Palaeontologia Electronica
http://palaeo-electronica.org

# NEW SPECIES OF *SINOCAPRA* (BOVIDAE, CAPRINAE) FROM THE LOWER PLIOCENE PANACA FORMATION, NEVADA, USA

### Jim I. Mead and Louis H. Taylor

## ABSTRACT

A new species of Caprini is described from the early Pliocene (Blancan NALMA) Meadow Valley deposits of Panaca, Nevada, USA, and probably represents the earliest caprine known from North America. The Meadow Valley fauna of the Panaca Formation existed between 4.95 and 4.50 Ma ago. Comparative data indicate that *Sinocapra willdownsi* sp. nov. most closely resembles the extinct caprine *Sinocapra minor,* known only from the Yushe Basin, China. The Mazegou Formation locality, from which *S. minor* was collected, was deposited about 3.5 Ma ago. Morphological analysis also indicates that *Sinocapra* is more closely allied to sheep than to goats. Basal caprine ancestors were present in Europe during the late Miocene, but the earliest sheep, *Ovis,* appears in China at approximately 2.42 Ma ago. The earlier presence of the sheep-like *Sinocapra* in North America is problematic and may indicate an early migration from China. However, it may also indicate that *Sinocapra* evolved in North America from an ancestor that migrated from China even earlier, and later dispersed back to Asia. We postulate that *Sinocapra* migrated to North America from northeastern China during the latest Miocene or earliest Pliocene (late late Hemphillian NALMA).

Jim I. Mead. Department of Geology and the Quaternary Sciences Program, Northern Arizona University, Flagstaff, Arizona 86011, and Museum of Northern Arizona, Flagstaff, Arizona, 86001, USA
James.Mead@nau.edu
Louis H. Taylor. Denver Museum of Nature and Science, Denver, Colorado, 80001, USA
taylorlh1@msn.com

**KEY WORDS:** *Sinocapra*, Bovidae, Caprinae, Pliocene, North America

PE Article Number: 8.1.11

Submission: 18 February 2004. Acceptance: 6 April 2005.

Mead, Jim I., and Taylor, Louis H., 2005. New Species of Sinocapra (Bovidae, Caprinae) from the Lower Pliocene Panaca Formation, Nevada, USA, *Palaeontologia Electronica* Vol. 8, Issue 1; 11A:20p, 768KB;
http://palaeo-electronica.org/paleo/2005_1/mead11/issue1_05.htm

## INTRODUCTION

Ruminants (Artiodactyla, Ruminantia) include the chevrotain, Family Tragulidae, and five families within Pecora, including the Family Bovidae. Based on horn core characteristics, the earliest member of the Bovidae is *Eotragus* (Boselaphini) from the early-middle Miocene of Europe and Pakistan (Solounias et al. 1995; Gentry 2000). Simpson (1945) and Vrba and Schaller (2000) suggest that classification of Bovidae is among the most difficult of all mammalian families. As a monophyletic group, the modern bovids can be divided into five or six subfamilies, including the monophyletic Caprinae (Gentry 1992; Gatesy et al. 1997; Vrba and Schaller 2000). The Caprinae include the wild sheep and true goats (Caprini), the muskoxen (Ovibovini), and the mountain goats, gorals, serows, and chamois of the non-monophyletic group 'Rupicaprini' (Gentry 1992). See Gentry (1992) and Grubb (2001) for discussions concerning the utility of 'Rupicaprini' and 'Naemorhedini'; here we use 'Rupicaprini' and 'rupicaprine' in quotes to designate confusion created by non-monophyly and the need for further work within the group.

North America today has a number of endemic and Holarctic species of bovids including the bison (*Bison*), muskox (*Ovibos*), wild sheep (*Ovis*), mountain goat (*Oreamnos*), along with many extinct forms (Kurtén and Anderson 1980). The timing of the arrival of bovids from Asia is still inadequately understood. Here we present a new species of Caprini from the early Pliocene, Blancan NALMA (North American Land Mammal Age), deposits of Panaca, Nevada, USA. This species likely is the earliest caprine to enter North America.

## EARLY CAPRINES

*Protoryx enanus* from MN-7 (European Faunal zone, Mammal Neogene 7 late-middle Miocene) is thought to represent the earliest occurrence of the Caprinae (Gentry and Heinzmann 1996; Köhler 1987). Gentry (1971) assigned *Pachytragus* from the late Miocene of Greece to Caprini, providing the earliest representative of the tribe (but see Gentry [1992] for discussion of the middle Miocene aegodont bovids). Questions about the subfamilial and tribal attribution of *Protoryx* and *Pachytragus* remain (see discussion in Gentry and Heinzmann 1996; Gentry 2000). Vrba and Schaller (2000) suggest that *Pachytragus* is ancestral to the Caprini and that the group *Pantholops*-Caprinae experienced rapid evolution during the late Miocene. Synapomorphies are difficult to find, but Gentry (2000) believes that living Caprinae, other than Caprini, may have had separate ancestries dating well back into the Miocene.

