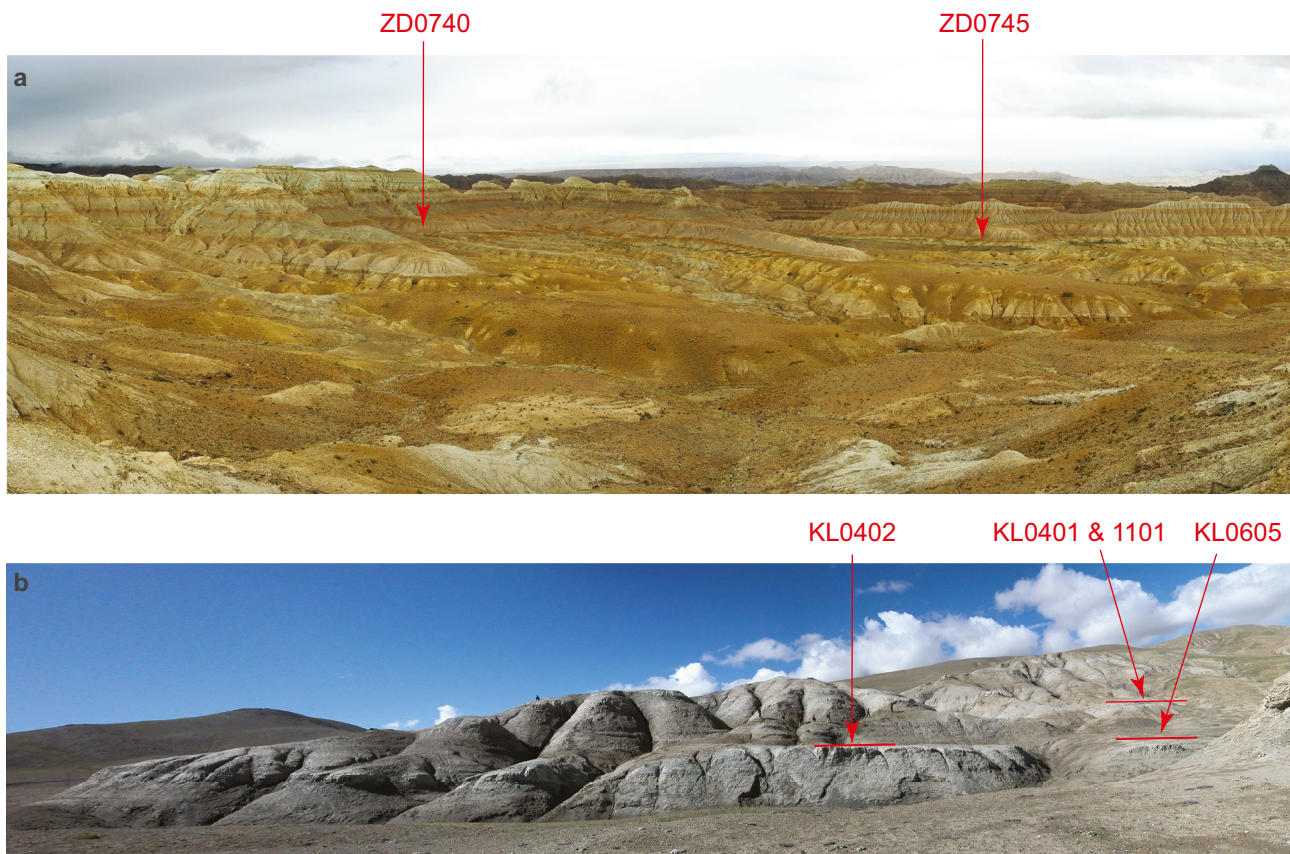


Fig. 2 a. Scenic View (Guanjingtai) exposures that produced the *Qurliqnorina hundesiensis* holotype at locality ZD0745 and *Coelodonta thibetana* (ZD0740); photo looking to the southwest by Xiaoming Wang on

July 23, 2007. b. Kunlun Pass Basin exposures and key localities; photo looking to the southeast by Qiang Li

Tseng et al. (2022) described the a much better sample of *Qurliqnorina cheni* from Qaidam Basin and established a phylogenetic framework of the *Qurliqnorina-Pantholops* lineage.

Geological setting

Type locality of *Qurliqnorina hundesiensis*

The holotype was acquired by Captain W. S. Webb and Mr. George Traill from Tibetan or Chinese traders at Niti village near Niti Pass at the present China-India border. In his descriptions of *Pantholops hundesiensis*, Lydekker, (1901:289) stated the type locality as “Hundes plain, on the far side of the Niti Pass”. Hundes (Undés, Híundes, and Hioondès) refers to modern Zanda Basin in the literature of early explorers (Strachey 1851b; Wang et al. 2020a) but became an obscured term from 1900s on. Falconer (1868) further established that Captain Webb and Mr. Traill’s fossil mammal collection must have come from the flat-lying strata about 20 miles north of the Niti Pass, with descriptions of

local topography and stratigraphy by Moorcroft (1816) and Batten (1838) perfectly matching the general geology and landscapes of Zanda Basin (Fig. 1). Herbert’s (1831) narratives help to narrow the locality down to possibly the village of Dongba (Dongpo). Wang et al. (2020a) further speculated that the original collections were likely to have been collected from hillside caves near the village of Dongba.

Faunas and ages

As verified by our own recent collections of *Qurliqnorina hundesiensis* from the Zanda Basin, we are reasonably confident that the British Museum holotype was from this basin (Wang et al. 2020a). Our own collection also helps to constrain the biostratigraphic occurrence of this species (Wang et al. 2013b) (Fig. 2). The updated faunal list of Zanda Basin fossil vertebrates include: Soricidae indet., *Aepyosciurus* sp., *Nannocricetus qiui*, *Aepyocricetus liuae*, *Prosiphneus eriksoni*, *Mimomys (Aratomys) bilikeensis*, *Apodemus* sp., *Trischizolagus mirificus*, *Trischizolagus* cf. *T. dumitrescuae*, *Ochotona* sp., *Meles* sp., *Panthera blytheae*, *Vulpes qiuzhudingi*, *Nyctereutes* cf. *N. tingi*, *Sinicuon* cf. *S.*

dubius, *Chasmaporthetes gangsriensis*, *Pliocrocuta perrieri*, *Qurlignoria hundesiensis*, *Antilospira* sp., *Protovis himalayensis*, *Metacervulus* sp., *Palaeotragus* sp., *Hipparion zandaense*, *Coelodonta thibetana*, Gomphotheriidae indet., and *Struthio* sp. (Li and Li 1990; Deng et al. 2011; Tseng et al. 2013a, b, 2016; Wang et al. 2013b, 2014a, b, 2016; Li and Wang 2015; Li et al. 2017). In addition, a bovid “as large as the Indian wild buffalo” was found among the early collections of Zanda fossils (Falconer 1868:173), which is not seen in our own collections and awaits future confirmation.

The age of the “Hundes plain” sediments had been speculated to be around 1 Ma (Pilgrim 1939) or 2 Ma (Lydekker 1901). Modern magnetostratigraphic correlations of the Zanda section are controversial. Qian’s (1999) first attempt arrived at an age range of 6.15–1.25 Ma, followed by Saylor et al.’s (2009) independent magnetic section that correlates to 9.2 to < 1 Ma. Another independent section by S. Wang et al. (2008a) yielded an age estimate of 9.5–2.6 Ma. Using fossil mammals as a constraint, Wang et al. (2013b) made a reinterpretation of previous magnetic correlations and suggested the 800-m Zanda section having an age range of ~6.4 Ma to 400 Ka, spanning from late Miocene to middle Pleistocene. Wang et al. (2013b:table 3) estimated an age span of 5.3–3.3 Ma for *Qurlignoria* based on three localities. With present recognition of seven specimens from six localities (ZD0624, 0636, 0745, 1001, 1055, 1202) (see Wang et al. 2013b:fig. 2 for a map of Zanda fossil localities), our new estimate for the Zanda Basin occurrences of *Qurlignoria* is in the range of 5.3–3.9 Ma in the early Pliocene.

The Kunlun Pass Basin (Figs. 1 and 2) has a much shorter history of exploration beginning in the early 2000s (Li et al. 2014). With an elevation of 4,786–4,923 m asl, the Kunlun Pass Basin contains vertebrate fossils from some of the highest elevations in the world (see Li et al. 2014:fig. 1 for a map of fossil localities). The Yuzhu Fauna preserved in the fine-grained lower Qiangtang Formation is a low-diversity assemblage with mammals such as *Petenya* sp., *Aepyosciurus* sp., *Nannocricetus mongolicus*, cf. *Orientalomys sinensis*, *Mimomys* sp., *Prosiphneus* cf. *P. eriksoni*, *Ochotona minor*, *Ochotona* cf. *O. lagreli*, Rhinocerotidae indet., *Hipparion* (*Proboscidihipparion*) *pater*, *Qurlignoria hundesiensis*, Bovidae indet., cf. *Panthera blytheae*, Hyaininae indet., *Vulpes qiuzhudingi*, and aff. *Arctomeles* sp. (Li et al. 2014; Wang et al. 2014b; Li and Wang 2015), as well as two fishes, *Gymnocypris* sp. and *Triplophysa* sp. (Wang and Chang 2010, 2012).

There have been multiple attempts at a Kunlun Pass magnetostratigraphic correlation. Qian et al. (1982) was the first to propose a composite section with an estimated age of 2.7–1.4 Ma. Qian and Zhang (1997) increased section lengths and sampling density and arrived at a longer age estimate of 2.90–0.65 Ma. Cui et al. (1998, 1999) also published a

magnetic section but failed to document it in detail. Constrained by ESR dates, Song et al. (2005) measured a more detailed magnetic section and concluded that the basin spans 3.6–0.5 Ma. Based on the fossil mammals, Li et al. (2014) attempted a reinterpretation of Song et al. section and arrived at a time span of ~4.2–3.6 Ma for the Yuzhu Fauna.

Material and methods

Specimen repository

Specimens from Zanda and Kunlun Pass basins described herein are deposited in the collections of Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (Beijing).

Dental terminology

Dental terminology follows those by Gentry (1994), Bärmann and Rössner (2011), Gustafson (2015), and Tong and Zhang (2019).

3D models by laser scans

Individual bones were scanned using a NextEngine scanner (model 2020i) in combination with ScanStudio software (version 2.0.2). Specimens were usually scanned in the highest resolution possible in the “Macro” setting, which has a 0.005” accuracy (~40,000–160,000 points/square inch). Typically, two sets of 360° scans (at intervals of 22.5°) were obtained, and manually aligned and fused into a single model. Scans were saved in the PLY format that preserves texture information. Size scale was captured by build-in calibrations of the NextEngine scanner.

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

MorphoSource repository

MorphoSource is a repository platform (www.morphosource.org) that holds digital data of biological specimens and cultural heritage objects contributed by museums, researchers, and scholars. We have placed files pertaining to *Qurlignoria hundesiensis* (<https://www.morphosource.org/dashboard/collections/000434456/edit?locale=en&>) onto this site to make them broadly available.

Systematic paleontology

Class MAMMALIA Linnaeus, 1758
 Order ARTIODACTYLA Owen, 1848
 Family BOVIDAE Gray, 1821
 Tribe CAPRINI Gray, 1821
 Genus *Qurlignoria* Bohlin, 1937

Type species. *Qurlignoria cheni* Bohlin, 1937.

Included species. *Qurlignoria cheni* Bohlin, 1937; *Q. hundesiensis* (Lydekker, 1881); *Q. bohlini* (Ozansoy, 1965).

Differential diagnosis. *Qurlignoria* differs from extant *Pantholops* in larger size, lacking a frontal spur between

the posterior ends of nasals, cranial roof more inclined by about 20°, cross-sections of horncores more flattened (greater anteroposterior length/transverse width ratio) toward the tops, and backwardly curved horncores.

Distribution and age. Qaidam Basin, Qinghai Province; Wuzhong, Ningxia Autonomous Region; Zanda Basin, Xizang (Tibet) Autonomous Region; and Kunlun Pass Basin, Qinghai Province; Middle Sinap Formation of Turkey. Late Miocene to Pliocene of north China and Tibetan Plateau and late Miocene of Turkey.

Qurlignoria hundesiensis (Lydekker, 1881)
 (Figs. 3, 4, 5, 6 and 7; Table 1)

“Antelope” and “fossil deer”: Royle 1839:xxix, pl. III.

