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### Journal

Journal of Vertebrate Paleontology, 36(5)

### ISSN

0272-4634

### Authors

Wang, Xiaoming  
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### Publication Date

2016-09-02

### DOI

10.1080/02724634.2016.1169190

Peer reviewed



# JVP

Journal of Vertebrate Paleontology



Volume 36, Number 5  
September 2016



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Print ISSN 0272-4634  
Online ISSN 1937-2809







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To cite this article: Xiaoming Wang, Qiang Li & Gary T. Takeuchi (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, *Journal of Vertebrate Paleontology*, DOI: [10.1080/02724634.2016.1169190](https://doi.org/10.1080/02724634.2016.1169190)

To link to this article: <http://dx.doi.org/10.1080/02724634.2016.1169190>

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## OUT OF TIBET: AN EARLY SHEEP FROM THE PLIOCENE OF TIBET, *PROTOVIS HIMALAYENSIS*, GEN. ET SP. NOV. (BOVIDAE, CAPRINI), AND ORIGIN OF ICE AGE MOUNTAIN SHEEP

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**ABSTRACT**—Modern wild sheep, *Ovis*, is widespread in the mountain ranges of the Caucasus through Himalaya, Tibetan Plateau, Tianshan-Altai, eastern Siberia, and the Rocky Mountains in North America. In Eurasia, fossil sheep are known at a few Pleistocene sites in North China, eastern Siberia, and western Europe, but are so far absent from the Tibetan Plateau. We describe an extinct sheep, *Protovis himalayensis*, gen. et sp. nov., from the Pliocene of the Zanda Basin in western Himalaya. Smaller than the living argali, this new form shares with *Ovis* posterolaterally arched horncores and partially developed sinuses and possesses several transitional characters leading to *Ovis*. *Protovis* likely subsisted on C<sub>3</sub> plants, which are the dominant vegetation in the Zanda area during the Pliocene. With the discovery of this new genus and species, we extend the fossil record for the sheep clade into the Pliocene of the Tibetan Plateau, consistent with our previous out-of-Tibet hypothesis. Ancestral sheep in the Pliocene were presumed adapted to high altitude and cold environments, and during the Ice Age, sheep became anatomically modern and dispersed outside of the Tibetan Plateau. Both this new fossil datum and the existing molecular phylogeny suggest that the Tibetan Plateau, possibly including Tianshan-Altai, represents the ancestral home range(s) of mountain sheep and that these basal stocks were the ultimate source of all extant species. Most sheep species survived along their Pleistocene route of dispersal, offering a highly consistent pattern of zoogeography.

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Citation for this article: Wang, X., Q. Li, and G. T. Takeuchi. 2016. Out of Tibet: an early sheep from the Pliocene of Tibet, *Protovis himalayensis*, gen. et sp. nov. (Bovidae, Caprini), and origin of Ice Age mountain sheep. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2016.1169190.

### INTRODUCTION

Wild sheep, *Ovis* Linnaeus, 1758, is part of the Ice Age megafauna that survived the end-Pleistocene extinction. Well adapted to mountainous terrains and high plateaus, six extant species span much of Eurasia and the Rocky Mountains of North America and their distribution strikingly reflects routes of dispersal (Rezaei et al., 2010). Recent molecular phylogenies increasingly indicate that *Ovis* is well embedded within the Caprini clade (the tribe including sheep, goats, muskox, and others) (Fernández and Vrba, 2005; Ropiquet and Hassanin, 2005; Hassanin et al., 2009; Shafer and Hall, 2010; Hassanin et al., 2012). The fossil history of the mountain sheep is, however, known only by a few isolated records in the Pleistocene of northern China, eastern Siberia, and western Europe, all outside of the Tibetan Plateau

(see below). We have previously proposed an out-of-Tibet hypothesis regarding the origins of Ice Age megaherbivores (Deng et al., 2011; Wang et al., 2014c), in which we considered other megafaunal elements, such as the bharal (*Pseudois*, also known as blue sheep) from the Pliocene Zanda Basin, as examples of mountain-adapted species originating from Tibet. In this paper, we make a detailed study of the horncore material and conclude that, rather than a bharal, the Zanda Basin horncores belong to a new genus and species that is more basal to *Ovis*. Both our fossil record and molecular phylogeny strongly suggest an out-of-Tibet scenario for the mountain sheep.

**Institutional Abbreviations**—**IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **KUMA**, Mammalogy Collection, University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A.; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; **NIPB**, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining, Qinghai Province, China; **PMU**, Palaeontological Museum, Uppsala University, Uppsala, Sweden.

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## MATERIALS AND METHODS

Our usage of the Plio-Pleistocene boundary at 2.6 Ma follows the recent decision by the International Commission on Stratigraphy (Gibbard et al., 2010; Pillans and Gibbard, 2012). X-ray photography was made with a digital soft X-ray machine (Softex model VIX-150).

Phylogenetic analysis was performed in MrBayes 3.2.0 (Ronquist et al., 2012), as well as through manual exploration in Mesquite (Maddison and Maddison, 2015). We used the default evolutionary model and runtime parameters in MrBayes (mcmcngen = 2,500,000, samplefreq = 500, printfreq = 500, diagnfreq = 1000).

## SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758  
Order ARTIODACTYLA Owen, 1848  
Family BOVIDAE Gray, 1821  
Subfamily ANTILOPINAE Gray, 1821  
Tribe CAPRINI Gray, 1821  
*PROTOVIS*, gen. nov.

**Type Species**—*Protovis himalayensis*, new genus and species.

**Etymology**—*prōtos*, Greek prefix for ‘primitive’ or ‘ancestral,’ combined with *Ovis* for living wild sheep.

**Diagnosis**—*Protovis* differs from basal caprins with primitive horncore morphology, such as *Rupicapra*, *Oreamnos*, *Nemorhaedus*, and *Pantholops*, in its much elongated and thickened horncores that are arching dorsally and laterally, have a slight homonymous torsion at the tips, and modest development of the sinus at the basal part of the horncores no more than 10 cm from the base of the horncore. *Protovis* is distinct from *Ovis* by its less thickened horncores, greater divergence of the horncores instead of a more posteriorly arched and spiraled condition in *Ovis*, nearly equal length and width at horncore base, and a less extensive development of the sinus within the horncores. *Protovis* is distinguishable from *Pseudois* in its long axis of the horn core rotated less strongly against the sagittal plane but more arched upward and posteriorly, less tapering off toward the tips, and smoother surface. *Protovis* differs from *Tossunnoria* in its much longer horncores that are not mediolaterally compressed.

*PROTOVIS HIMALAYENSIS*, sp. nov.