*Tossunnoria* (late Miocene; Tsaidam Basin, China; Bohlin 1937) may be the predecessor of *Sivacapra* (late Pliocene; Pinjor Formation, Siwaliks, Pakistan; Pilgrim 1939) possibly the predecessor of the extant and extinct forms of *Hemitragus* (Himalayan tahr), part of a goat lineage within Caprini. Early caprine taxa are relatively rare in China and differ from contemporary European taxa. There is little question that basal Caprini existed by the late Miocene. Unfortunately late Miocene, Pliocene, and early Pleistocene caprines are extremely rare in the fossil record of northeastern Asia and North America, rendering their evolutionary history poorly understood; any record is noteworthy.

## FAUNAL INTERCHANGE EVENTS

The late Miocene Hemphillian NALMA begins at approximately 9 Ma with the immigration of mammals from Asia and South America (Tedford et al. 2004; part of the larger Interchange Event 10 of Woodburne and Swisher 1995). The immigration event of the late early Hemphillian (Hh2, approximately 7.5 to 6.8 Ma of Tedford et al. 2004) marks the arrival of the first bovid, *Neotragocerus*, to North America (Matthew and Cook 1909). Its affinity to other bovids has yet to be adequately established, yet it is the only bovid in North America during the late Miocene.

Deposits in the Yushe Basin of Shanxi Province, China, show major periods of faunal turnovers. The first takes place over a short period of time across the Mahui-Gaozhuang hiatus at approximately 5.8 to 5.9 Ma (Flynn et al. 1991; Tedford et al. 1991; chronology updated in Flynn 1997). Large mammal faunas show an abrupt turnover at the transition between Gaozhuang and Mazegou Formations (dating approximately 4.0 Ma) and illustrate a distinct immigration event (Flynn et al. 1991). Another major turnover event takes place during the Mazegou-Haiyan hiatus, which cannot be pinpointed but falls in the interval of 3.0 to 2.0 Ma (Tedford et al. 1991).

These turnover events in eastern Asia and North America not only illustrate extinctions, but also reflect faunal exchange between the two continents. We infer that the new species of caprine from the Panaca Formation described here immigrated from the general region of northeastern Asia during the latest Miocene or earliest Pliocene, i.e., late late Hemphillian, Hh4 equivalent (Tedford et al. 2004).

**Figure 1.** Type locality (star) for *Sinocapra willdownsi* sp. nov. at the Limestone Quarry of the Panaca Formation in southern Nevada, USA (see text for details).

## PANACA FORMATION, NEVADA

The Panaca Formation is exposed in Lake, Meadow, and Spring Valleys, Lincoln County, southeastern Nevada, USA (Figure 1), and represents basin-fill deposition. The caprine remains reported here are from Meadow Valley, a feature formed during middle to late Miocene crustal extension (Bartley et al. 1988). Phoenix (1948) estimated the total thickness of the Panaca Formation to be approximately 427 m. Sedimentological studies by Pederson et al. (1999) indicate that the deposit consists of horizontally stratified siltstones, sandstones, and mudstones, with occasional small artesian spring-formed lacustrine deposits (see review in Lindsay et al. 2002).

Stock (1921) first recovered and briefly described fossils from the Panaca Formation. White (1987, 1991) reported the leporids *Hypolagus edensis*, *Lepoides lepoides*, *Pewelagus dawsoni*, and *Nekrolagus progressus* and considered them characteristic taxa of the Blancan. Repenning (1987) placed the fauna in the early Blancan, based on his study of *Repomys panacaensis* and arvicolid (microtine) rodents *Mimomys* (*Ophiomys*) *magilli* and *Pliopotamys meadensis*. Mou (1997) described the primitive arvicolid *Mimomys panacaensis* from UALP locality 8197, a site correlative with and adjacent to Stock's AMNH Limestone Corner locality (Lindsay et al. 2002). The caprine specimens reported here were recovered from the Limestone Corner locality in 1940 and reportedly were recovered as a single cluster of skeletal elements, implying that they are related and represent a single individual (a premise followed here). This concept is consistent with the state of preservation and age of growth for various skeletal elements. All the small mammals and the artiodactyls from the Panaca Formation in Meadow Valley are more characteristic of the Blancan than of the previous Hemphillian Age and are part of the Rodent Ravine section of Lindsay et al. (2002).

The stratigraphic interval preserved in Meadow Valley spans about one million years, from approximately 5.5 Ma (upper part of chron C3r GPTS [Geomagnetic Polarity Time Scale]) to about 4.5 Ma (chron C3n.2n GPTS), as interpreted by Lindsay et al. (2002). Their work places the fauna of the Panaca Formation in Blancan I of Repenning (1987), its base in eastern Nevada being approximately 4.95 Ma. The age of the caprine remains reported here are between approximately 4.95 and 4.50 Ma (chron C3n.3r GPTS), immediately above the Hemphillian/Blancan NALMA boundary (Lindsay et al. 2002).

### Abbreviations

AMNH, American Museum of Natural History, New York, USA; GRCA, Grand Canyon National Park; NAUQSP, Northern Arizona University Quaternary Sciences Program, Laboratory of Quaternary Paleontology; PLWZM UM, Philip L. Wright Zoological Museum, University of Montana; UALP, University of Arizona Laboratory of Paleontology, Tucson, Arizona, USA.

## SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Suborder RUMINANTIA Scopoli, 1777
Superfamily BOVOIDEA Gray, 1821
Family BOVIDAE Gray, 1821
Subfamily CAPRINAE Gray, 1821
Tribe CAPRINI Gray, 1821
Genus *SINOCAPRA* CHEN, 1991
*Sinocapra willdownsi* sp. nov.

**Holotype:** AMNH 52139: left horn core and portion of orbit (52139A), fragmentary right horn core and corresponding frontal (52139A), fragmentary occipital region of skull (52139C, D), fragmentary right maxillary tooth row with P3-4, M1-2, isolated P2, and isolated left M1 (52139B), distal fragments left and right humerus (52139E), proximal fragment left ulna (52139E), distal fragment right metacarpal (52139E), first phalanx manus (52139E), first phalanx unknown position (52139E), second phalanx manus (52139E), fragmentary third phalanx manus (52139E), proximal fragment left and right femur (52139E), right metatarsal (52139E), right navicular-cuboid (52139E), right lunar (52139E).

**Type Locality and Age:** AMNH Limestone Corner locality (equivalent to UALP 8197 locality). Magnetozone C of chron C3n.3r GPTS. Approximately 4.95 to 4.50 Ma, immediately above the Hemphillian/Blancan boundary (as described in Lindsay et al. 2002).

**Etymology:** Named in honor of our late colleague and friend Will Downs, who worked extensively at the type locality of Panaca, Nevada (USA).

**Diagnosis:** An extinct Caprini of moderate size, but smaller than typical living members of the tribe, including *Sinocapra minor.* Horn core is short, nearly straight (no divergence), with a slight posterior curvature, moderately medio-laterally compressed, without transverse ridges, longitudinal grooves, or torsion, and hollow at base. Differs from S. minor in lacking a postcornual fossa. Specimen appears to represent adult female individual. P3-M2 are mesodont. Strong labial ribs occur between the parastyle, mesostyle, and metastyle. Distinct internal cavities occur between the protocone and metaconule on the M1-2. The metacarpal has a distinctive sulcus with slight crests (not sharp) parallel to the sulcus and is widely open (sagittal groove) at the distal epiphysis. The metatarsal has a sulcus on the dorsal surface, which extends from proximal to distal epiphyses, is apparent most of its length, and is prominent and open the distal third, with crests on both sides of the sulcus, and widely open (sagittal groove) at the distal epiphysis.

## DESCRIPTION AND COMPARISONS

### Horn Core

The left horn core (52139A) is complete and contains some fragmentary adjoining frontal bone (Figure 2). The horn core is short, nearly straight (no divergence), with a slight posterior curvature (recurved). The horn core is medio-laterally (transversely) compressed, with the medial side somewhat flattened and the lateral side more convex, producing an ovate cross section. The relatively smooth surface lacks both anterior and posterior keels and longitudinal grooves. There is no evidence of torsion (spiral twist to horn core and horn sheath). Sinus cavities extend into the basal portion of the horn core (Figure 2). The cranium is broken immediately adjacent to the position of a postcornual fossa (pf, Figure 2). If this fossa was small, it would probably be absent from the portion of the fossil preserved. Until more complete specimens can be located, there is no evidence that a postcornual fossa occurred on *Sinocapra willdownsi* Extant *Ovis, Capra, Hemitragus,* and *Oreamnos* have a highly reduced to absent postcornual fossa, whereas a shallow yet distinct fossa occurs on the holotype of *S. minor* (Figure 3; Chen 1991).

The horn core length is measured from the pedicle base (where the burr would be located; arrows in Figure 2; equals base of horn sheath) to the tip. Medio-lateral and nasal-nuchal (antero-posterior) measurements, taken at pedicle base, are included in Table 1.

**Discussion**: Although the horn core of *Sinocapra willdownsi* is unusually small relative to those of living caprines and the extinct *S. minor* (Table 1), we interpret that the small horn cores do not indicate a juvenile growth stage. Figure 4 contains a series of skulls showing ontogenetic growth stages for male and female *Ovis canadensis* (Rocky Mountain bighorn) and illustrates the sexual dimorphism that is expressed at an early age. Using even this small series of skulls, it is easy to determine the sex and approximate age of the wild sheep. At about three months of age, the horn core begins to appear on the frontal (Figure 4A). The horn core develops more rapidly on males. At an early age the horn core has a wide pedicle base yet little length (male and female); torsion begins early for males (arrow in Figure 4C). The young female (Figure 4B) still has a wide base to the horn core yet no torsion develops. These sexual dimorphic traits occur because the horn core and horn sheath in male *Ovis* spp. is highly twisted at maturity, providing the characteristic lateral curl to wild sheep rams (Figures 4E, 5I-L). Horn cores of female *Ovis* spp. are not twisted and are more-or-less straight with a slight posterior curvature (Figure 4D). The horn sheaths (therefore the horn cores also) of adult female *Ovis* spp. show little growth after about 2.5 years age (Geist 1971). Using horn growth of *Ovis* as a model for *Sinocapra*, it would appear that the individual from Panaca was likely at full growth stage of development.