Fig. 3 *Qurlignoria hundesiensis* (Lydekker, 1881), BMNH PV M10888, holotype, partial cranium. **a.** right lateral view; **b.** left lateral view with the broken right horncore removed. Scale bar equals 30 mm. Photographs by X. Wang

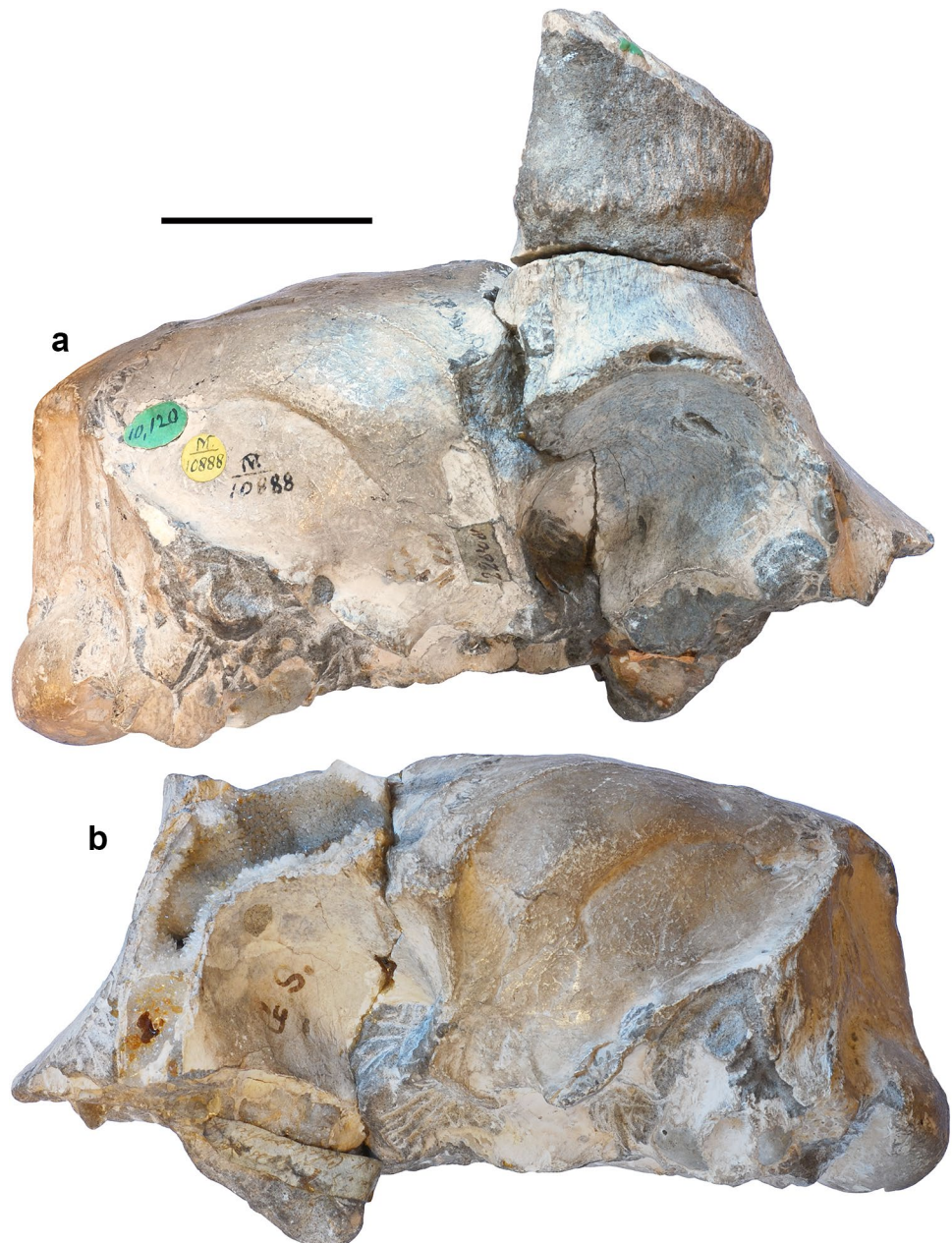
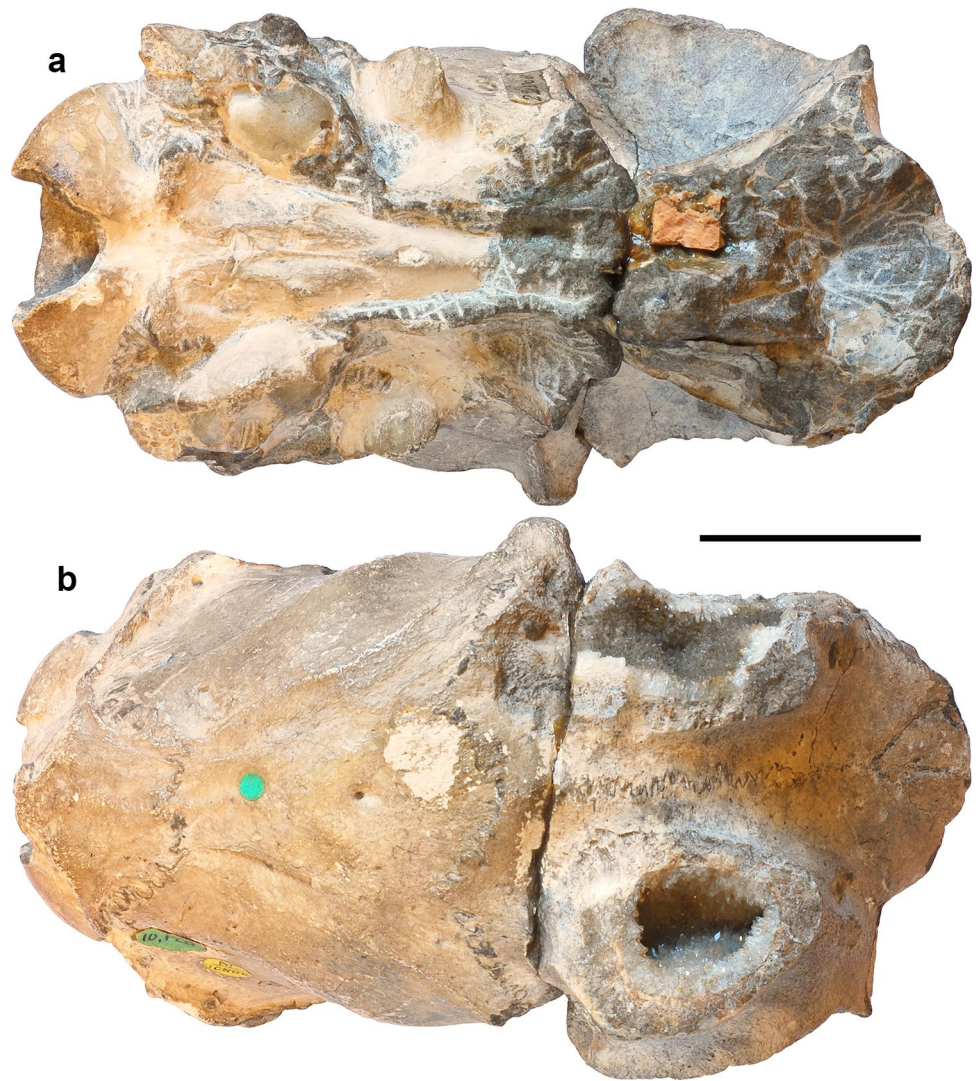


Fig. 4 *Qurlignoria hundesien-*
sis (Lydekker, 1881), BMNH
PV M10888, holotype, partial
cranium. **a.** ventral view; **b.**
dorsal view with the broken
right horncore removed. Scale
bar equals 30 mm. Photographs
by X. Wang



Pantholops hundesiensis Lydekker, 1881: Lydekker 1901:289; Pilgrim 1939:61; Leslie and Schaller 2008:4. *Qurlignoria hundesiensis* (Lydekker, 1881): Wang et al. 2020a, b:1; Tseng et al. 2022:13.

Qurlignoria sp.: Wang et al. 2013a, b, c:93, 2014a, b; Li et al. 2014:51.

Holotype. BMNH M10888, partial cranium with broken left and right horncores (Figs. 3, 4 and 5). Lydekker's (1881) initial naming of this species was based on an illustration by Royle (1839:xxix, pl. III), which included a partial skull (BMNH M10888) and a left palate with P2-M3 (BMNH M10889). Initially deposited in the Museum of the Geological Society, London, the type specimens were subsequently acquired by the British Museum of Natural History (now Natural History Museum, London) in 1911, where they have resided since. Although Royle's illustration contains two specimens of median-sized bovid and Lydekker did not specifically assign a type, the latter's descriptions left no doubt that he had erected a new species based solely on the

partial cranium—the upper teeth on the left palate was not mentioned. Therefore, Lydekker apparently did not consider the dental materials as potentially belonging to *Pantholops hundesiensis* and BMNH M10888 is by default the holotype (as it was labeled as the “type”). We suspect that BMNH M10889 belongs to the same individual as BMNH M10888, i.e., all BMNH specimens came from a single complete skull that was broken during excavation or subsequent handling (see Comparisons under cf. *Qurlignoria hundesiensis*).

Differential diagnosis. Differing from *Pantholops hodgsonii*, *Qurlignoria hundesiensis* has relatively longer and more slender braincase, longer parietal, relatively higher and narrower occipital, horncore situated more obliquely to the sagittal plane and forming a right angle with the plane of the parietal, parietal-frontal suture pointing forward at a more acute angle, basioccipital subtriangular with anterior tuberosities less expanded laterally and shallower median furrow, auditory bulla broader (Pilgrim 1939). Differing from *Q. cheni*, *Q. hundesiensis* has more elevated orbit in lateral

Fig. 5 *Qurlignoria hundesien-*
sis (Lydekker, 1881), BMNH
PV M10888, holotype, right
horncore removed from skull.
a. lateral view (see Fig. 3A for
its location on skull); **b.** medial
view; **c.** distal view (lower end
is toward lateral side); and **d.**
proximal view (lower end is
toward medial side). Scale bar
equals 20 mm. Photographs by
X. Wang



view. *Q. hundesienensis* has horncore cross sections with sharp keels on anterior edge in contrast to a more rounded leading edge in *Q. cheni* and *P. hodgsonii*, and its horncores are also less divergent than those seen in *Q. cheni*. *Q. hundesienensis* has straighter horncores than those in *Q. bohlini*.

Referred specimens. Zanda Basin: IVPP V31222, partial left horncore, orbit, and part of braincase (Fig. 6a, b), locality ZD0745 (Fig. 2), collected by Yang Wang on August 26, 2007; IVPP V31223, partial left and right horncores plus orbits and braincase (Fig. 6c, d), locality ZD1202, collected by Guangpu Xie, on July 4, 2012; IVPP V31224, basal horncore fragment, locality ZD1055, collected by Guangpu Xie on July 4, 2012.

Kunlun Pass Basin: IVPP V19072, isolated partial left and right horncores (Fig. 7a, b), from locality KL1101 (Fig. 2); IVPP V19073, partial right horncore with orbit and part of braincase (Fig. 7c, d), from locality KL1101.

Description. The holotype skull (BMNH M10888) is still the best cranial materials for this species. The skull is preserved in a greyish matrix and bone cavities are extensively filled with calcite crystals, such as inside the frontal sinus (Fig. 3b) and basal horncores (Figs. 4b and 5d). The left and right upper cheek teeth of BMNH M10889 are also preserved in grey matrix and likely belong to the same individual as the skull (see Comparison and Comments for more details).

Skull

With limited material available, the skull of *Qurlignoria hundesienensis* is broadly comparable to those of living chiru, as noted by Lydekker (1881, 1901). There are, however, two notable differences. In lateral view, if the facial region is aligned with modern chiru, the cranial roof behind the horncores is inclined by approximately 45 degrees. Such a moderate inclination is probably the primitive condition, and in some derived bovids, it either inclines in a greater (more steeply inclined) or lesser (becoming horizontal) angle (characters 15 and 16 of Calamari 2021). The cranial roof in *Pantholops* is somewhat more horizontal (by about 20° relative to that of *Qurlignoria*) but was still coded as primitive by Calamari (2021). Such a more horizontal orientation is presumably a derived condition relative to *Qurlignoria*. Another distinct cranial character in *Qurlignoria* is a lack of a frontal spur between the posterior ends of the nasal. Presence of such a spur in *Pantholops* is illustrated by Lydekker (1901:fig. 1B) and also seen in USNM 122758 (Fig. 8a).

Lydekker's (1901) illustrations show additional differences in cranial sutures in dorsal view. However, he acknowledged that his artist did not precisely align the two skulls for *Qurlignoria* and *Pantholops* to allow for accurate comparison.