(Figs. 2–4)

*Pseudois* sp.: Deng et al., 2011:1287, fig. 2D; Wang et al., 2013a:table 3; Tseng et al., 2013a:6.

*Pseudois* n. sp.: Wang et al., 2014c:table 2.

**Holotype**—IVPP V18928, nearly complete male left and right horncores (Figs. 2, 3), collected by Qiang Li on August 19, 2007.

**Type Locality**—IVPP locality ZD0712, N31°33′55.6″, E79°51′53.4″, Guanjingtai, Zanda County, Tibetan Autonomous Region (Fig. 1).

**Referred Specimen**—From IVPP locality ZD0604, N31°27′27.2″, E79°43′59.2″, an uncatalogued horncore fragment collected by Gary Takeuchi on September 2, 2006 (Fig. 2C).

**Etymology**—The species came from the Himalaya Mountains.

**Diagnosis**—Same as for genus.

**Age and Associated Fauna**—At an elevation of 4295 m above sea level, IVPP locality ZD0712 (Fig. 1) was correlated to the 568 m level of the South Zanda section by Saylor et al. (2010a, 2010b), which was correlated to Chron 2An.1r with a calibrated age of 3.10 ± 0.2 Ma (Hilgen et al., 2012; Wang et al., 2013c). IVPP locality ZD0604 is much lower (3803 m) in elevation and correlated to C3r with a calibrated age of 5.46 ± 0.2 Ma (Wang

et al., 2013a:table 1). *Protovis himalayensis* thus spans much of the Zanda section from latest Miocene through much of the Pliocene, although the horncore fragment (Fig. 2C) from IVPP locality ZD0604 is less secure in identification. Assuming an age range of 5.46–3.10 Ma, *P. himalayensis* is associated with nearly all taxa from the Zanda Basin, with the exception of the Pleistocene part of the section, including published taxa such as *Coelodonta thibetana* (Deng et al., 2011), *Hipparion zandaense* (Deng et al., 2012), *Chasmaporthetes gangriensis* (Tseng et al., 2013), *Pliocrocota perrieri* (Tseng et al., 2016), *Panthera blytheae* (Tseng et al., 2013a), *Vulpes qiuzhudingi* (Wang et al., 2014b), *Sinicuon* cf. *S. dubius* (Wang et al., 2014a), *Prosiphneus eriksoni* (Li and Wang, 2015), as well as many unpublished taxa: *Meles* sp., *Nyctereutes* cf. *N. tingi*, *Qurlignoria* sp., *Antilospira* sp., *Aepyosciurus* sp., *Nannocricetus* sp., *Mimomys* (*Aratomys*) *bili-keensis*, *Apodemus* sp., *Trischizolagus mirificus*, *Ochotona* sp., and others (see fig. 4 in Wang et al., 2013c).

## DESCRIPTION

The holotype horncores, IVPP V18928, form the main basis of this new species. The referred specimen from IVPP locality ZD0604 is consistent in size to a distal segment of the horncore in IVPP V18928 but has a slightly straighter curvature than the holotype, although it is too fragmentary to be certain about its identity. The holotype specimen, IVPP V18928, is a male (see Comparison with Extant Forms section), and with a total horncore upper curve length of 443 mm, this individual is similar in size to some extant species of *Ovis*. The holotype suffered from extensive damage to the dorsal surface of the right horncore (Fig. 1, inset), which is partially restored with plaster.

Surface texture of the horncores is mostly smooth and lacking fine grooves (especially along the proximal half) seen in many living sheep. Toward the distal half and more visible on the ventral surface, fine grooves are present (Fig. 3B). The grooves also indicate a slight homonymous torsion (i.e., left horncore twisting clockwise from the base up as defined by Kostopoulos, 2014) of the horncores by no more than half a turn, which is also seen in living bharals.

The horncores rise from the top of the skull roof. Initially diverging laterally and somewhat upward, the horncores gently curve backward and once reaching the highest point, arch downward and backward. The angle of horncore divergence in anterior view is 84°, and the width of the frontals between the horncores is 27 mm. This initial lateral splay makes a strikingly laterally expanded horn in dorsal view (Figs. 3, 4), somewhat like modern *Pseudois*, although the posterior bending of the distal half of the horncores is different from the latter, which continues to project laterally.

The cross-sections of the horncores are quite rounded, although a vague keel on the posteroventral side can be detected, and combined with a slightly flattened surface on the medial and lateral sides, a very faint triangular cross-section is also discernable (Fig. 2). The maximum cross-sectional (anteroposterior) length and (mediolateral) width at the base of the horncore is 78 mm by 75 mm, close to a living male individual of *Pseudois* but far smaller than most *Ovis* (Table 1). The tapering off, or thinning, of the horncores toward the tips is very gradual compared with those of *Ovis* and *Pseudois*.

At the proximal end, where the base of the horncore is broken off the skull, the front wall of the horncore (~10–20 mm) is generally twice as thick as the hind wall (~5–10 mm), probably due to the impact of horn clashing. X-ray images reveal a modest development of sinuses along the ventral margin of the horncore, mostly restricted to the basal part (Fig. 3A), which is more extensively developed in some Pleistocene bharals (Xu, 2009) and almost all *Ovis* (Wang, 1984, 1988). As shown in X-ray images, individual sinuses appear to be separated by struts that extend about 10 cm into the horncore.



FIGURE 1. Exposures near IVPP locality ZD0712 looking toward the west. Basement rocks (dark areas in mid-ground to the right, outlined by white lines) crop out in deeply cut valleys and are overlain by lacustrine sediments of the Zanda Formation. A distant mountain in the background is the Himalaya Range. Inset (lower right): the type specimen of *Protovis*, exposed dorsal side up, is preserved in greenish or rusty-yellow siltstones of near-shore facies. Photos taken by Qiang Li on August 19, 2007.

**Comparison with Extant Forms**—There are six living genera of bovids on the Tibetan Plateau: bharal (*Pseudois*), argali (*Ovis*), chiru (*Pantholops*), Tibetan gazelle (*Procapra*), takin (*Budorcas*), and yak (*Bos*). The latter four are easily ruled out from the new Zanda species due to their radically different horn-core morphology, and only *Pseudois* and *Ovis* need to be considered here.