Table 1 illustrates the small size of the Panaca caprine horn core in comparison to horn cores of other adult caprines including *Sinocapra minor* (sex not designated by Chen [1991]; see discussion below), *Ovis dalli* (Dall's bighorn; male and female), *Ovis nivicola* (Snow sheep; male), and

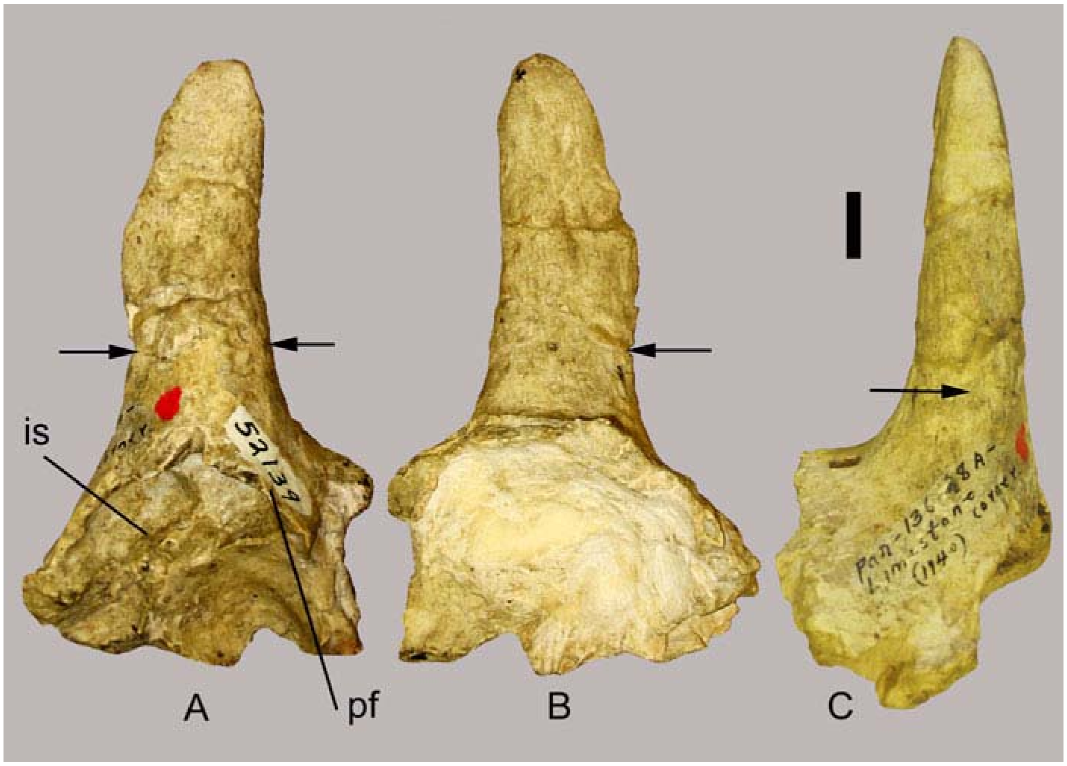

**Figure 2**. Left horn core of *Sinocapra willdownsi* (52139A). **A**, lateral view showing location of burr and base of pedicle (arrows) and the base of the horn sheath; anterior to left; **B**, medial view; anterior to right; **C**, anterior view. All views illustrate the straight horn core (no torsion) with only slight recurvature. Abbreviation: pf, postcornual fossa; is, internal sinus area exposed by breakage. Scale bar equals 10 mm.

*Ovis shantungensis* (extinct bighorn; assumed to be male), and the two 'rupicaprines' *Neotragocerus* (two species, extinct) and *Oreamnos* (two species, one extinct; male and female). Clearly the horn cores of the Panaca caprine are small, yet based on length and diameter measurements, the horn core is considered to be from an adult individual (a determination that is supported by tooth eruption; see below).

There is a slight posterior curvature orientation to the horn core of *S. willdownsi*, with no indication of torsion (such as would be found with the *Oioceros* (extinct) and members of the Bovini, Ovibovini, and many males of taxa within Caprini; e.g., *Ammotragus* (aoudad), *Pseudois* (bharal), *Ovis*, and some forms of *Capra* (goat); Figure 5). The surface of the horn core of *S. willdownsi* is relatively smooth (as is found in *Capra*, *Hemitragus* (tahr), *Oreamnos*, *Ovis*, and *Sinocapra minor*) and lacks the deep grooves found with members of the Bovini, Ovibovini, *Oioceros*, and *Saiga*.

The horn core of *S. willdownsi* is medio-laterally flattened (ovate cross section), typical of most Caprini and unlike the circular to nearly circular horn cores found within the 'rupicaprine' *Capricornis* (serow), *Nemorhaedus* (goral), *Neotragocerus*, and *Oreamnos*, and also within *Pachygazella* (extinct), *Oioceros*, *Saiga*, and the ovibovines. Medio-laterally compressed horn cores occur on female caprines (e.g., *Ovis* and *Hemitragus*), perhaps because their small horns are not used for extreme butting. In contrast, adult males of the living Caprini use their horns for extensive butting. Their horn cores typically have rounded lateral surfaces and anterior surfaces (contact when butting) that range from comparatively flat (*Ovis*, *Ammotragus*, *Pseudois*, and some forms of *Capra*) to highly ridged, forming an acute triangular cross section (*Hemitragus*, most forms of *Capra*; Figure 5 shows the horn sheath expressions of the horn cores).