Fig. 6 **a.** anterior and **b.** lateral views (both inversed from left side) of *Qurlignoria hundsensis* (Lydekker, 1881), IVPP V31222, loc. ZD0745, left horncore and orbit. **c.** anterior and **d.** lateral views of *Qurlignoria hundsensis* (Lydekker, 1881), IVPP V31223, loc. ZD1202, left and right partial horncores and top of skull. **e.** anterior and **f.** lateral views (both inversed from left side) of living *Pantholops hodgsonii* (Abel, 1826), left horncore from Kunlun Pass area; note

the slight lateral bend in anterior view toward the top of this horncore is likely caused by postmortem uneven desiccation after the horn sheath was shed, i.e., horn sheath in living Tibetan antelopes is straight in this segment of the horn. Horncore cross sections are derived from 3D models of laser scans (see [Material and method](#)). Scale bar equals 50 mm. Photographs by X. Wang

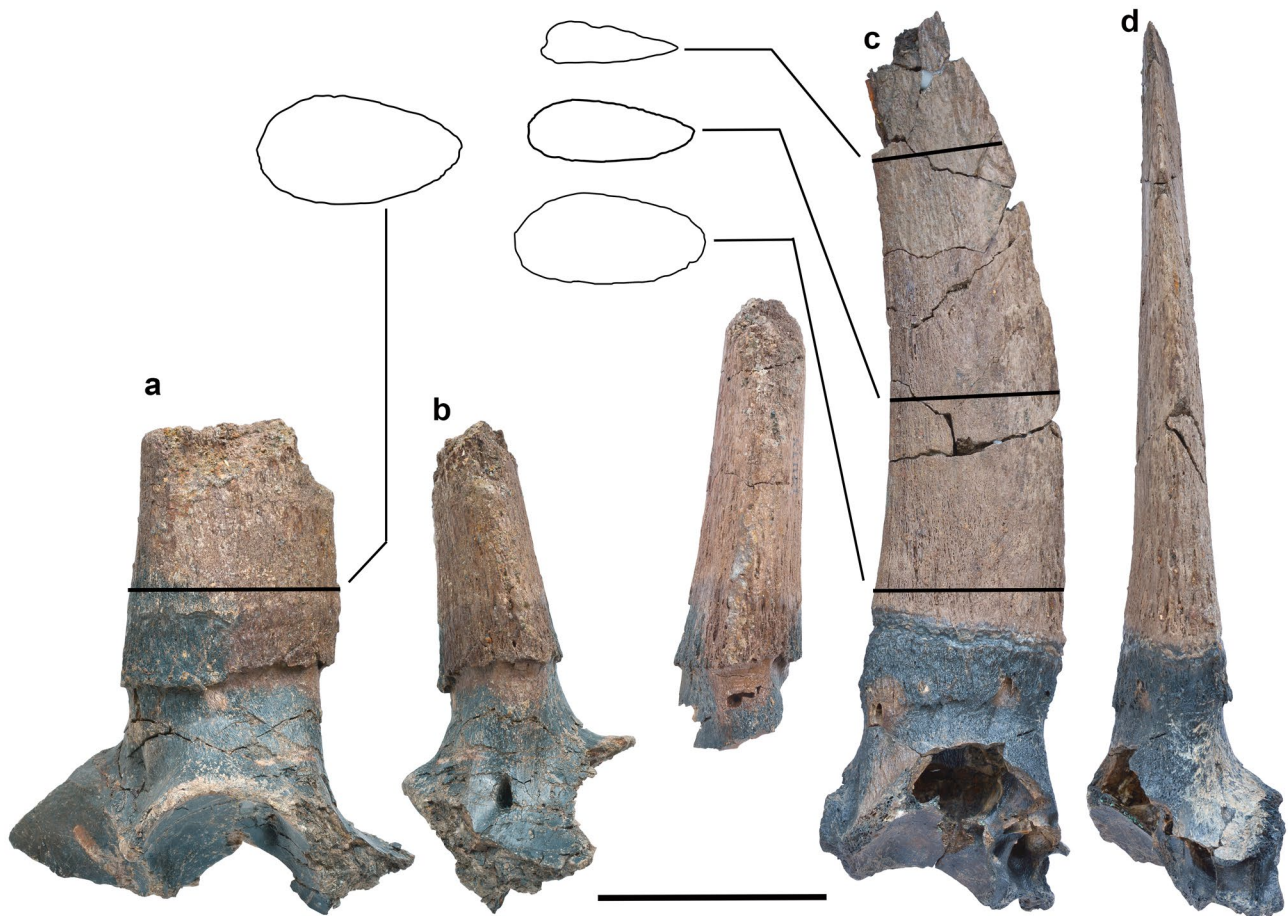


Fig. 7 a. lateral and b. anterior views of *Qurliqnoria hundsensis* (Lydekker, 1881), IVPP V19072, loc. KL1101, left and right isolated horncores and right orbit. c. lateral and d. anterior views of *Qurliqnoria hundsensis* (Lydekker, 1881), IVPP V19073, loc. KL1101, right

partial horncore and orbit. Horncore cross sections are derived from 3D models of laser scans (see [Material and method](#)). Scale bar equals 50 mm. Photographs by X. Wang

Although the posterior edge of the palatine in BMNH M10889 is broken, it does appear to end anterior to the M3 posterior margin. Such a condition is in contrast to a more posteriorly positioned caudal end of the palatine in living *Pantholops*. Although the median parts of the left and right halves of the maxillae are missing, the palatine-maxillary suture appears to form a V-shaped angle (Fig. 9), whereas that in *Pantholops* has a more gently curving suture.

Horncore

The horncores are situated directly above the orbit, a primitive condition for bovids (Calamari 2021). Aligning the preserved facial parts in BMNH M10888 to living *Pantholops*, the horncores seem to have a similar orientation in lateral view as that in *Pantholops*, which has a backward inclination of around 40° from vertical (assuming the cheek teeth and occipital condyles are flat on a level surface). However, with

limited facial region preserved in the holotype, the above comparison needs to be confirmed in better-preserved skulls.

The horncore sizes in *Qurliqnoria hundsensis* are roughly similar to those in *Q. cheni*, although one individual of the former taxon, IVPP V31222, has a noticeably larger (much greater girth) horncore (Table 1). The average horncore base long-axis length in *Q. hundsensis* is 44.9 mm ($N=5$) as compared to 42.6 mm for *Q. cheni* ($N=5$) and 35.9 for living chiru ($N=1$; the long, slender horn sheaths in museum collections of living chiru do not easily detach from horncores, thus the small sample size).

In all horncores that reveal their basal internal structure, the horncore sinus is typically a single large chamber that extends to the base of the burs. In the case of the holotype (BMNH M10888), the sinus is filled with calcite crystals (Fig. 5d). Above the sinus, the horncores consist of solid bone (Fig. 5c). The surface texture of the horncores is also somewhat different. In *Qurliqnoria hundsensis*, the base

Table 1 Measurements (in mm) of horncores

	<i>Qurlignoria cheni</i>					<i>Qurlignoria hundesiensis</i>					<i>P. hodgsoni</i>
	Wuzhong	Qaidam Basin				Zanda Basin			Kunlun Pass Basin		Kunlun Pass
	IVPP V7164	IVPP RV-37100	IVPP RV-37102	IVPP V169652	IVPP V169649	BMNH M10888	IVPP V31223	IVPP V31222	IVPP V19072	IVPP V19073	
Horncore base across pedicles	85.0	88.0	88.0	80*	86.5		76.3				
Horncore base between pedicles	14.0	14.0	17.0	18.7	13.0		21.0				
Horncore base long-axis length	43.0	48.0	40.0	37.7	44.2	41.4	38.5	55.3	47.0	42.1	35.9
Horncore base short-axis width	26.5	30.0	28.0	25.7	27.3	24.8	25.3	33.6	28.1	25.3	25.9
Horncore length 60 mm above base	31.8	42.3	33.8					47.6		37.9	29.7
Horncore width 60 mm above base	23.1	24.6	23.4					23.4		14.9	16.2

of the horncores below the burs is more elongated than in *Pantholops*. There is also a distinct surface texture where the growth ring at the base is shown. The depth of such a growth ring is deeper in *Qurlignoria hundesiensis* than in *Pantholops*. Above the growth ring, the horncore surface consists of fine grooves paralleling the length of the horncores with the anterior and posterior aspects of the horncores having deeper grooves.

In anterior view, the horncores have a slightly less lateral splay than in living *Pantholops*, but such a more upright orientation in *Qurlignoria* may have been due to its basal segment being more upright and divergence of its upper segments begins shortly above (Fig. 6c). Furthermore, this change in orientation also appears to vary among our sample (contrast IVPP V31223 in Fig. 6c with other horncores in Figs. 6 and 7), i.e., other than the slightly laterally curved IVPP V31223 (ZD1202), all other individuals seem to have more straight horncores as in living *Pantholops*. Ancestrally, *Q. cheni* has a similarly divergent horncores as in living *Pantholops* (Tseng et al., 2022:fig. 5), which is assumed to be the primitive condition for the chiru lineage.

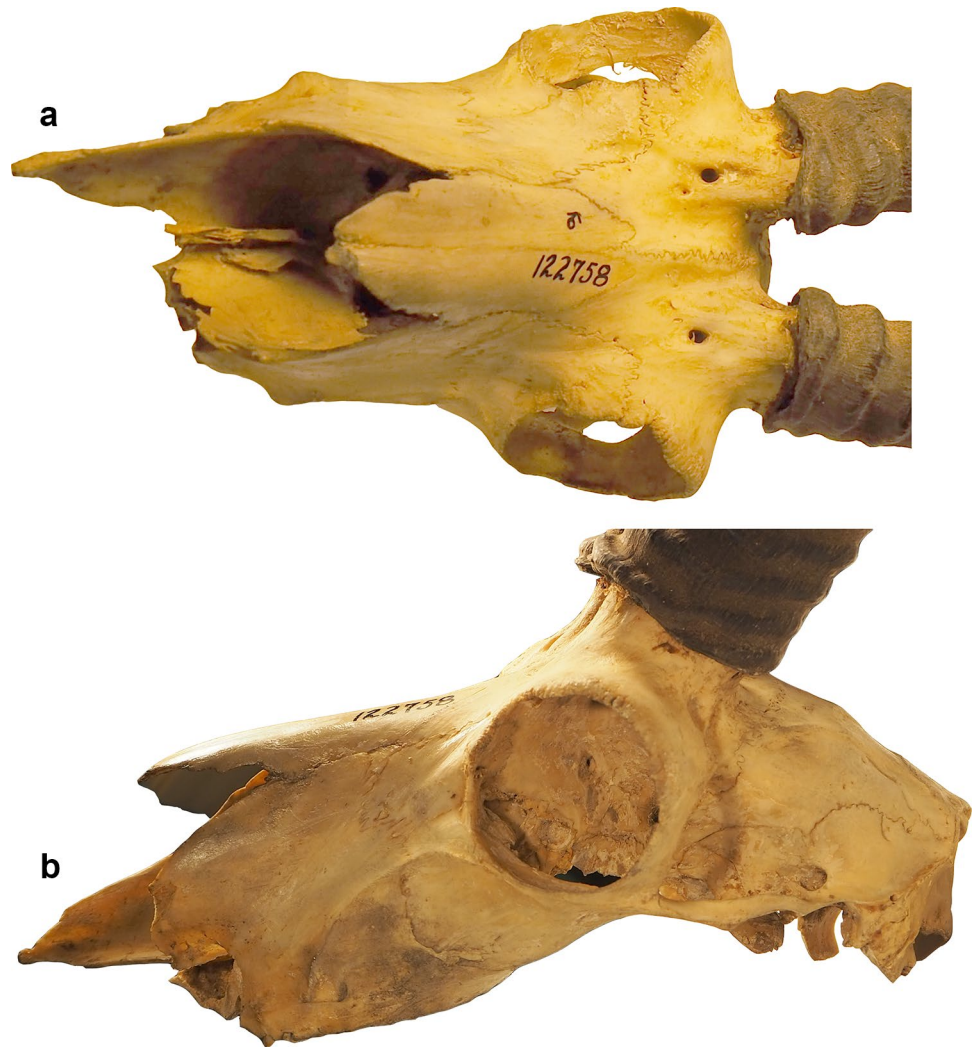
Perhaps the greatest horncore differences between *Qurlignoria* and *Pantholops* lie in the curvature and cross-sectional shape. A slightly backwardly curving horncore in *Qurlignoria cheni* (Tseng et al., 2022) is in contrast to the very straight ones of *Pantholops* in lateral view (see Fig. 6).

Within the large sample of *Q. cheni* from Qaidam Basin, this curvature varies slightly with some individual having nearly straight horncores (such as IVPP V16952; see Tseng et al. 2022:fig. 2) and others having similar curvatures as the Pliocene *Q. hundesiensis*.

Horncore cross sections in *Qurlignoria hundesiensis* are also substantially different from those of living *Pantholops*. In *Q. hundesiensis*, the horncores has an oval cross section at the base and becomes more elongated toward the top. The anterior edge also becomes progressively sharp, forming a keel. In extreme cases, this keel has a sharp blade followed behind by a very flat lateral surface, as seen in IVPP V19073 (see cross sections in Fig. 7c). Such a trend toward a flattened, laterally compressed horncore is in contrast to living *Pantholops*, in which the cross sections are not flattened (elongated) toward the top nor does it acquire a sharp anterior edge (Fig. 6f). Such a relatively uniformly elongated horncore in *Pantholops* suggests a somewhat different direction of evolution.

None of the horncores of *Qurlignoria hundesiensis* preserves the tips, with IVPP V19073 from the Kunlun Pass Basin (Fig. 7c, d) being the most complete. The general trends of tapering in all known horncores are similar to those in *Q. cheni* as seen in IVPP RV-37100 from the Qaidam Basin (Bohlin's Nr. 441) (Bohlin 1937:pl. III, figs. 6 and 7), which is still the most complete horncore so far known. The

Fig. 8 *Pantholops hodgsonii* (Abel, 1826), USNM 122758, male skull lacking teeth. **a.** dorsal view; **b.** left lateral view. Photos by B. Santaella Luna



ratio of total horncore length (height) to maximum anteroposterior diameter is approximately 4.3 for the holotype of *Q. cheni*, which is probably similar to those of *Q. hundesiensis*, in contrast to a much higher ratio of 7.2 for modern *Pantholops hodgsonii* (Fig. 6f). Such a high ratio is also reflected in the slender and elongated appearances in the horn sheaths of the living chirus (chirus' characteristically straight horn had been described as "unicorn of the Himalayas" in early literatures; Abel 1826).