The laterally diverging and upward arching horn-core configuration in *Protovis* is best compared with those of *Pseudois* and *Ovis*, both also extensively overlapping with each other in the entire Tibetan Plateau. The predominantly backwardly spiraling horns with triangular cross-section in the proximal segment and mediolaterally compressed cross-section in the distal segment in *Ovis* contrasts strongly with the laterally diverging horns with almost equal dimensions across the horn-core base in *Pseudois* (Table 1). Although *Protovis* does not match exactly with either one, overall it seems closer to *Ovis* in several ways (Fig. 4). The basal part of the horncores in *Protovis* are more posteriorly and upwardly projected, conditions somewhat similar to that in *Ovis* but in sharp contrast to the upward and lateral curvature in *Pseudois*. This is particularly obvious in lateral and dorsal views (Fig. 4). The relatively flat anterior surface of the horn core (widest part anteriorly) in cross-section is also more *Ovis*-like in

comparison with *Pseudois*, which has a more rounded section. Sinuses in *Protovis* horncores have struts, as does *Ovis*, in contrast to hollow pedicel sinuses in basal caprins. The sinuses in *Protovis*, however, are confined to the ventral portion (Fig. 3A), instead of the far more elaborately developed sinuses within the entire horn-core in *Ovis*, possibly due to its behavior of full-blown head clashing during rut (Wang, 1984, 1988), but see Farke (2010). Xu (2009:fig. 4) has documented an extensive sinus system with struts in fossil *Pseudois* from the late Pleistocene of western Beijing. *Protovis*, however, differs from both *Pseudois* and *Ovis* in its far more gradual tapering of the horncores, resulting in a very gentle narrowing of the horncores toward the tips. This is in contrast to a more dramatic thinning of the horns with sharp contrast in girths between the bases and tips for *Pseudois* and especially *Ovis*.

*Protovis* is also quite comparable to the North African Barbary sheep (aoudad), *Ammotragus*, which is also adapted to rocky terrains. In fact, external horn morphology of the Barbary sheep is remarkably similar to that of bharals, with upwardly and laterally arching horns (Gray and Simpson, 1980), and both morphological and molecular phylogenies tend to place *Ammotragus* and *Pseudois* near each other, but they are not sister groups (Fernández and Vrba, 2005; Ropiquet and Hassanin, 2005;



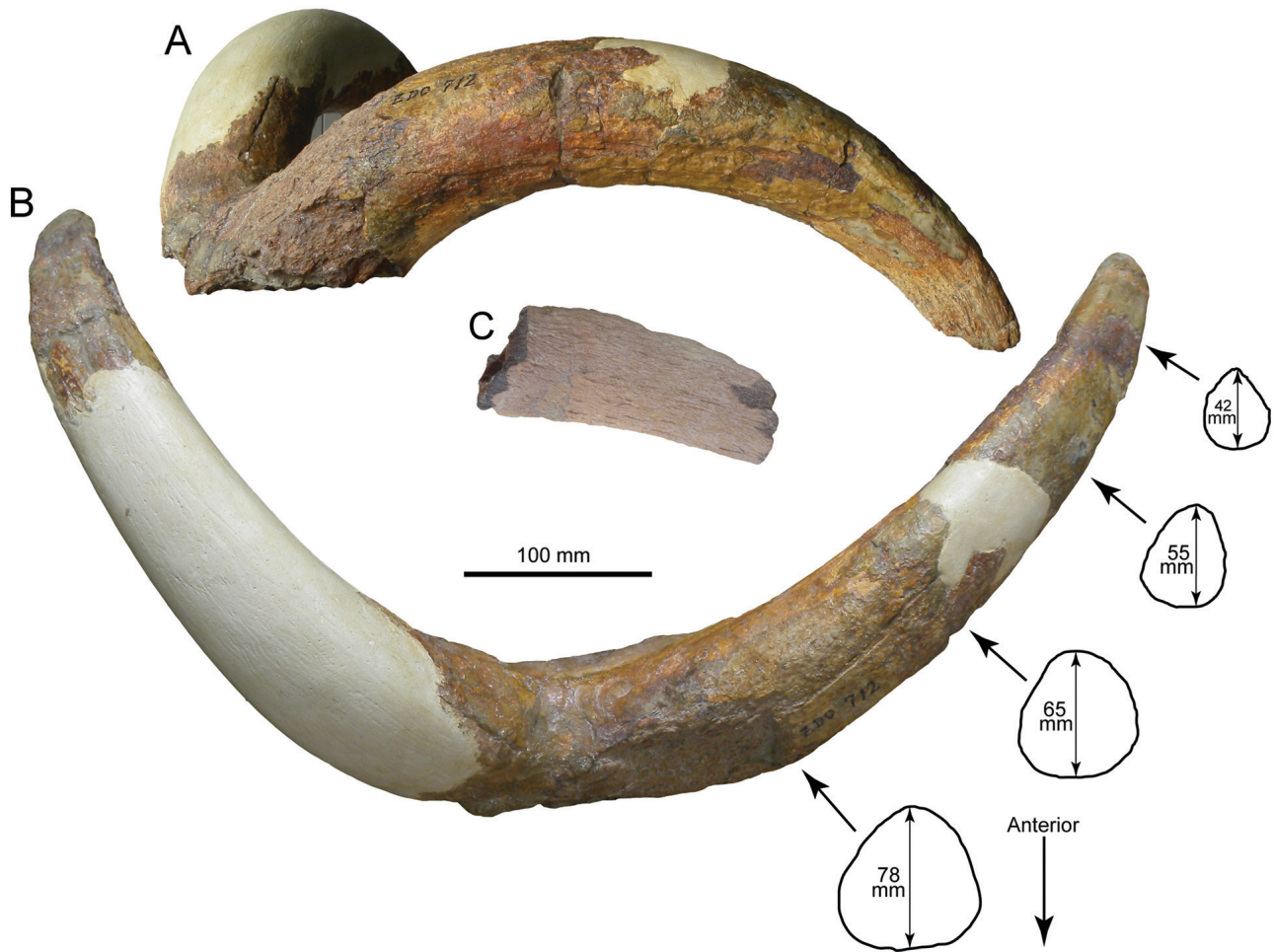


FIGURE 2. *Protovis himalayensis*, IVPP V18928, holotype. **A**, frontal-lateral view; **B**, dorsal view of horncores and cross-sectional shapes at four intervals along left horn; **C**, lateral view of horncore fragment from IVPP locality ZD0604 (uncatalogued).

Cantalapiedra et al., 2006; Hassanin et al., 2009, 2012), i.e., their horn similarities were possibly independently acquired. Based on the external horn morphology, the main differences between *Pseudois* and *Ammotragus* seem to be the former's more keeled horn sheath with more torsion and backward flare at the tips.