The horn core, type, for *Sinocapra minor*, is larger than that of *S. willdownsi*, yet it, too, shows little posterior curvature and lacks torsion (Figure 3). Similar horn cores were referred to *Sinocapra minor* by Chen (1991; see Teilhard de Chardin and Trassaert 1938). They are all short, moderately straight with minor posterior curvature, lack divergence, and have a comparatively wide pedicle base (one with a postcornual fossa; Figure 3). Because of this wide pedicle base, we assume that the illustrated horn cores for *S. minor* are from male members of a genus with relatively small horn

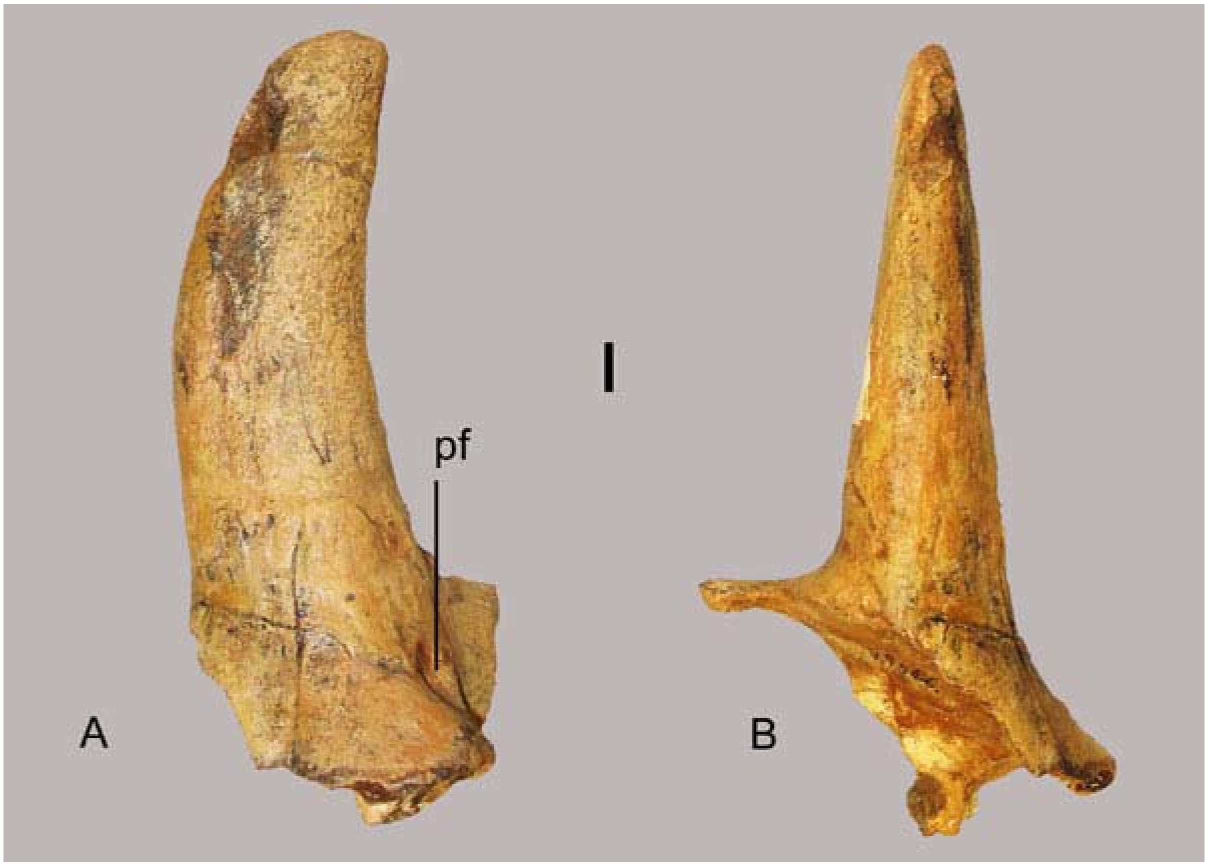

**Figure 3.** Left horn core of *Sinocapra minor* (cast of type; V 9546; Chen 1991). **A**, lateral view, anterior to the left; **B**, anterior view. Abbreviation: pf, postcornual fossa. Scale bar equals 10 mm.