Comparison. In his original erection of the new species, *Pantholops hundesiensis*, based on Royle's (1839) illustration, Lydekker (1881) thought the fossil species may not be distinguishable from the living chiru. In his subsequent comparison, this time with the actual specimen on hand, Lydekker (1901) did detect some differences, i.e., smaller size, more forward inclination and greater lateral splay of the horncores. To these, we can add the following cranial characters: the presences of a frontal spur inserted between posterior ends of the nasals, more anteriorly positioned

horncores, relatively longer skull portion behind the horncores, more erect supraoccipital shield. With the availability of more complete materials reported in this study, the horncores of *Qurlignoria hundesiensis* are demonstrably quite different from those of the living chiru: such as a more mediolaterally compressed, backwardly curved horncores that may also be shorter.

Compared to skulls of *Qurlignoria cheni* described by Tseng et al. (2022), the holotype skull (BMNH M10888) of *Q. hundesiensis* shows a very similar lateral profile (Fig. 3a) for the posterior part of the cranium. BMNH M10888, however, does have a slightly more erect occipital shield in lateral view, i.e., the occipital in *Q. cheni* sloping more forward by about 10° (compare Tseng et al. 2022:figs. 2B and 3B). In dorsal view, the patterns for sutures between the frontals, between frontal and parietal, and between parietal and supraoccipital are also similar to those in *Q. cheni* (Tseng et al. 2022:fig. 2C), although the interfrontal suture in *Q. cheni* (Tseng et al. 2022:fig. 3A) seems more elevated than

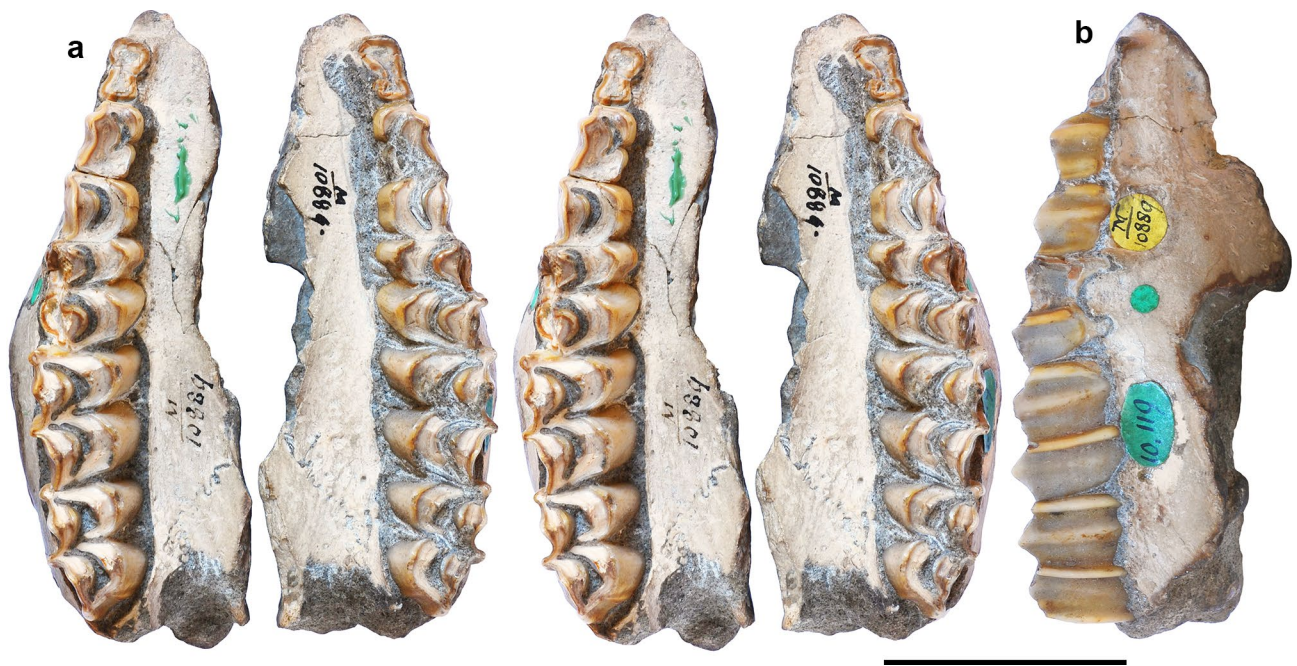


Fig. 9 cf. *Qurlignoria hundsensis* (Lydekker, 1881), BMNH PV M10889, partial left and right palate with nearly complete cheekteeth. **a.** stereo photos of occlusal view; **b.** labial view of the left cheekteeth. Scale bar equals 30 mm. Photographs by X. Wang

in *Q. hundsensis*. The most conspicuous difference in *Q. hundsensis* lies in the more elevated orbit in lateral view, which is markedly higher than in those of *Q. cheni*.

cf. *Qurlignoria hundsensis*

(Figs. 9, 10 and 11; Tables 2 and 3)

Capricornis roylei Pilgrim, 1939:57.

Referred Specimens. Zanda Basin: BMNH M10889, partial palate with left and right P2-M3 (holotype of *Capricornis roylei* Pilgrim, 1939) (Fig. 9); IVPP V31232, partial left dentary with p2–m3 (Fig. 11d, e, f), locality ZD1001.55, collected by Z. Jack Tseng and team; IVPP V31233, partial right dentary with p2–3 alveoli and p4–m3 (Fig. 11a–c), locality ZD1001.71, collected by Z. Jack Tseng and team; IVPP V31225, isolated left m3, locality ZD0624 (mistaken for ZD0604 in Wang et al. 2013a, b, c:table 3, fig. 4), collected by Z. Jack Tseng on September 4, 2006; IVPP V31226, isolated right M2 (Fig. 10c, d), locality ZD0636, collected by Z. Jack Tseng on September 7, 2006.

Kunlun Pass Basin: IVPP V31227, isolated right m3 (Fig. 10a, b), locality KL0504, collected by Z. Jack Tseng on July 20, 2005; IVPP V19071, three broken lobes of one or two right lower molars, locality KL0607, collected on August 26, 2006.

Description. For lack of definitive association of cranial and dental materials, we treat the dental materials separately to convey uncertainties in our taxonomic assignment, as did

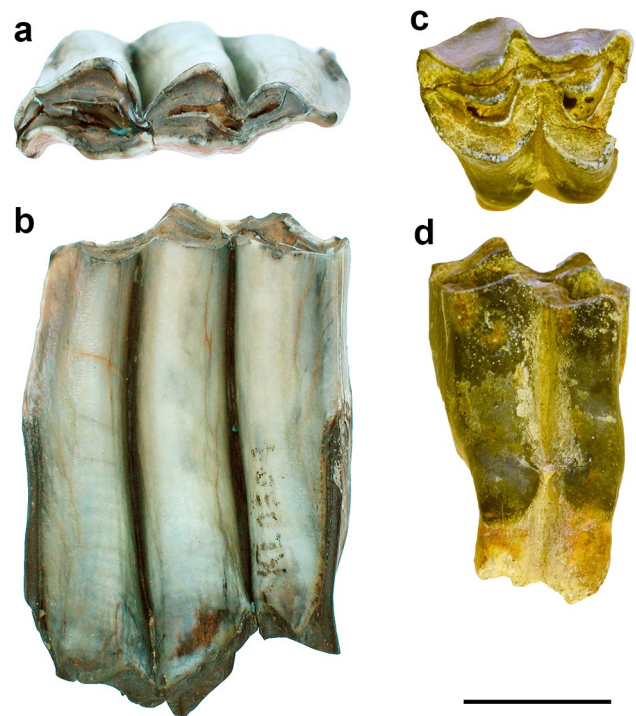


Fig. 10 cf. *Qurlignoria hundsensis* (Lydekker, 1881), isolated cheekteeth. **a.** occlusal and **b.** labial views of right m3, IVPP V31227, from KL0504 locality in Kunlun Pass Basin. **c.** occlusal and **d.** labial views of right M2, IVPP V31226, from ZD0636 locality in Zanda Basin. Scale bar equals 10 mm. Photographs by X. Wang



Fig. 11 cf. *Qurlignoria hundsensis* (Lydekker, 1881) lower jaws and teeth. **a.** labial, **b.** lingual, and **c.** occlusal views (inverted) of IVPP V31233, locality ZD1001.71, all reversed from right side;

d. occlusal, **e.** lingual, and **f.** labial views of IVPP V31232, locality ZD1001.55. Scale bar equals 50 mm. Photographs by X. Wang

Table 2 Dental measurements (in mm) of upper teeth of cf. *Qurlignoria hundsensis*

	<i>Q. hundsensis</i>	
	BMNH M10889	IVPP V31226
Cheek toothrow length (P2-M3)	73.30	
Right P2 length x width	8.2×5.7	
Right P3 length x width	9.3×7.2	
Right P4 length x width	9.0×8.9	
Right M1 length x width	13.6×11.6	
Right M2 length x width	17.2×11.8	14.6×10.0
Right M3 length x width	16.1×10.6	

in our treatment of cf. *Qurlignoria cheni* (Tseng et al. 2022). Dentally, cf. *Qurlignoria hundsensis* retains a P2 and p2, in contrast to the loss of these teeth in *Pantholops*, and has a distinct internal cleft on P3 absent in *Pantholops*.

Upper teeth

See Comparison section below for our argument that the upper palate in BMNH M10889 may belong to the same individual as the holotype skull and horncores (BMNH M10888). The following description of the upper teeth is based on BMNH M10889 (Fig. 9), which features a number of differences from those of *Pantholops* and need to be confirmed by future discoveries of associated teeth with horncores. BMNH M10889 has substantial wear on the premolars and modest wear on the molars. The upper molars are modestly hypsodont with the crown height increasing from M1 to M3, the latter being still buried in matrix and its full crown height unknown (Fig. 9b).

Both P2s are broken off at the base. However, the left P2 was intact when Royle (1839) initially illustrated it, but unfortunately the broken P2 appears to be lost when the lead author examined it in 2007 (and again verified by another senior author, ZJT, in 2010). In the oblique view of Royle's

illustration, the P2 is slightly smaller and seems to have a triangular outline but with an anterolingual spur, in contrast to a complete loss of this tooth in *Pantholops*. The P3s, better preserved on that of the right one, are anteroposteriorly longer than its width and have a strong mesostyle. The lingual edge is relatively straight and has a highly distinct cleft interrupting the lingual surface and sending a longer anterior and a shorter posterior branch. In living *Pantholops*, the P3s are highly reduced (Leslie and Schaller 2008) and apparently loosely rooted, and so are missing in the modern specimens we examined—whether or not *Pantholops* has a cleft on their P3s is not known. The P4s have a modest parastyle and metastyle. Besides a vague lateral curve on the lingual surface, the P4s have no indication of a cleft.

There is no indication of an entostyle (basal pillar) in upper molars, although the matrix on the lingual side of the upper teeth is not fully cleared to be certain of this fact. The M1-3 s are broadly similar, all having a distinct parastyle and mesostyle and a modest rib on the labial surface of anterior lobes. In living *Pantholops*, the parastyles and mesostyles are even more prominent, to the point that the labial surface of the anterior lobe is concave.

Based on above analysis, we also refer an isolated right M2 to *Qurlignoria hundsensis* (IVPP V31226) from Zanda Basin. This tooth (Fig. 10c, d) has the characteristically distinct parastyle and mesostyle, a weak labial rib on anterior lobe, and a lack of a basal pillar.

Lower teeth

We still do not have associated lower teeth with upper teeth, or with skull or horncores. There are three partial lower jaws (IVPP V31232, V31233, V31234) that belong to medium-sized bovids and we tentatively assign two of these (IVPP V31232 and V31233) to cf. *Qurlignoria hundsensis* for the following reasons. The lower teeth are of similar size and occlude well with the upper teeth in BMNH M10889, with similar mesowear patterns. The

Table 3 Dental measurements (in mm) of lower teeth of cf. *Qurlignoria hundsensis*, those for IVPP V16954, V16956, and V16961 follow Tseng et al. (2022)

	cf. <i>Qurlignoria hundsensis</i>				cf. <i>Qurlignoria cheni</i>		
	IVPP V31233	IVPP V31232	IVPP V31225	IVPP V31227	IVPP V16954	IVPP V16956	IVPP V16961
p2-m3 length	78.0	76.7			99.2		
p2 length x width		6.9×4.0					8.8×6.7
p3 length x width		9.1×5.1				12.2×6.3	12.7×7.8
p4 length x width	10.5×6.1	9.8×6.2					13.9×8.7
dp4 length x width						20.1×9.3	
m1 length x width	12.1×8.9	13.2×9.6			16.1×9.9	17.4×12.5	15.1×11.3
m2 length x width	16.4×9.6	15.3×9.7			19.7×13.3		
m3 length x width	23.7×8.9	22.6×9.8	24.1×7.9	22.8×7.2	26.7×12.8		

dentary has similar shape as living *Pantholops* with mediolaterally thickened cheekteeth section (especially near m2-3; Fig. 11c, d). Dental morphology is consistent with those of cf. *Q. cheni* from Qaidam Basin referred by Tseng et al. (2022) and to some extent the living *Pantholops*. Finally, the relative abundance among medium-sized bovids in Zanda Basin is highest for *Qurlignoria* (in terms of identifiable horncores), which is consistent with a similarly high frequency in the lower jaws and isolated teeth.