As in many modern bovids whose horns are intensely selected for intraspecific (sexual) competition, extant *Ovis* and *Pseudois* are strongly dimorphic both in body size and horn shape (Fig. 4). Males are typically larger than females by ~15% in linear dimensions and by ~35% in body weight in *Pseudois* (Wang and Hoffmann, 1987), and by 23–38% of body weight in *Ovis* (Schaller, 1977:table 11). Horncore dimorphism is even more pronounced, with those of males being not only much more massive but also more laterally or posteriorly arched, so much so that males and females were given separate species names in late Pleistocene *Pseudois* or even given different generic names in fossil sheep (see below). In light of the dimorphism in fossil and extant bharals and sheep, IVPP V18928 is undoubtedly a male because of its large horncore size (Table 1) and prominent lateral arching of the horncores.

**Comparison with Fossil *Ovis***—Assuming *Protovis* is closer to *Ovis* than *Pseudois*, the following comparisons are concentrated on the fossil sheep record. There is a modest fossil record for the *Ovis* clade in the Plio-Pleistocene of North China, France, Russian Siberia, and North America. Matsumoto (1926:39) was first to describe a fossil subspecies of argali, *Ovis ammon shantungensis*, from “later Pleistocene” loess of Wanchiagna, near Qingzhou

(Chinchou), Shandong Province. Shortly thereafter, Teilhard de Chardin and Piveteau (1930) elevated it to species rank and referred cranial material to it from the early Pleistocene Nihe-wan Basin. Young (1932) reported horncore and dental materials of *Ovis* cf. *O. ammon* from the middle Pleistocene Peking Man site at Zhoukoudian, which apparently extended to the Upper Cave site in the late Pleistocene (Dong et al., 2009). This was followed by additional references from the Yushe Basin to *O.* cf. *O. shantungensis* (Teilhard de Chardin and Trassaert, 1938), although this latter reference was based on dental and postcranial remains. Teilhard de Chardin and Trassaert (1938) did note that the Nihewan form may be a different species from *O. shantungensis*. Qiu (2000) considered that the Nihewan *Ovis* is more derived than that from Senèze, France (Delson et al., 2006; Cregut-Bonnoure, 2007).

Bohlin (1938) described *Ovis zdanskyi* based on a fairly complete skull, plus cervical vertebrae, from Yangshao Village of Mianchi County in Henan Province (locality 18, Yang-shao-tsun, Mien-chih-hsien). The associated fauna from locality 18 includes *Bos* sp., and the latter may indicate a late Pleistocene age. He also identified several specimens as *Ovis* cf. *O. ammon* from several sites (localities 2 and 25) from Xuanhua and Chicheng (formerly Longguan) counties in Hebei Province and Hallong Usu (Durbo-duggar-urto) of Inner Mongolia. Archaeological records from Yulin, Shaanxi Province, also record fossil *Ovis* (Hu et al., 2008).

The Nihewan materials, now defined as the Xiashagou Fauna (Qiu and Qiu, 1995; Cai et al., 2013), was viewed as the earliest

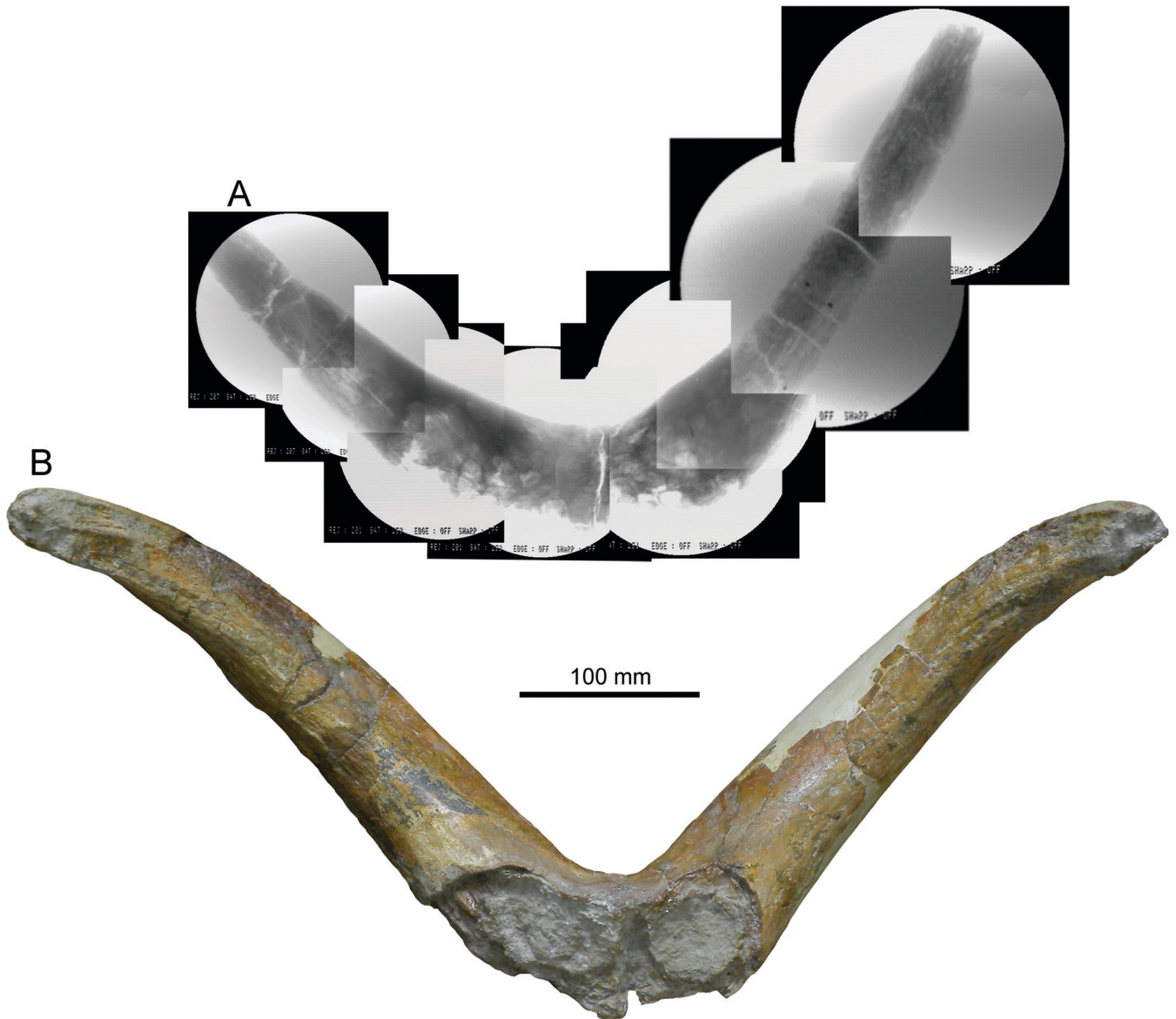


FIGURE 3. *Protovis himalayensis*, IVPP V18928, holotype. **A**, composite digital X-ray images of the horncores, dorsal view; **B**, posteroventral view of horncores.

record of *Ovis* until more recent reports from the early Pliocene Udungu in western Trans-Baikal region of Russian Siberia (Vislobokova et al., 1995; Erbajeva and Alexeeva, 2013; Kalmykov, 2013). However, only a short segment of horncore described by Kalmykov has the robust morphology of an *Ovis*, whereas those by Vislobokova et al. (occipital part of a skull and an isolated horncore) are not quite *Ovis*-like, as the authors themselves were doubtful about their own identification (Vislobokova et al., 1995:157). The Lake Baikal region has also produced some late Pleistocene *Ovis* materials (Shchetnikov et al., 2015). See Fedosenko and Blank (2005) for other miscellaneous fossil records of *Ovis*.