**Table 1.** Measurements (mm) of the horn core. *, estimated measurement; †, fossil taxon; 1, range of measurements from Valdez (1982); 2, Matthew and Cook (1909) data not useable, data here from cast, tip near complete, all measurements are minimum or estimates; 3, Merriam (1918), data here from cast, tip near complete, all measurements are minimum or estimates. Measurements for *Sinocapra minor* from Chen (1991). Measurements for *Ovis shantungensis* from Matsumoto (1926). Measurements for *Oreamnos* species from Mead and Lawler (1994) and Jass et al. (2000).

| | **Nas.Nuc.** | | **Med.Lat.** | |
|---|---|---|---|---|
| | **Circum.** | **Dia.** | **Dia.** | **Length** |
| *Neotragocerus improvisus*†[2] | 105 | 37.2 | 25.5 | 92.6 |
| *N. lindgreni*†[3] | 117 | 41.7 | 29.4 | 84.3 |
| *Oreamnos americanus* | 96-150 | 31.3-48.3 | 26.8-41.4 | 84.5-101.0 |
| *O. harringtoni*† | 59-108 | 19.0-36.0 | 15.9-34.8 | 35.8-114.0 |
| *Ovis dalli dalli* (male)[1] | 330-388 | – | – | – |
| *O. dalli stonei* (female) | 108 | 36.2 | 28.7 | 67.0 |
| *O. dalli stonei* (male)[1] | 343-414 | – | – | – |
| *O. nivicola* (male)[1] | 338-368 | – | – | – |
| *O. shantungensis*† | 250 | – | – | – |
| ***Sinocapra willdownsi*† type** | **69** | **23.4** | **12.6** | **48.0** |
| *S. minor* † holotype | 104* | 40.0 | 28.0 | 84.0 |
| *S. minor* † (RV 38050) | 121* | 52.0 | 27.0 | 104.0 |

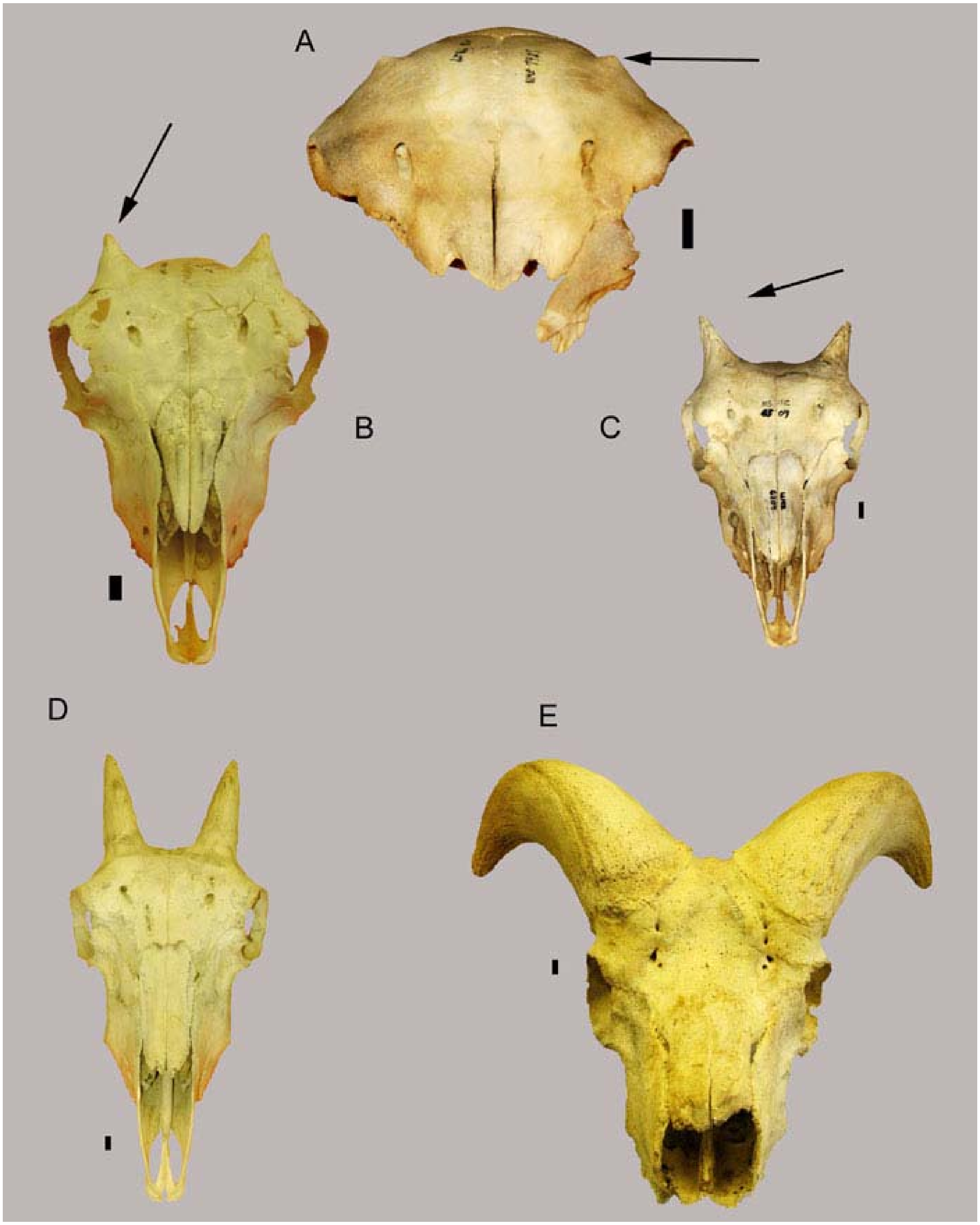

**Figure 4**. Frontal views of an ontogenetic series of horn core growth within *Ovis*. **A**, *Ovis canadensis*, 2-3 months old (PLWZM UM 7927); arrows locate the incipient horn core developments on the frontals. **B**, *Ovis dalli*, female, 11.5 months old (PLWZM UM 11688); horn cores are wider than long and are posteriorly directed (arrow). **C**, *Ovis canadensis*, male, 5 months old (PLWZM UM 6307); horn cores are better developed than on the female in B; horn cores (arrow) are still wide for their length, and show incipient torsion (outward turning). **D**, *Ovis dalli*, female, adult (NAUQSP 2780); horn cores are fully developed and directed posteriorly without torsion. **E**, *Ovis canadensis*, male, adult (NAU QSP 7325); note the torsion of the horn cores. Scale bars equal 10 mm.