A modest-sized, double-rooted p2 (6.9 mm long) is present in the two lower jaws (or at least the alveoli in the case of IVPP V31233), in contrast to the loss of this tooth in *Pantholops*. The p2 in cf. *Qurlignoria hundesiensis* shows no sign of reduction relative to the rest of cheek teeth compared to that in *Q. cheni* (Tseng et al., 2022), i.e., cf. *Q. hundesiensis* is not trending toward modern chiru. The p2 has modest wear and its cusp morphology is largely intact. A discrete paraconid bends slightly lingually. The protoconid is the largest cusp of the tooth, followed behind by a short talonid.

The p3 has a discrete parastylid and paraconid, both closely pressed together and separated by a shallow groove visible on lingual side. Heavy wear on the p3 crown does not permit observation of protoconid and metaconid. As in the p2, the talonid appears short and its cusp morphology not readily distinguishable.

The p4 has distinct parastylid and paraconid, both reaching to the lingual border. The metaconid, on the other hand, is not well developed, forming a modest lingual swelling from the protoconid base. A prominent entoconid is both larger than metaconid and more lingually expanded. Posterior to the entoconid is a discrete entostylid on lingual side and hypoconid on labial side.

The m1s on both specimens suffer from extensive wear. A variation between these two specimens is the presence of a spur on the anterior aspect of the hypoconid in IVPP V31232 in contrast to the lack of it in IVPP V31233, which does show a minute spur near the base of the crown.

The m2 lacks the anterior spur on hypoconids of both specimens. On the less worn specimen (IVPP V31233), a small remnant of an anterior cingulid is visible on the labial side.

The m3s in both IVPP V31232 and V31233 possess a distinct anterior cingulid, with the less worn specimen (IVPP V31233) showing a more prominent one that is also visible on the lingual side as a distinct rib. The occlusal outlines of the hypoconulid-entoconulid lobes also differ between these two specimens, one being more rounded at posterior end (IVPP V31232) as opposed to more pointed in IVPP V31233.

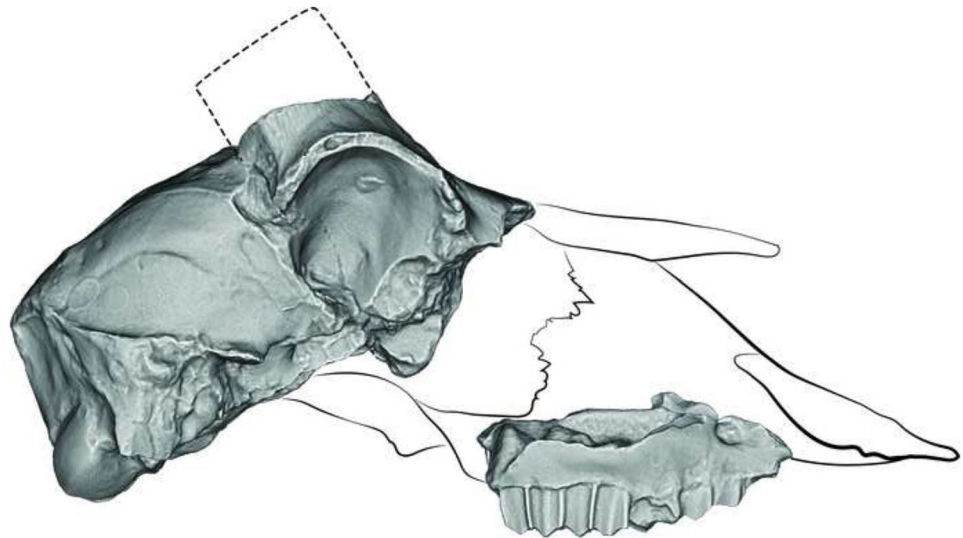
We refer two isolated m3s from Zanda and Kunlun Pass basins to cf. *Qurlignoria hundesiensis* (Fig. 10a, b). Both have high crowns and are relatively narrow (high ratio of length vs width; Table 2). Both also have a third lobe of m3

consisting of a hypoconulid, a derived character for Caprini (Calamari 2021). The hypoconulid is offset labial-wards, as also seen in *Pantholops*, but this feature is not seen on IVPP V31233 (Fig. 11c). If our reference of the two m3s is correct, these teeth will make an interesting contrast with those described for cf. *Qurlignoria cheni* (Tseng et al. 2022). Notably, the relatively narrow proportions as indicated in an average length/width ratio of 3.1, as compared to 2.1 for *Q. cheni* (IVPP V16954).

Comparison—BMNH M10889 was among the first fossil collections made from the Zanda Basin and was figured as “fossil deer” by Royle (1839:pl. III, fig. 2). Commenting on Royle’s illustrations, Falconer (1868:179) regarded the partial skull (BMNH M10888) as belonging to “the Cervine group” whereas the partial palate as “the Caprine group.” While correcting Falconer’s identification of a cervid and erecting a new name (*Pantholops hundesiensis*) for the partial skull, Lydekker (1881) did not comment on the partial palate, nor did he mention it when he had a chance to examine the specimen in person (Lydekker 1901). Pilgrim (1939:58) was the first to treat BMNH M10889 in detail, assigning it as the holotype of his newly named *Capricornis roylei*. He contrasted it with *Pantholops* in the following way: “the sharp narrow folds (parastyles and mesostyles of modern terminology) on the external surface of the molars indicate that the specimen belongs to the Aegodon section of the Bovidae. It is not only too large for *Pantholops*, but in that genus the narrower molars, the concavity of the outer lobes, the absence of median ribs and the reduction of the premolars, of which P2 is missing, sharply distinguish it from the present palate.”

We suggest that BMNH M10889 may belong to the same species, if not the same individual, as the holotype (BMNH M10888) of *Qurlignoria hundesiensis* for the following reasons. Firstly, BMNH M10888 and M10889 seem complement each other as a single skull with similar color of the matrix and no duplicate parts. Our digital assembly of these three components does seem to suggest a single individual (Fig. 12). Secondly, our own expeditions to Zanda Basin have not discovered any horncore resembling *Capricornis*. Instead, medium-sized bovids include *Qurlignoria*, *Protovis*, and a spiral horned taxon that we tentatively called *Antilospira* (Wang et al., 2013b, 2016). Thirdly, although we still do not have associated teeth with horncores for *Qurlignoria*, dental characters of BMNH M10889 do not preclude it from being compared to those of *Pantholops*. Upper teeth of BMNH M10889 are characterized by prominent folds at parastyles and mesostyles, a rib on the labial surface of anterior lobe of molars, lack of entostyle (basal pillar) in upper molars, a deep cleft on lingual side of P3, and presence of P2. Of these, *Pantholops* has even more prominent parastyle and mesostyle folds to the point that the labial surface is concave between the folds, a derived character

Fig. 12 *Qurliqnorina hundesiensis* (Lydekker, 1881), right lateral view of 3D models of skull (BMNH M10888) and upper palate (BMNH M10889) as reconstructed based on the skull outline of a living *Pantholops*. 3D laser scans by Narimane Chatar. MeshLab digital assemblage by Stuart White



shared with *Naemorhedus*, *Rupicapra*, *Ovibos*, *Budorcas*, *Capra*, and *Ovis* (Gentry 1992). The loss of second premolars apparently occurred independently in *Antelope*, *Saiga*, and *Pantholops* (Gentry 1992), in light of phylogenetic trees derived from mtDNA (Bibi 2013). The loss of this tooth could conceivably occur within the chiru lineage, i.e., its presence in BMNH M10889 does not preclude its inclusion in *Qurliqnorina*. Finally, the P3s in living *Pantholops* are so reduced that they are often missing in published figures (e.g., Leslie and Schaller 2008) and thus its morphology is difficult to evaluate. A lingual cleft occurs on the P2s of *Capricornis* (Pilgrim 1939) and *Turcocerus* (Pilgrim 1934) and its presence on P3 seems likely to be another independently evolved character. Recent phylogenetic analyses based on mtDNA (Bibi 2013), heuristic-hierarchical Bayesian approach on all mammalian species (Faurby and Svenning 2015), genomic analysis (Chen et al. 2019), and total evidence (Calamari 2021) all place *Pantholops* at the base of the Caprini clade. Its dental similarity with that of *Capricornis* is perhaps not surprising but represents shared primitive characters (synplesiomorphies) for basal caprines. In absence of a *Capricornis*-like horncore from Zanda Basin, it seems reasonable to assume that BMNH M10889 more likely belongs to *Qurliqnorina*.

Tseng et al. (2022) referred four lower jaws from Qaidam Basin to “cf. *Qurliqnorina chen*”. Given a lack of direct association of cranial and dental materials from Qaidam Basin, Tseng et al.’s tentative assignment was largely based on relative abundance of jaws and horncores in Qaidam bovid sample, plus slightly shortened premolar rows, diminutive basal pillars in lower molars, and a posterior position of p4 metaconid, dental features that characterize basal caprines. The present referral of two partial lower jaws from Zanda Basin plus three m3s is largely consistent with the above treatment.

If these referrals are correct, it further reinforces our idea that *Q. hundesiensis* is not in the direct line of descent to living *Pantholops* because it shows no sign toward the loss of p2. In addition, *Pantholops* has more distinct ribs for the anterior and posterior cingulids on molars.

Discussion

Ozansoy (1957) named a new species, *Qurliqnorina* (= *Ouirliknorina*) *şenyüreki*, from locality XXXb in the middle Sinap beds in Turkey. No description or figure was provided by Ozansoy (1957). This name appeared in the faunal list again in Ozansoy (1965) and Tekkaya (1974), but again, no mention was made about the nature of the materials (see also Kostopoulos et al. 2020). Nor did the taxon appear in subsequent systematic treatments of ruminants from Sinap Formation (Gentry 2003). Tseng et al. (2022) thus treated it as a *nomen nudum*.

In his monographic treatment of Cenozoic mammals of Turkey, Ozansoy (1965) named a new species, *Capra bohlini*, from the lower and middle layers of the middle Sinap strata, based on a skull fragment with partial left and right horncores (see more discussion in Kostopoulos et al. 2020). Ozansoy did not mention his previous taxon, and it is not possible to know if his holotype of *Capra bohlini* was related to his earlier name *Qurliqnorina şenyüreki*. However, Ozansoy did compare *C. bohlini* to “*Antelope* gen. and sp. indet. II” from Qaidam (Bohlin 1937), which, in his opinion, was closest in morphology.

Bohlin’s “*Antelope* gen. and sp. indet. II” was based on a right horncore (Bohlin 1937:pl. VI, figs. 7, 8), plus two more fragmentary horncores. Labeled as Nr. 479, this horncore was collected on May 26, 1932 from “hill of point

42” in the “General Strips” (Wang et al. 2011:fig. 7), the same strata where the majority of *Qurlignoria cheni* was collected both by the Bohlin party and by us (Tseng et al. 2022). Bohlin was especially impressed by the deep grooves and noticeable heteronymous torsion, which differ from other mid-sized bovids from Qaidam Basin. Ozansoy’s (1965) *Capra bohlini*, however, lacks both of these features. More recently, Bouvrain et al. (1994) also expressed doubts about the generic assignment of *Capra bohlini*, whereas Gentry (2003:367) tentatively referred this taxon to *Pseudotragus* aff. *P. capricornis* Schlosser (1904). Most recently, Kostopoulos et al. (2020) re-figured the holotype of *Capra bohlini* (MNHN TRQ/1955–15-31), and moved it to *Qurlignoria*, i.e., *Q. bohlini*. Based on the published figures (Ozansoy 1965; Kostopoulos et al. 2020), the holotype of *Capra bohlini* is consistent with the basic morphology of *Qurlignoria*, although its horncores curve more backward than its Tibetan counterparts do. If this is the case, *Q. bohlini* represents the western-most occurrence of this genus. Its stratigraphic occurrence is still vaguely defined, although Gentry (2003:table 15.6) listed his *Pseudotragus* aff. *P. capricornis* in the MN 9–12 part of the middle Sinap strata but Kostopoulos et al. (2020:633) suggested that specimens of *Q. bohlini* are from both Lower and Middle Sinap (likely older than 9.5 Ma), equivalent to part of the Qaidam *Qurlignoria* occurrences.

Kostopoulos et al. (2020) named a new species, *Qurlignoria chorakensis*, from the late Miocene Çorakyerler in Çankırı Basin, Anatolia, Turkey. However, as pointed out by Kostopoulos et al. (2020), this species has very divergent horncores ($> 45^\circ$), especially toward their distal parts, which also taper off less quickly than the Tibetan forms, weaker anterior keels, stronger and thicker interfrontal suture, unreduced P2, and P3 lacking a lingual cleft. These characters are distinctly different from the general morphological trends among the Tibetan forms, and we are thus doubtful that this new species from Çorakyerler belongs to *Qurlignoria*.

While describing their new species of *Qurlignoria chorakensis*, Kostopoulos et al. (2020) also referred to this species some horncore materials from Platania fossil site in northern Greece. These materials were originally identified as *Tragoreas?* aff. *T. oryxoides* by Vasileiadis et al. (2019). We have not seen these materials and following our above assessment, we tentatively exclude the Greek specimens from *Qurlignoria*.