Mead and Taylor (2005) described a new species, *Sinocapra willdownsi*, from the early Pliocene of Nevada. They regard the rather straight and small horncores in *Sinocapra*, originally described from Yushe Basin by Chen (1991), as representing those of an adult female sheep. Such recognition, if correct, poses interesting chronological and geographic problems that place North America, not Asia, as having the earliest, or at least as early, and the most primitive sheep record.

In Europe, *Ovis* was first reported in early Pleistocene Senèze (~2 Ma), France (Delson et al., 2006; Cregut-Bonnoure, 2007). By the middle Pleistocene, abundant materials of *Ovis ammon antiqua* were found in the Caune de l'Arago in southern France (Rivals and Deniaux, 2003; Rivals et al., 2006). European *Ovis* appears to be a later expansion of sheep from Central Asia.

Except for the Yushe and North American *Sinocapra*, the above northern Chinese Plio-Pleistocene fossil records of *Ovis* are all very modern in their horncore morphology and their identity as *Ovis* is not in doubt. They differ from *Protovis* in similar ways as the extant *Ovis* (see above). This suggests that the sheep lineage was possibly developed within the Tibetan Plateau some time during the Pliocene (see below), reaching its present morphological condition by the Pleistocene. Assuming such a scenario, when they expanded outside of the Tibetan Plateau during the Ice Age, they were probably anatomically modern in horncore morphology, except for a slightly larger size. The Udungu record (Vislobokova et al., 1995; Erbajeva and



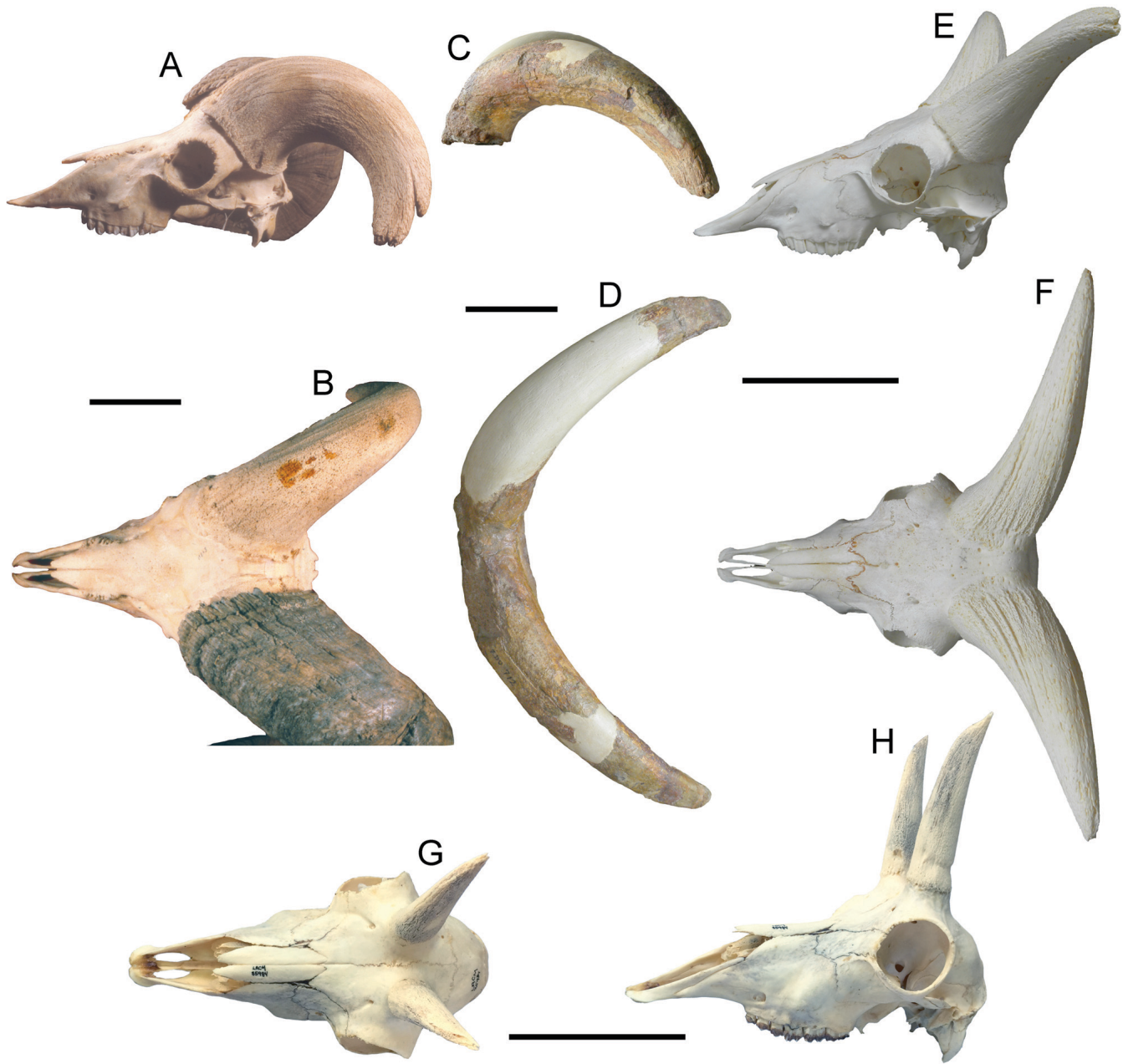


FIGURE 4. Comparison of *Protovis himalayensis* with male specimens of a basal caprin, *Rupicapra*, an extant bharal, *Pseudois*, and a bighorn sheep, *Ovis*. **A**, lateral (mirrored from right side) and **B**, dorsal views of *Ovis canadensis mexicana* (KUMA 54861 from Hidalgo County, New Mexico); **C**, lateral and **D**, dorsal views of *Protovis himalayensis* (IVPP V18928); **E**, lateral and **F**, dorsal views of a male *Pseudois nayaur* (NIPB KX1, from Kekexili in Qinghai Province); **G**, lateral and **H**, dorsal views of a male *Rupicapra rupicapra* (LACM 85984 from the San Diego Zoo). To facilitate comparison, all specimens are scaled to approximately the same size. Scale bars equal 10 cm.