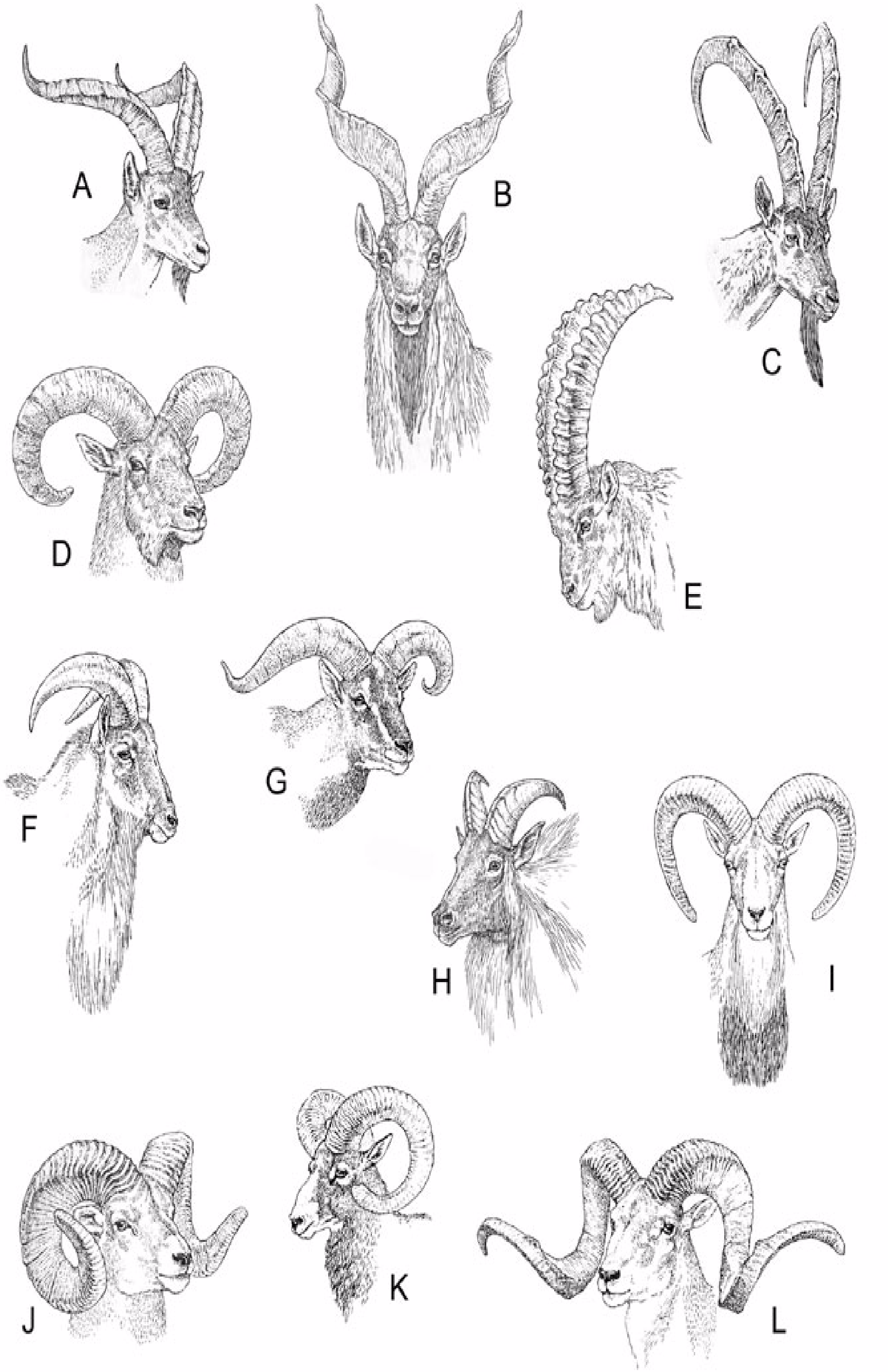

**Figure 5.** Line drawings by Richard Keane of various male members within the living Caprini. Taxonomy follows Grubb (1993), although see Valdez (1982). **A**, *Capra pyrenaica* (Spanish goat); **B**, *Capra falconeri* (markhor); **C**, *Capra hircus* (wild goat); **D**, *Capra cylindricornis* (tur); **E**, *Capra ibex* (ibex); **F**, *Ammotragus lervia* (aoudad); **G**, *Pseudois nayaur* (bharal); **H,** *Hemitragus jemlahicus* (Himalayan tahr); **I**, *Ovis aries* (=*orientalis* of Valdez 1982; urial); **J**, *Ovis canadensis* (Rocky Mountain bighorn); **K**, *Ovis aries* (=*orientalis* of Valdez 1982; mouflon); **L**, *Ovis ammon* (Marco Polo argali). Note the variation within the group, especially within the genus *Capra*. What is shown are the animals with their horn sheaths. Horn cores will not have the same length as the horn sheath; however, horn sheaths with torsion will have horn cores with torsion. Adapted from Schaller (1977, 1980).