Qiu et al. (1987) described a pair of partial left and right horncores (IVPP V7164) from Wuzhong, Ningxia Hui Autonomous Province, and referred it to *Qurlignoria cheni*. They estimated an early late Miocene (Bahean) age and correlated the 20 m yellow sandstones to the Ganhegou Formation, a vague term often used in southern Ningxia regional geology. Recently, S. Wang et al. (2018) compared

the Wuzhong Fauna with Tuosu Fauna in Qaidam Basin, based on their discovery of a shared taxon, *Olonbulukia*, previously known in Qaidam Basin only. Tseng et al. (2022) cautiously interpreted a younger age for the Wuzhong strata than the Qaidam forms based on paleomagnetic works by Shen et al. (2001).

Tseng et al. (2022) provided the latest summary of *Qurlignoria cheni*, adding substantial materials from the Qaidam Basin and providing a biostratigraphy of this species. They also placed this species in a phylogenetic framework, as a distant sister-group of the living chirus, a conclusion we follow here.

Evolution of Tibetan antelope

Pantholops is arguably one of the mammals best adapted to the harsh life on the high plateau. As an open terrain grazer, the chiru has acquired adaptations for enhanced oxygen transport against hypoxia (Ge et al. 2013; Ma et al. 2014; Signore and Storz 2020), dense under furs for thermal insulation against hypothermia (Rollins and Hall 1999), and an enlarged air sac in the nasal passage to enhance breathing (Hodgson 1833; Schaller 1998; Leslie and Schaller 2008). All of these presumably were evolved over long periods of geologic time, as its ancestors became ever more adapted to higher elevations.

Bohlin (1937) thought *Qurlignoria* was possibly a goat-like form but believed the materials at hand too incomplete to speculate further. In a brief note, Gentry (1968) was first to single out several features of *Qurlignoria* that are shared with the living *Pantholops* and proposed a tentative relationship to the Tibetan chiru. In describing additional materials of *Qurlignoria* from Qaidam Basin and placing them within modern phylogenetic framework, Tseng et al. (2022) re-affirmed Gentry’s proposal of a chiru relationship and placed the Tibetan antelope clade at the base of the caprine clade. We follow Tseng et al.’s phylogeny and note that Calamari (2021) estimated an initial divergence time for *Pantholops* around 9 Ma (Calamari did not use *Qurlignoria* in his fossil calibration), which is roughly consistent with our fossil records.

If we take the Wuzhong record of *Qurlignoria cheni* and *Q. bohlini* from Turkey as early indications of its initial evolution in and outside the Tibetan Plateau, the *Qurlignoria* lineage then became isolated within the plateau during the Pliocene (Fig. 13).

Our present records of *Qurlignoria hundsensis* in the Pliocene add an important time dimension. The two known Tibetan species of *Qurlignoria* may be a chronospecies succession from *Q. cheni* to *Q. hundsensis* (Fig. 13). It also suggests that *Qurlignoria* represents a side branch of the

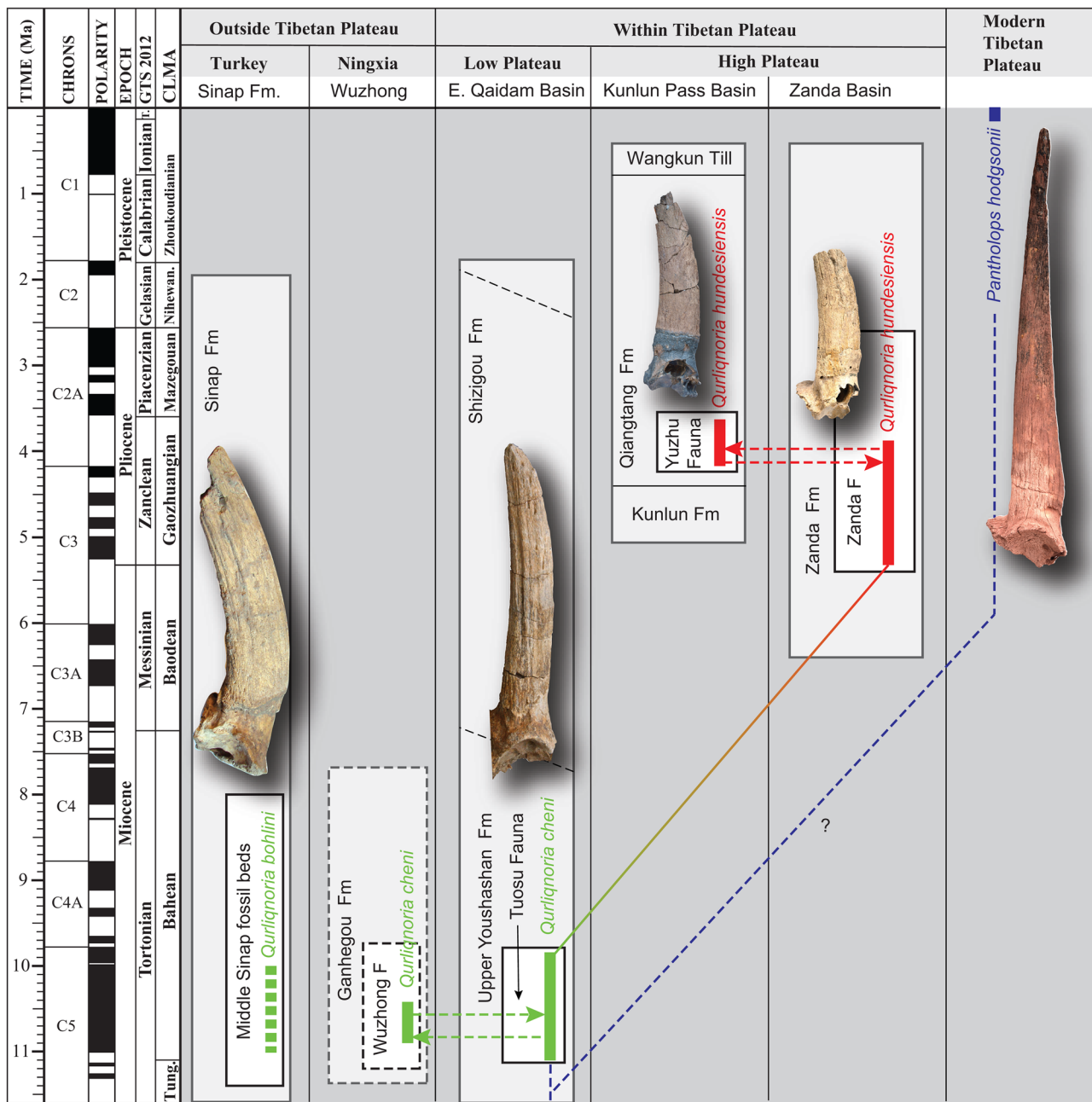


Fig. 13 Geologic and geographic occurrences and evolution of *Qurliqnorina* and *Pantholops*. Geochronology of Qaidam Basin strata and fauna is based on Fang et al. (2007) and Wang et al. (2007) plus relocation of historical collections (Wang et al. 2011), those for Zanda Basin strata and fauna by Wang et al. (2013b), and those for Kunlun Pass Basin fauna and strata by Song et al. (2005) and Li et al. (2014). The Wuzhong Fauna in Ningxia is still poorly constrained by

magnetostratigraphy (Shen et al. 2001) and its age is estimated to be equivalent to Tuosu Fauna in Qaidam Basin (Wang et al. 2018). The precise occurrence of *Q. bohlini* (Ozansoy 1965) from the Middle Sinap Formation in Turkey is not available and its chronologic range follows that by Wang et al. (2013a). Photo of *Q. bohlini* courtesy of Dimitris S. Kostopoulos

Tibetan antelope clade and did not directly give rise to modern *Pantholops*. It appears that throughout its 8-million-year evolution on the Tibetan Plateau, *Qurliqnorina* remained in stasis (Fig. 13). Both its horncore and dental morphologies have changed little, and for those features that do change,

they are not in a direction toward the morphology of modern *Pantholops*. For example, the horncores of *Qurliqnorina* did not become straightened and elongated from late Miocene to Pliocene. Dentally, it shows no sign of progressive reduction and loss of p2, nor does it acquire more prominent parastyles

and mesostyles on the upper molars and anterior/posterior cingulids on the lower molars, some of which are key characters of *Pantholops*.

True fossil *Pantholops*, or its direct ancestors, is yet to be discovered. If modern chiru necessarily took millions of years of evolution to acquire their adaptations to living in the high plateau, we expect a parallel lineage to *Qurlignoria* in the plateau possibly with equal antiquity (Fig. 13).

Remarks on early controversies of paleoelevation and paleoenvironment

Zanda fossils are remarkable not only for their contribution to Tibetan vertebrate paleontology but also for their role in early controversies over paleoelevations and environments. Besides a theological antediluvian interpretation of the Zanda fossils (Buckland 1823), Falconer (1868:173) (according to Lydekker 1881, this paper was possibly written in as early as 1839 and posthumously published in 1868) first recognized that at an lofty elevation of “15,000 feet above the sea, and that the natural vegetation at present hardly anywhere attains the size of a shrub—not to mention the Polar severity of the climate”, a rhinoceros (likely *Coelodonta thibetana* Deng et al. 2011) could not have existed in such a habitat. Remarkably, he did envision that the rhinoceros could have been clothed in a dense fur like in late Pleistocene woolly rhinoceros. Falconer therefore concluded that Zanda Basin must have been much lower than it is at present.

Lydekker (1881), however, challenged Falconer’s view with an alternative interpretation of a mild and moist environment prevailing in Zanda Basin that stayed in the same elevation (or slightly lower). To further strengthen Lydekker’s stable basin hypothesis, Lydekker cited Strachey’s (1851a, b) observation that Zanda strata are almost perfectly horizontal with no sign of tectonic disturbance. One of his strongest arguments was that given its similar morphology to the living Tibetan antelope, the ancestral chiru that he just named *Pantholops hundsensis* must have been adapted to similarly high altitudes as its modern descendants. This, Lydekker argued, must be true for most of other Zanda faunas with the possible exception of the rhinoceros. Unfortunately, Falconer, who by then had passed away, was never afforded a chance to respond to Lydekker, and as far as we are aware, this controversy has not been further addressed ever since.

Independently, Chinese vertebrate paleontologists advanced a strikingly similar argument to that by Falconer. During the Tibetan Plateau expedition by the Chinese Academy of Sciences in 1975, Ji et al. (1980) described late Miocene fossils of *Hipparion* horse from the Gyirong Basin (elevation 4,100–4,300 m asl) at the foothills of the Mount Xixiabangma along the Himalaya Range. They reckoned

that this basin must have been 2,500–3000 m lower than it is today because known Chinese hipparionine horses were from localities that are in the range of 500–1,000 m asl (Huang and Ji 1979; Huang et al. 1980). Interestingly, the Chinese vertebrate paleontologists were apparently unaware of the Falconer-Lydekker controversy and independently arrived at a similar conclusion as that by Falconer (1868) more than a century later.

Lydekker’s (1881, 1901) case against such claims can equally be employed for the low elevation arguments by Falconer (1868) and Chinese paleontologists above. Indeed, there is no compelling reason to think Mio-Pliocene equids and bovids, being endothermic as other eutherian mammals, could not survive in high altitude environments as living Tibetan ass and chiru can. However, it seems likely true that the modern-day dry climate and low shrub vegetation in Zanda Basin are indeed unlikely able to support a rhinoceros, let alone gomphothere proboscideans and an ancestral browsing giraffe (*Palaeotragus*). It is thus likely that elevation and climate changes both played a role, with the latter considerably more important than the former in supporting a fauna and flora that is so different from that of modern-day Zanda Basin.

More recently, Deng et al. (2012) advanced another hypothesis on paleoelevation based on Zanda fossil horses. But instead of arguing for lower elevation, Deng et al. suggested that the cursorial nature of Zanda three-toed horse, *Hipparion zandaense*, demonstrates the attainment of modern horse level of cursorial specialization, implying adaptations in open terrains high above timberline. Such arguments, however, suffer from similar logical setbacks as above because highly cursorial horses are equally at ease in both high and low altitudes, as modern *Equus* demonstrates. In any case, browsing gomphotheres and giraffe suggest the presence of trees, distributions of which are controlled by amount of precipitation in addition to elevation.

More than 150 years after the Falconer-Lydekker debate, modern geochemistry offers better hopes for tackling the questions of paleoelevation, but considerable controversies remain. For Qaidam Basin, fossil leaves indicate attainment of its present-day elevation of about $3,000 \pm 1,400$ m asl by Oligocene (Song et al. 2020) but studies of the dialkyl glycerol tetraethers suggest a relatively low elevation of ~1,500 m asl during the early Miocene (Tian et al. 2021). For Zanda Basin, based on stable isotopes from fossil mollusks, Saylor et al. (2009) estimated an elevation at least as high as, and possibly up to 1.5 km higher than today, and the climate was cold and arid, indistinguishable from modern. Wang et al. (2013c), on the other hand, suggest a similar to or slightly (less than ~1 km) lower than present-day elevation based on carbon and oxygen stable isotopes from mammalian herbivores. Most recently, using clumped isotope thermometry on living and fossil snails,

Wang et al. (2020b), suggests a similar Pliocene elevation as modern.