Alexeeva, 2013; Kalmykov, 2013) is too fragmentary to evaluate, and its true status remains to be revealed in future discoveries.

#### PHYLOGENY

Recent molecular phylogenies consistently place *Ovis* in the caprins (Hassanin et al., 1998; Fernández and Vrba, 2005; Cantalapiedra et al., 2006; Bibi, 2013). Based on the complete mitochondrial genome, Hassanin et al. (2009) placed the sister group *Ovis* + *Oreamnos* near the base of the Caprina clade, although such a sister relationship no longer exists when placed in a larger context of Cetartiodactyla (Hassanin

et al., 2012). Although *Ovis* is increasingly positioned more basal to *Pseudois* relative to the adjacent *Pantholops* and *Rupicapra*, *Ovis* horncore morphology is highly derived, as seems consistent with an animal that is known for its high impact clashing (and related behaviors) during rut. It thus seems safe to assume that a ‘goat-like’ horncore with simple, thin, short, upright, and slightly backwardly arching tips, such as those in *Rupicapra* (chamois), *Oreamnos* (mountain goat), and *Naemorhedus* (goral), are the primitive plans for the basal caprin clade (Ropiquet and Hassanin, 2005; Shafer and Hall, 2010). From such a basal configuration, we might envision a morphological transformation toward modern *Ovis*,

TABLE 1. Measurements of the horncores (in mm).

Dimension	<i>Tossunoria pseudibex</i>		<i>Protovis himalayensis</i> IVPP V18928		<i>Ovis shantungensis</i>		<i>Ovis zdanskyi</i>	<i>Ovis ammon</i>
	No. 481	No. 449	Left	Right	Left	Right		
Horncore base length	77	70	78	82	115	118		101
Horncore base width	43	37	75	82	93	84		73
Circumference of horncore base			240	251	320	313	318	274
Length of horncore along upper curve			438	443	210	340	310	285

Measurements for *Ovis shantungensis* are adopted from Matsumoto (1926), *O. zdanskyi* and *O. ammon* from Bohlin (1938), and *Tossunoria pseudibex* from Bohlin (1937).

with *Protovis* occupying a transitional position (Fig. 4). However, depending on the evolutionary scenario, it is also conceivable that *Protovis* may be related to *Pseudois*.

Sokolov (1959) postulated that the ancestor of *Capra* and *Ovis* was close to *Tossunoria* from the late Miocene of Qaidam Basin in the northern Tibetan Plateau (Bohlin, 1937), an idea also followed by Kalmykov (2013). In his description of *T. pseudibex*, Bohlin (1937) made extensive comparisons with the Siberian ibex, *Capra sibirica*, and concluded that *Tossunoria* is close to a goat (caprin), but he was unable to place it in a particular lineage. Similarities shared by *Tossunoria* and *Protovis* include a large lateral component in the horncore orientation and the massiveness of the horncores. There are, however, enough detailed differences to suggest that *Tossunoria* and *Protovis* probably are not in a direct ancestor-descendant relationship: the keeled dorsal surface, more compressed cross-sections, and short and abrupt tapering in *Tossunoria* horncores all indicate a distinct lineage of its own. Given the limited knowledge about *Tossunoria*, its robust horncores, which have a posterolateral orientation, do seem to be distantly related to the sheep clade. If this is the case, initial divergence of the sheep clade has a minimum age of ~10 Ma, because *Tossunoria* came from the Tuosu Fauna (Fang et al., 2007; Wang et al., 2007, 2011, 2013a).

Within the genus *Ovis*, Rezaei et al. (2010) recognized six species groups within two major clades: a central and western Asian clade of argali (*O. ammon*), urial (*O. vignei*), and mouflon (*O. orientalis*), and an eastern Asian–North American clade of snow sheep (*O. nivicola*), Dall sheep (*O. dalli*), and bighorn (*O. canadensis*), with a divergence time between these clades at 2.42 Ma. Bibi et al. (2012) combined mitochondrial DNA with morphological characters and arrived at essentially the same relationship.

To place *Protovis* in a phylogenetic framework, we coded horncore characters for *Protovis* and added them to Bibi et al.'s (2012) morphological matrix. Of the 52 characters, only 9

horncore characters can be coded and these are 30(2), 31(2), 32(0), 33(0), 36(0), 37(2), 39(2), 40(0), and 45(0) based on Bibi et al.'s (2012) character number scheme (numbers within parentheses are character states for *Protovis*) (see Bibi et al., 2012:1846, for links to their supermatrix archived in TreeBase). The resulting matrix can be downloaded from Supplemental Data. We used the default evolutionary model and runtime parameters in MrBayes 3.2.0 (Ronquist et al., 2012) (mcmc ngen = 2,500,000, samplefreq = 500, printfreq = 500, diagnfreq = 1000). The resulting tree is very similar to that of Bibi et al. (2012) and *Protovis* falls in the *Ovis* clade (Fig. 5A). Further manual exploration in Mesquite (Maddison and Maddison, 2015) constrained by Bibi et al.'s (2012:fig. 2) topology yields a similar tree of 195 steps, although a sister relationship of *Protovis* and *Ovis* is of equal length (Fig. 5B).

We would like to emphasize that Bibi et al.'s (2012) data matrix adopted here was designed to elucidate relationships of a new African fossil caprin, *Capra wodaramoya*, and transitional characters in and around the *Ovis* clade cannot easily be added without examination of all taxa in their matrix, a task that is beyond the scope of this study. The lack of resolution at the base of the *Ovis* clade in our analysis can be attributed to the poor conditions of preservation in Zanda fossils (only 9 of the 52 morphological characters can be coded) and our inability to add transitional characters in the matrix (outlined in Diagnosis for Genus section). Pending a more comprehensive phylogenetic analysis that includes fossil/transitional taxa and additional discoveries of new materials, our phylogenetic result must be considered an approximate solution. If our diagnostic characters for *Protovis* are taken into consideration, i.e., small size and thinner horncore (relative to larger and thicker horncores in living *Ovis*), more laterally oriented horncore (in contrast to more posteriorly oriented horncores in all extant *Ovis*), relatively weak horncore sinuses (extensive in *Ovis*), and equal distance in width and length of

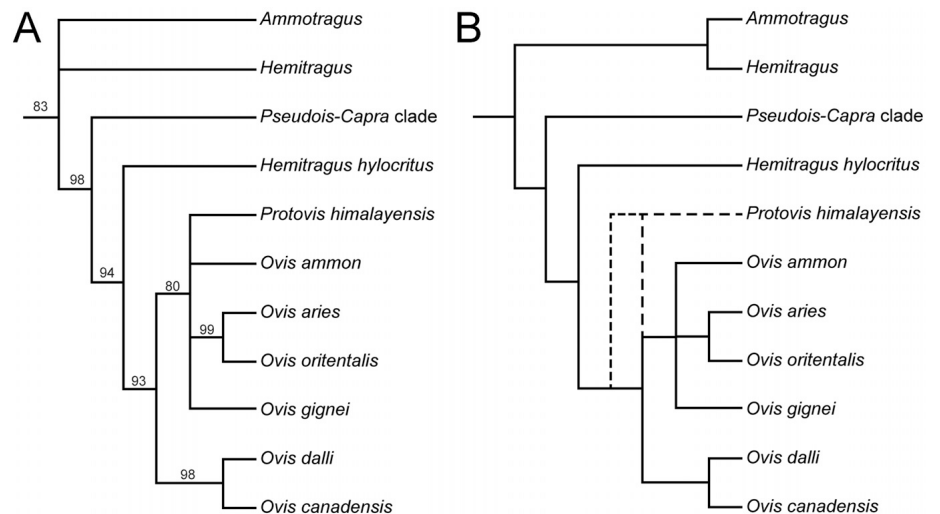


FIGURE 5. **A**, partial tree (*Capra-Ovis* clade) of Bayesian analysis of a modified supermatrix of cytochrome b plus 52 morphological characters by Bibi et al. (2012) with the addition of *Protovis* (see text); numbers at nodes are clade credibility values; **B**, partial shortest trees (*Capra-Ovis* clade) of 195 steps from manual manipulation in Mesquite (Maddison and Maddison, 2015) based on 52 morphological character matrix and constrained by a Bayesian tree topology from Bibi et al. (2012:fig. 2).



horncore cross-section (as opposed to more elongated in extant *Ovis*), all seem to point to a more primitive condition for *Protoavis*, falling outside of *Ovis*. We thus feel justified to choose one of the shortest trees in Figure 5B as our preferred evolutionary scenario (Fig. 6).

The above phylogenies from both living and fossil taxa are strikingly consistent with progressive dispersals from a Tibetan Plateau (or Central Asian) ancestral stock toward the west and east (see below; Fig. 6). Given our fossil sheep from Zanda, the ancestral sheep probably occupied a similar habitat as extant argali in the Tibetan Plateau and Altai ranges.

### ZOOGEOGRAPHY AND PALEOECOLOGY

Although dental remains for *Protoavis* are not available so far, studies on carbon isotopes on fossil mammalian herbivores from

Zanda Basin indicate that  $C_3$  vegetation formed the dominant plant community during the Pliocene (Wang et al., 2013b, 2014c). It is likely that *Protoavis*, too, had a  $C_3$  diet, as do the modern bovids within the Tibetan Plateau.

Situated between the Himalayas and Ayilariju ranges, Zanda Basin was formed in a tectonically active region (Saylor et al., 2007, 2010B), and throughout the basin development, basement outcrops from residual topography and surrounding mountains offered plenty of rugged terrain and gentle hills along the shores of the paleo-Zanda lake (Wang et al., 2013c). The type locality (IVPP locality ZD0712) of *Protoavis* is not far from one of the paleo-islands formed by metamorphic basement rock (Fig. 1), and these cliffs probably provided protection from predators in times of danger (Fig. 7).

With the present discovery of a primitive sheep in the Himalaya, we thus offer another example of our out-of-Tibet