For the Kunlun Pass Basin, on the other hand, Wang et al. (2008b) estimated that the basin was once a hospitable place with a much warmer and wetter climate in the late Pliocene. They further suggested that the elevation of the basin has increased by $\sim 2700 \pm 1600$ m since $\sim 2\text{--}3$ Ma compared to its current elevation of 4,700–4,900 m asl (Fig. 1).

The above geochemical evidence seems to indicate that Zanda and Kunlun Pass faunas must have endured significantly high elevations. Unfortunately, there are still no known osteological characters that are reliably associated with high altitude adaptations, much less with precision. An enlarged air sac in the nasal passage in living chiru (Hodgson 1833; Schaller 1998; Leslie and Schaller 2008) is a potential morphological character, but its osteological connection (if any) is yet to be investigated. The shortening of cheektooth row and the loss of the P2/p2 in the chiru lineage are also presumably related to diet, potentially offering information related to the vegetation.

Conclusion

We transfer *Pantholops hundsensis* Lydekker, 1881 to the genus *Qurlignoria* Bohlin, 1937. We re-describe the holotype partial skull of *Qurlignoria hundsensis* (Lydekker, 1881) from the BMNH collection, the first fossil mammal from Tibet in the scientific literature going back to as early as 1839, and regarded as a fossil ancestor of modern Tibetan chiru. With the addition of new materials collected during the past 20 years, including tentatively assigned lower jaws and teeth, this primitive Tibetan chiru is now substantially better known. The original type locality of “Hundes Plains” is undoubtedly Zanda Basin at the northern foothills of the Himalaya Range, and likely to have been collected from hillside caves near the village of Dongba. We tentatively assign the holotype of *Capricornis roylei* Pilgrim, 1939, an upper palate obtained at the same time as the holotype of *Q. hundsensis*, to the latter although we still lack definitively associated horncores and upper teeth.

We also describe horncore and dental materials of *Qurlignoria hundsensis* from Kunlun Pass Basin in the interior of Tibetan Plateau, representing one of the highest late Cenozoic sites in the world. Our records of *Qurlignoria* thus span much of the Tibetan Plateau ranging from relatively low-elevation Qaidam Basin to high elevation Kunlun Pass Basin. The chronologic occurrences show a progressive adaptation to higher elevations.

Phylogenetic analysis of *Qurlignoria* suggests a sister-group relationship to living *Pantholops*, as recently published by Tseng et al. (2022). While this framework is still

valid, the Pliocene materials described herein show no sign of transitions to living chiru. It appears that *Qurlignoria* is a side branch of the chiru lineage that persisted throughout late Miocene and Pliocene of the Tibetan Plateau with minimal changes. *Q. cheni* and *Q. hundsensis* thus appear to form a chronospecies succession. The Pliocene *Q. hundsensis* probably did not directly give rise to *Pantholops*. A direct ancestor of *Pantholops* is yet to be found.

Qurlignoria hundsensis played a key role in informing early controversies of paleoelevations of Zanda Basin and by extension, the rest of the Himalaya Range. Fossil mammals and their modern descendants offer the first scientific arguments in this century-old controversy over their elevational and environmental implications and are still being marshalled to lend support to various elevational models. Despite their often-flawed presentation, *Qurlignoria*, along with other ancient megaherbivores, is still relevant in the scientific discourse about paleoenvironments.

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

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Data availability 3D models of specimens described are available for download at <https://www.morphosource.org/dashboard/collections/000434456/edit?locale=en&> (see Material and method section).

Declarations

Competing interests The authors declare no conflicts of interest.

References

- Abel C (1826) On the supposed unicorn of the Himalayas. *Phil Mag* 68:232-234
- Bärmann EV, Rössner G (2011) Dental nomenclature in Ruminantia: Towards a standard terminological framework. *Mamm Biol* 76:762-768
- Batten JH (1838) Note of a visit to the Níti pass of the grand Himálayan chain. *J Asiatic Soc Bengal* 7:310-316
- Bibi F (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. *BMC Evol Biol* 13:166
- Bohlin B (1937) Eine Tertiäre säugetier-fauna aus Tsaidam. *Sino-Swedish Exped Publ* 1:3-111
- Bouvrain G, Sen S, Thomas H (1994) Un nouveau genre d'Antilope dans le Miocene superieur de Sinap Tepe en Turquie. *Rev Paléobiol Genève* 13:375-380
- Buckland W (1823) *Reliquiae Diluvianae; or, Observations on the Organic Remains Contained in Caves, Fissures, and Diluvial Gravel, and on Other Geological Phenomena, Attesting the Action of an Universal Deluge.* John Murray, London
- Buho H, Jiang Z, Liu C, Yoshida T, Mahamut H, Kaneko M, Asakawa M, Motokawa M, Kaji K, Wu X, Otaishi N, Ganzorig S, Masuda R (2011) Preliminary study on migration pattern of the Tibetan antelope (*Pantholops hodgsonii*) based on satellite tracking. *Adv Space Res* 48:43-48. <https://doi.org/10.1016/j.asr.2011.02.015>.
- Calamari ZT (2021) Total evidence phylogenetic analysis supports new morphological synapomorphies for Bovidae (Mammalia, Artiodactyla). *Am Mus Novitat* 3970:1-38
- Chen L, Qiu Q, Jiang Y, Wang K, Lin Z, Li Z, Bibi F, Yang Y, Wang J, Nie W, Su W, Liu G, Li Q, Fu W, Pan X, Liu C, Yang J, Zhang C, Yin Y, Wang Y, Zhao Y, Zhang C, Wang Z, Qin Y, Liu W, Wang B, Ren Y, Zhang R, Zeng Y, da Fonseca RR, Wei B, Li R, Wan W, Zhao R, Zhu W, Wang Y, Duan S, Gao Y, Zhang YE, Chen C, Hvilson C, Epps CW, Chemnick LG, Dong Y, Mirarab S, Siegmund HR, Ryder OA, Gilbert MTP, Lewin HA, Zhang G, Heller R, Wang W (2019) Large-scale ruminant genome sequencing provides insights into their evolution and distinct traits. *Science* 364:eaav6202. <https://doi.org/10.1126/science.aav6202>.
- Cui Z-j, Wu Y-q, Ge D-k, Liu G-n (1999) Environmental change of Kunlun Pass area since Quaternary. *Marine Geol Quat Geol* 19:53-62
- Cui Z-j, Wu Y-q, Liu G-n, Ge D-k, Pang Q-q, Xu Q-h (1998) The "Kunlun-Huanghe Movement". *Sci China (Ser D)* 28:53-59
- Deng T, Li Q, Tseng ZJ, Takeuchi GT, Wang Y, Xie G, Wang S, Hou S, Wang X (2012) Locomotive implication of a Pliocene three-toed horse skeleton from Tibet and its paleo-altimetry significance. *Proc Nat Acad Sci* 109:7374-7378 <https://doi.org/10.1073/pnas.1201052109>
- Deng T, Wang X, Fortelius M, Li Q, Wang Y, Tseng ZJ, Takeuchi GT, Saylor JE, Säilä LK, Xie G (2011) Out of Tibet: Pliocene woolly rhino suggests high-plateau origin of Ice Age megaherbivores. *Science* 333:1285-1288 <https://doi.org/10.1126/science.1206594>
- Falconer H (1868) VII. On the fossil rhinoceros of central Tibet and its relation to recent upheaval of the Himalayahs. *Palaeontological Memoirs and Notes of the Late Hugh Falconer, Volume 1, Fauna Antiqua Sivalensis* 1:173-185
- Fang X-m, Zhang W-l, Meng Q-q, Gao J-p, Wang X-m, King J, Song C-h, Dai S, Miao Y-f (2007) High-resolution magnetostratigraphy of the Neogene Huaitoutala section in the eastern Qaidam Basin on the NE Tibetan Plateau, Qinghai Province, China and its implication on tectonic uplift of the NE Tibetan Plateau. *Earth Planet Sci Lett* 258:293-306
- Faurby S, Svenning J-C (2015) A species-level phylogeny of all extant and late Quaternary extinct mammals using a novel heuristic-hierarchical Bayesian approach. *Mol Phyl Evol* 84:14-26 <https://doi.org/10.1016/j.ympev.2014.11.001>
- Ge R-L, Cai Q, Shen Y-Y, San A, Ma L, Zhang Y, Yi X, Chen Y, Yang L, Huang Y, He R, Hui Y, Hao M, Li Y, Wang B, Ou X, Xu J, Zhang Y, Wu K, Geng C, Zhou W, Zhou T, Irwin DM, Yang Y, Ying L, Bao H, Kim J, Larkin DM, Ma J, Lewin HA, Xing J, Platt RN, Ray DA, Auvil L, Capitanu B, Zhang X, Zhang G, Murphy RW, Wang J, Zhang Y-P, Wang J (2013) Draft genome sequence of the Tibetan antelope. *Nat Commun* 4:1858 <https://doi.org/10.1038/ncomms2860>
- Gentry AW (1968) The extinct bovid genus *Qurliqnoria* Bohlin. *J Mammal* 49:769
- Gentry AW (1992) The subfamilies and tribes of the family Bovidae. *Mamm Rev* 22:1-32
- Gentry AW (1994) The Miocene differentiation of Old World Pecora (Mammalia). *Hist Biol* 7:115-158
- Gentry AW (2003) 15. Ruminantia (Artiodactyla). In: Fortelius M, Kappelman J, Sen S, Bernor RL (eds) *Geology and Paleontology of the Miocene Sinap Formation, Turkey.* Columbia University Press, New York, pp 332-379
- GeoMapApp (Version 3.6.14) (2021) Available from <http://www.geomapapp.org> Accessed in April 2015.
- Google Earth Pro (Version 7.3.3.7786) (2020) Available from <https://www.google.com/work/earthmaps/earthpro.html>. Mountain View, CA: Google Inc. Accessed on December 24, 2021.
- Gray JE (1821) On the natural arrangement of vertebrate animals. *London Med Reposit* 15:296-310
- Gustafson EP (2015) An early Pliocene North American deer: *Bretzia pseudalces*, its osteology, biology, and place in cervid history. *Bull Mus Nat Hist Univ Oregon* 25:1-75
- Hedin S (1922) Southern Tibet: Discoveries in Former Times Compared with My Own Researches in 1906-1908. Vol. IV, Kara-Korum and Chang-Tang. Lithographic Institute of the General Staff of the Swedish Army, Stockholm
- Herbert JD (1831) On the organic remains found in the Himalaya. *Glean Sci* 3:265-272
- Hodgson BH (1833) Further illustrations of the *Antilope hodgsonii*, Abel. *Proc Zool Soc London* 1:110-111
- Huang W-b, Ji H-x (1979) Discovery of *Hipparion* fauna in Xizang. *Chin Sci Bull* 24:885-888
- Huang W-b, Ji H-x, Chen W-y, Hsu C-q, Zheng S-h (1980) Pliocene stratum of Guizhong and Bulong Basin, Xizang. In: Qinghai-Tibetan Plateau Comprehensive Scientific Investigation Team of Chinese Academy of Sciences (ed) *Paleontology of Tibet, Part 1.* Science Press, Beijing, pp 4-17
- Ji H-x, Hsu C-q, Huang W-b (1980) The *Hipparion* fauna from Guizhong Basin, Xizang. In: Qinghai-Tibetan Plateau Comprehensive Scientific Investigation Team of Chinese Academy of Sciences (ed) *Paleontology of Tibet, Part 1.* Science Press, Beijing, pp 18-32
- Kostopoulos DS, Erol AS, Mayda S, Yavuz AY, Tarhan E (2020) *Qurliqnoria* (Bovidae, Mammalia) from the Upper Miocene of Çorakyerler (Central Anatolia, Turkey) and its biogeographic implications. *Palaeoworld* 29:629-635 <https://doi.org/10.1016/j.palwor.2019.10.003>
- Leslie DM, Schaller GB (2008) *Pantholops hodgsonii*. *Mamm. Species* 817: 1-13
- Li F-l, Li D-l (1990) Latest Miocene *Hipparion* (*Plesiohipparion*) of Zanda Basin. In: Yang Z, Nie Z (eds) *Paleontology of the Ngari Area, Tibet (Xi Zang).* China University of Geological Science Press, Wuhan, pp 186-193
- Li Q, Stidham TA, Ni X, Li L (2017) Two new Pliocene hamsters (Cricetidae, Rodentia) from southwestern Tibet (China), and their implications for rodent dispersal 'into Tibet'. *J Vert*