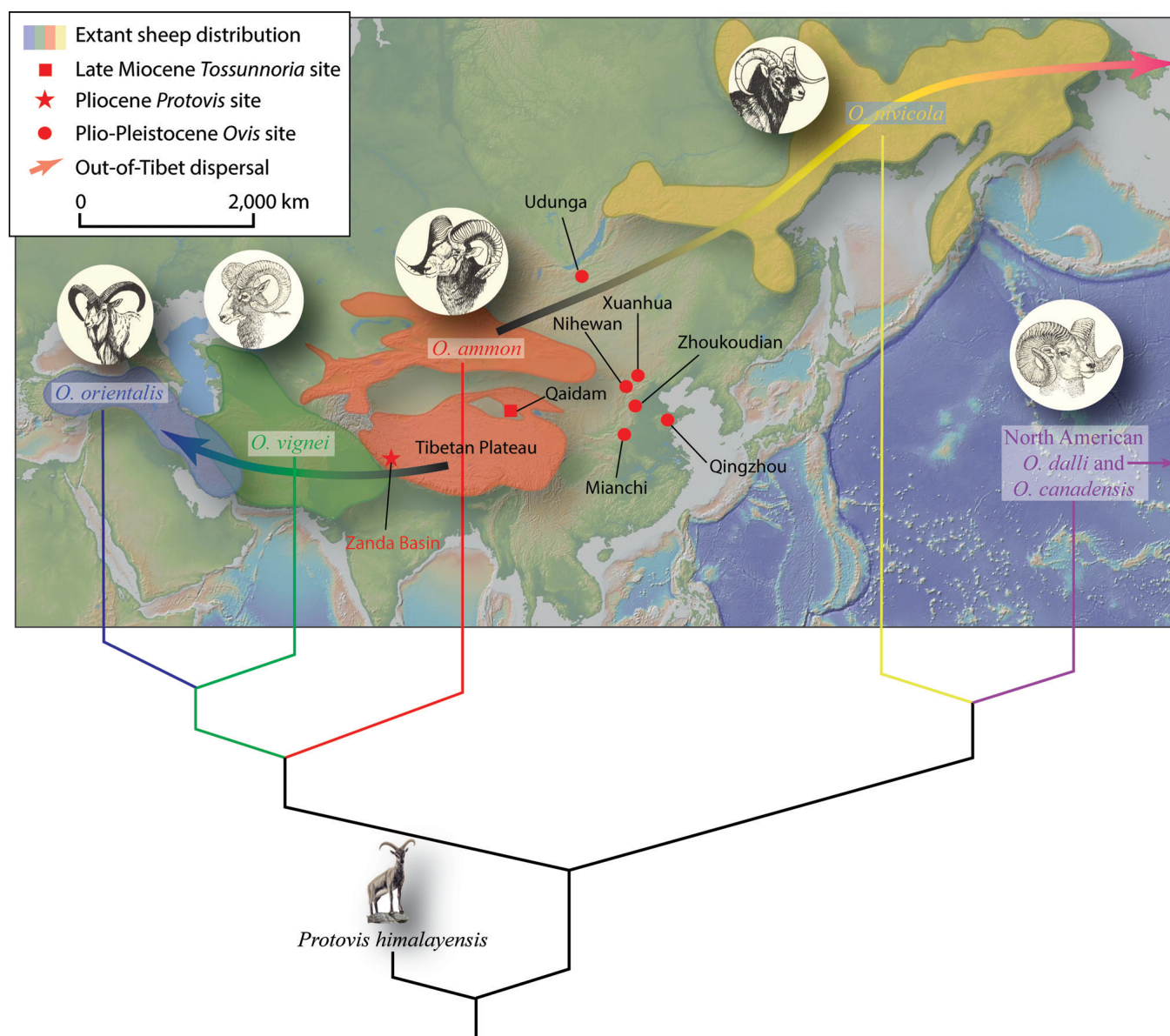


FIGURE 6. Map of extinct and extant species of *Ovis* in Eurasia and their evolutionary relationships. Topographic map was generated by GeoMap-App (version 3.5.1) (Ryan et al., 2009). Distribution of extant species of *Ovis* was simplified from those by Fedosenko and Blank (2005) and Rezaei et al. (2010). Phylogenetic relationship and classification of living *Ovis* follows those of Rezaei et al. (2010) and Bibi et al. (2012), and our own analysis of Zanda *Protoavis* based on Bibi et al.'s (2012) data matrix (Fig. 5). We adopt one of the alternative topologies shown in Figure 5B, which best accounts for the evidence at hand (see text for explanations). Head illustrations adapted from Geist (1971:figs. 43, 46) and Schaller (1977:fig. 7).



FIGURE 7. Artist reconstruction of a male Zanda sheep, *Protovis*, placed in a modern Zanda basement outcrop that was widely exposed during basin formation. Art by Julie Selan and photo background by Xiaoming Wang.

hypothesis (Deng et al., 2011; Wang et al., 2014c)—ancestral sheep were adapted to high-elevation cold environments in the Pliocene, and during the Pleistocene, they began to disperse outside their ancestral home range in Tibet to northern China, northern Siberia, and western Asia. The sheep thus joined several other mammals, such as big cats (Tseng et al., 2013), arctic foxes (Wang et al., 2014b), hypercarnivorous hunting dogs (Wang et al., 2014a), and woolly rhinoceros (Deng et al., 2011) in their expansion out of Tibet during the Ice Age and gave rise to elements of the Pleistocene megafauna.

Living argali prefer high rolling or broken hills on the upper slopes of mountain ranges (Schaller, 1998). With their long, thin legs, they are capable of fleeing danger in open terrain and are less dependent on rugged cliffs for escape than the bharals. Such adaptability enables the wild sheep to be excellent long-distance dispersers, crossing large open country areas between mountains. It is perhaps no surprise that the distribution of wild sheep presently stretches across much of the mountainous regions of

Eurasia and North America, and among Pleistocene megafauna, it's range is exceeded by only *Mammuthus* and *Bison* (Fig. 6). The potential route of Pleistocene dispersal in North China follows mountainous terrain, through Loess Plateau, and reaching Yanshan Mountains (including caves west of Beijing).

Geist (1971:313) remarked that primitive species or relict forms, such as *Rupicapra*, *Capricornis*, and *Hemitragus* from “south of the Himalayas,” are stagnant in evolution, in contrast to species to the north, which have undergone rapid morphological change. More broadly, Fortelius et al. (2014) suggested that physical forcing under harsh environmental conditions is the driver of evolution in Eurasia during the Neogene, which is consistent with our out-of-Tibet hypothesis (Wang et al., 2014c). Mountain sheep may represent a prime example of such a process. Ancestral sheep in the Tibetan Plateau, occupying a similar range as the extant argali, were adapted to high-elevation, cold environments during the Pliocene, when conditions elsewhere (including the high Arctic



regions) were much warmer (Ballantyne et al., 2010). These ancestral stocks evolved rapidly to morphological conditions similar to that of living *Ovis*. By the time the Ice Age arrives around 2.6 Ma, *Ovis* possessed a competitive advantage for surviving in freezing environments and spread rapidly to regions surrounding the Plateau and beyond, reaching North America during the late Pleistocene (Wang, 1988). As noted by Rezaei et al. (2010), the phylogenetic relationships and distribution of modern wild sheep strongly reflect their dispersal route—sheep species that succeeded in expanding to new ranges were able to stay there to found new species, despite the extremely harsh environments, such as snow sheep habitat in northeastern Siberia and Dall sheep habitat in the mountains of Alaska (Fig. 6). This high fidelity to their ancestral home ranges, often bound to particular mountain ranges, offers an excellent model for studying their Pleistocene dispersals. Fortunately, wild sheep were able to take refuge in mountain ranges, possibly an important contributing factor in protection against early human hunting, and they have largely survived the end-Pleistocene extinction that befell many of their megafaunal contemporaries.

#### ACKNOWLEDGMENTS

Materials described in this study were collected during the 2006 and 2007 field seasons, and we are indebted to the dedication by field participants and drivers that made our trip possible: Z. J. Tseng, Y. Wang, F.-q. Shi, W.-q. Feng, R. Laba, B. Sang, and L. Jie. We are indebted to J.-s. Dong, who provided numerous assistances in obtaining field permits. Y. Kimura provided assistance in Japanese literatures. We thank H.-w. Tong and Z.-j. Xu for permission to photograph living bharal specimens that they borrowed from the NIPB. J. Dines of Natural History Museum of Los Angeles County helped in loaning the *Rupicapra* specimen. We thank W.-d. Zhang of IVPP for assistance in X-ray photography. We are indebted to F. Bibi, who provided his supermatrix for a phylogenetic analysis as well as technical help in running MrBayes. We are grateful to two anonymous reviewers for criticism and suggestions that greatly improved the clarity of this paper. Financial support is provided by Strategic Priority Research Program of the Chinese Academy of Science (XDB03020104), Major Basic Research Projects of Ministry of Science and Technology of China (973 Program, No. 2012CB21904), CAS/SAFEA International Partnership Program for Creative Research Teams, Chinese National Natural Science Foundation (Nos. 41430102 and 40702004, and 41472002 to Q. L.), Chinese Academy of Science Outstanding Overseas Scholar Fund (KL205208), National Science Foundation (U.S.A.) (EAR-0446699, 0716507, 0958704, and 1227212 to X.W.), and National Geographic Society (nos. 6004–97 and 6771–00 to X. W., W22-08 to Q.L.).

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Submitted July 27, 2015; revisions received February 16, 2016;

accepted February 17, 2016.

Handling editor: Marcelo Sánchez-Villagra.