- Paleontol 37:e1403443 <https://doi.org/10.1080/02724634.2017.1403443>
- Li Q, Wang X (2015) Into Tibet: An early Pliocene dispersal of fossil zokor (Rodentia: Spalacidae) from Mongolian Plateau to the hinterland of Tibetan Plateau. PLoS ONE 10:e0144993 <https://doi.org/10.1371/journal.pone.0144993>
- Li Q, Xie G-p, Takeuchi GT, Deng T, Tseng ZJ, Grohé C, Wang X (2014) Vertebrate fossils on the Roof of the World: Biostratigraphy and geochronology of high-elevation Kunlun Pass Basin, northern Tibetan Plateau, and basin history as related to the Kunlun strike-slip fault. Palaeogeog Palaeoclim Palaeoecol 411:46-55 <https://doi.org/10.1016/j.palaeo.2014.06.029>
- Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale. Editio decima, 1758. Societatis Zoologicae Germanicae, Stockholm
- Lydekker R (1881) Observations on the ossiferous beds of Húndes in Tibet. Rec Geol Surv India 14:178-184
- Lydekker R (1901) On the skull of a chiru-like antelope from the ossiferous deposits of Hundes (Tibet). Quart J Geol Soc 57:289-292
- Ma L, Shao X, Wang Y, Yang Y, Bai Z, Zhao Y, Jin G, Ga Q, Yang Q, Ge R-L (2014) Molecular cloning, characterization and expression of myoglobin in Tibetan antelope (*Pantholops hodgsonii*), a species with hypoxic tolerance. Gene 533:532-537 <https://doi.org/10.1016/j.gene.2013.09.030>
- Moorcroft W (1816) A journey to Lake Mánasaróvara in Ún-dés, a province of little Tibet. Asiatic Res 12:375-534
- Owen R (1848) Description of teeth and portions of jaws of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyopotamus bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. Contrib Hist British Fossil Mamm (First Ser) Part VII:30-71
- Owen R (1870) On fossil remains of mammals found in China. Quart J Geol Soc London 26:417-434
- Ozansoy F (1957) Faunes de mammifères du Tertiaire de Turquie et leurs révisions stratigraphiques. Bull Mineral Res Expl Inst Turkey 49:29-48
- Ozansoy F (1965) Étude des gisements continentaux et des mammifères du Cénozoïque de Turquie. Mém Soc Géol France 44:1-92
- Pilgrim GE (1934) Two new species of sheeplike antelope from the Miocene of Mongolia. Am Mus Novit 716:1-29
- Pilgrim GE (1939) The fossil Bovidae of India. Palaeont Indica 26: 1-356
- Qian F (1999) Study on magnetostratigraphy in Qinghai-Tibetan plateau in late Cenozoic. J Geomech 5:22-34
- Qian F, Ma X-h, Wu X-h, Pu Q-y (1982) Magnetostratigraphy of the Qiangtang and Quguo formations. In: Editorial Committee (ed) Collected Papers of Geology of the Qinghai-Tibetan Plateau. Geology Publishing House, Beijing, pp 121-130
- Qian F, Zhang J (1997) Study on the magnetic stratigraphy of the Qiangtang Formation and the neotectonism. J Geomech 3:50-56
- Qiu Z-x, Ye J, Jiang Y-j (1987) Some mammalian fossils of Bahe Stage from Wuzhong, Ningxia. Vert Palasiat 25:46-56
- Rawling CG (1905) The Great Plateau. Being an Account of Exploration in Central Tibet, 1903, and of the Gartok Expedition, 1904-1905. London Edward Arnold
- Rollins CK, Hall DM (1999) Using light and scanning electron microscopic methods to differentiate ibex goat and Tibetan antelope fibers. Textile Res J 69:856-860
- Royle JF (1839) Illustrations of the Botany and Other Branches of the Natural History of the Himalayan Mountains, and of the Flora of Cashmere, Volume I. Wm. H. Allen and Co., London
- Saylor JE, Quade J, Dettman DL, DeCelles PG, Kapp PA, Ding L (2009) The late Miocene through present paleoelevation history of southwestern Tibet. Am J Sci 309:1-42.
- Schaller GB (1996) Realm of the snow antelope. Nat Hist 1996:48-52
- Schaller GB (1998) Wildlife of the Tibetan Steppe. University of Chicago Press, Chicago, Illinois
- Schlosser M (1904) Die fossilen Cavicornier von Samos. Beitr Paläontol Geol Österreich-Ungarns Oriens 17:28-118
- Sclater PL, Thomas O (1897) The Book of Antelopes, Vol. III. R. H. Porter, London
- Shen X, Tian Q, Ding G, Wei K, Chen Z, Chai C (2001) Late Cenozoic stratigraphic sequence and its implication to tectonic evolution, Hejiakouzi Area, Ningxia Hui Autonomous Region. Earthquake Res China 15:380-389
- Signore AV, Storz JF (2020) Biochemical pedomorphosis and genetic assimilation in the hypoxia adaptation of Tibetan antelope. Sci Adv 6:eabb5447 <https://doi.org/10.1126/sciadv.abb5447>
- Smith AT, Xie Y (2013) Mammals of China. Princeton University Press, Princeton
- Song B, Spicer RA, Zhang K, Ji J, Farnsworth A, Hughes AC, Yang Y, Han F, Xu Y, Spicer T, Shen T, Lunt DJ, Shi G (2020) Qaidam Basin leaf fossils show northeastern Tibet was high, wet and cool in the early Oligocene. Earth Planet Sci Lett 537:116175 <https://doi.org/10.1016/j.epsl.2020.116175>
- Song C-h, Gao D-l, Fang X-m, Cui Z-j, Li J-j, Yang S-l, Jin H-b, Burbank DW, Kirschvink JL (2005) Late Cenozoic high-resolution magnetostratigraphy in the Kunlun Pass Basin and its implications for the uplift of the northern Tibetan Plateau. Chin Sci Bull 50:1912-1922
- Strachey R (1851a) On the geology of part of the Himalaya Mountains and Tibet. Proc Geol Soc 7:292-310 <https://doi.org/10.1144/GSL.JGS.1851.007.01-02.54>
- Strachey R (1851b) On the physical geography of the provinces of Kumáon and Garhwál in the Himálaya mountains, and of the adjoining parts of Tibet. J Roy Geog Soc London 21:57-85
- Tekkaya İ (1974) The Bovidae fauna of middle Sinap of Turkey. Bull Geol Soc Turkey 17:173-186
- Tian Q, Fang X, Bai Y, Chen C, Hou J, Zhang T (2021) An early Miocene lowland on the northeastern Tibetan Plateau. Frontiers Ear Sci 9:759319. <https://doi.org/10.3389/feart.2021.759319>
- Tong H-w, Zhang B (2019) New fossils of *Eucladoceros boulei* (Artiodactyla, Mammalia) from Early Pleistocene Nihewan Beds, China. Palaeoworld 28:403-424
- Traill GW (1832) Statistical report on the Bhotia Mehals of Kumaon. Asiatic Res 17:1-50
- Tseng ZJ, Li Q, Wang X (2013a) A new cursorial hyena from Tibet, and analysis of biostratigraphy, paleozoogeography, and dental morphology of *Chasmaporthetes* (Mammalia, Carnivora). J Vert Paleontol 33:1457-1471 <https://doi.org/10.1080/02724634.2013.775142>
- Tseng ZJ, Wang X, Li Q, Xie G-p (2022) *Qurlignoria* (Mammalia: Bovidae) fossils from Qaidam Basin, Tibetan Plateau and deep-time endemism of the Tibetan antelope lineage. Zool J Linnean Soc:1-23 <https://doi.org/10.1093/zoolin/zlab117>
- Tseng ZJ, Wang X, Li Q, Xie G (2016) Pliocene bone-cracking Hyaeninae (Carnivora, Mammalia) from the Zanda Basin, Tibet Autonomous Region, China. Hist Biol 28:69-77
- Tseng ZJ, Wang X, Slater GJ, Takeuchi GT, Li Q, Liu J, Xie G (2013b) Himalayan fossils of the oldest known pantherine establish ancient origin of big cats. Proc Royal Soc B 281: 20132686 <https://doi.org/10.1098/rspb.2013.2686>
- Vasileiadis N, Tsoukala E, Kostopoulos DS (2019) The late Miocene bovids from Platania (Drama Basin, Greece), with description of a new species of *Palaeoryx*. Geobios 55:57-76 <https://doi.org/10.1016/j.geobios.2019.06.005>

- Wang N, Chang M-m (2010) Pliocene cyprinids (Cypriniformes, Teleostei) from Kunlun Pass Basin, northeastern Tibetan Plateau and their bearings on development of water system and uplift of the area. *Sci China Earth Sci* 53:485–500 <https://doi.org/10.1007/s11430-010-0048-5>
- Wang N, Chang M-m (2012) Discovery of fossil Nemacheilids (Cypriniformes, Teleostei, Pisces) from the Tibetan Plateau, China. *Sci China Earth Sci* 55:714–727 <https://doi.org/10.1007/s11430-012-4368-5>
- Wang S-Q, Yang Q, Zhao Y, Li C-X, Shi Q-Q, Zong L-Y, Ye J (2018) New *Olonbulukia* material and its related assemblage reveal an early radiation of stem Caprini along the north of the Tibetan Plateau. *J Paleontol*:1–13 <https://doi.org/10.1017/jpa.2018.65>
- Wang S, Zhang W, Fang X, Dai S, Kempf O (2008a) Magnetostratigraphy of the Zanda basin in southwest Tibet Plateau and its tectonic implications. *Chin Sci Bull* 53:1393–1400
- Wang X, Flynn LJ, Fortelius M (2013a) Introduction. Toward a continental Asian biostratigraphic and geochronologic framework. In: Wang X, Flynn LJ, Fortelius M (eds) *Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology*. Columbia University Press, New York, pp 1–25
- Wang X, Jukar AM, Tseng ZJ, Li Q (2020a) Dragon bones from the heavens: European explorations and early palaeontology in Zanda Basin of Tibet, retracing type locality of *Qurlignoria hundesensis* and *Hipparion (Plesiohipparion) zandaense*. *Hist Biol* 33:1–11 <https://doi.org/10.1080/08912963.2020.1777551>
- Wang X, Li Q, Takeuchi GT (2016). Out of Tibet: an early sheep from the Pliocene of Tibet, *Protovis himalayensis*, genus and species nov. (Bovidae, Caprini), and origin of Ice Age mountain sheep. *J Vert Paleontol* 36:e1169190 <https://doi.org/10.1080/02724634.2016.1169190>
- Wang X, Li Q, Xie G-p, Saylor JE, Tseng ZJ, Takeuchi GT, Deng T, Wang Y, Hou S-k, Liu J, Zhang C-f, Wang N, Wu F-x (2013b) Mio-Pleistocene Zanda Basin biostratigraphy and geochronology, pre-Ice Age fauna, and mammalian evolution in western Himalaya. *Palaeogeog Palaeoclim Palaeoecol* 374:81–95 <https://doi.org/10.1016/j.palaeo.2013.01.007>
- Wang X, Li Q, Xie G (2014a) Earliest record of *Sinicuon* in Zanda Basin, southern Tibet and implications for hypercarnivores in cold environments. *Quat Int* 355:3–10 <https://doi.org/10.1016/j.quaint.2014.03.028>
- Wang X, Qiu Z-d, Li Q, Wang B-y, Qiu Z-x, Downs WR, Xie G-p, Xie J-y, Deng T, Takeuchi GT, Tseng ZJ, Chang M-m, Liu J, Wang Y, Biasatti D, Sun Z, Fang X, Meng Q (2007) Vertebrate paleontology, biostratigraphy, geochronology, and paleoenvironment of Qaidam Basin in northern Tibetan Plateau. *Palaeogeog Palaeoclim Palaeoecol* 254:363–385
- Wang X, Tseng ZJ, Li Q, Takeuchi GT, Xie G (2014b) From ‘third pole’ to north pole: a Himalayan origin for the arctic fox. *Proc Royal Soc B* 281:20140893 <https://doi.org/10.1098/rspb.2014.0893>
- Wang X, Xie G-p, Li Q, Qiu Z-d, Tseng ZJ, Takeuchi GT, Wang B-y, Fortelius M, Rosenström-Fortelius A, Wahlquist H, Downs WR, Zhang C-f, Wang Y (2011) Early explorations of Qaidam Basin (Tibetan Plateau) by Birger Bohlin -- reconciling classic vertebrate fossil localities with modern biostratigraphy. *Vert PalAsiat* 49:285–310
- Wang Y, Passey B, Roy R, Deng T, Jiang S, Hannold C, Wang X, Lochner E, Tripathi A (2020b) Clumped isotope thermometry of modern and fossil snail shells from the Himalayan-Tibetan Plateau: Implications for paleoclimate and paleoelevation reconstructions. *Geol Soc Am Bull* 133:1370–1380 <https://doi.org/10.1130/b35784.1>
- Wang Y, Wang X, Xu Y, Zhang C, Li Q, Tseng ZJ, Takeuchi GT, Deng T (2008b) Stable isotopes in fossil mammals, fish and shells from Kunlun Pass Basin, Tibetan Plateau: Paleoclimatic and paleoelevation implications. *Earth Planet Sci Lett* 270:73–85
- Wang Y, Xu Y, Khawaja S, Passey BH, Zhang C, Wang X, Li Q, Tseng ZJ, Takeuchi GT, Deng T, Xie G (2013c) Diet and environment of a mid-Pliocene fauna from southwestern Himalaya: Paleoelevation implications. *Earth Planet Sci Lett* 376:43–53 <https://doi.org/10.1016/j.epsl.2013.06.014>
- Zhang H-b, Li W-d, Liu Z-h (2003) Tibetan antelope (*Pantholops hodgsoni*). *Chin J Zool* 38:74
- Zhang Q-s, Wang F-b, Ji H-x, Huang W-b (1981) Pliocene stratigraphy of Zhada Basin, Tibet. *J Stratigr* 5:216–220

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