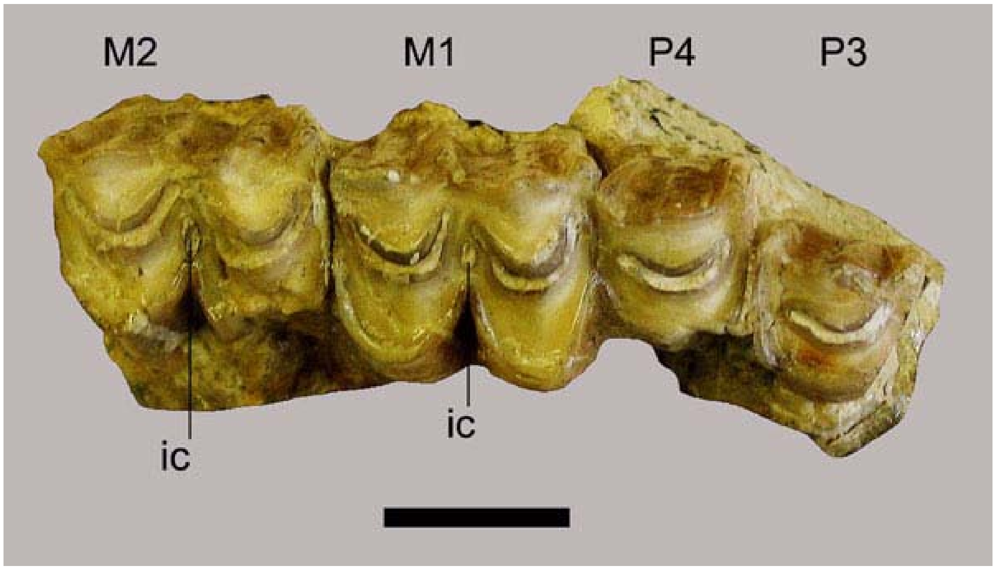

**Figure 6.** Right maxillary tooth row *Sinocapra willdownsi* (52139B) containing the P3-4 and M1-2. Scale bars equal 10 mm.

sheaths that are curved posteriorly and exhibit no torsion. Because the pedicle base on the type for *S. willdownsi* is not significantly larger than the burr base, as observed on *S. minor* horn cores and typically found on male caprines, the Panaca caprine specimen is considered to be a female.

### Maxillary Teeth

The right P3-M2 (52319 B) were recovered together in a small fragment of the maxilla (Figure 6). The posterior edge of the M2 has a contact mark showing that there was an M3 in the toothrow; this tooth was not recovered. The right P2 and left M1 were recovered as isolated teeth. The molars lack entostyles. Crown height is relatively low, mesodont. Strong labial ribs occur between the parastyle, mesostyle, and metastyle. Distinct internal cavities occur between the protocone and metaconule on the M1-2 (Figure 6).

**Discussion**: The teeth do not show extreme wear, indicating that the low crowns on the Panaca caprine are not to the result of abrasion (Figure 6). The M2 comes into full functional wear at about two years of age, and the M3 is in complete functional wear at about 3.0 to 3.5 years in *Ovis* spp. (Cowan 1940). Assuming a similar tooth eruption phase in *Sinocapra*, the individual from Panaca would have been at least three years old.

The observed occlusal characters of *Sinocapra willdownsi* are consistent within Caprini but appear undiagnostic to genus. Measurements of the molars and premolars of *S. willdownsi* are compared with *Ovis ammon* (argali), *O. canadensis*, *O. catclawensis* (extinct bighorn), *O. dalli* (female), *O. shantungensis*, and *O. zdanskyi* (extinct bighorn) in Table 2 (no dentition is known for *S. minor*). The length and width of the premolars of *S. willdownsi* fit within the variability observed among these taxa. The size of the molars indicates some variation among genera. These initial data imply that the teeth and toothrow of *S. willdownsi* are at the small end of the observable range of living and some fossil caprines. The mesodont characteristic may be of importance as the teeth of *Sinocapra willdownsi* are distinctly lower crowned than any living *Ovis* spp. or *Oreamnos* spp.

### Humerus

Fragmented left and right humeri (52319E) are known (Figure 7). The left humerus preserves the distal three-fourths while the right humerus is represented by only the distal quarter. Measurements are shown in Table 3.

### Ulna

A fragment of the proximal end of the left ulna (52319E) is recovered (Figure 8). The conical impression on the medial surface (Figure 8.1), is consistent with a canine impaction but there is no corresponding indentation on the lateral side.

### Lunar

The right lunar (52319E) is complete but not remarkably different from that of other taxa.

### Metacarpal

The distal fragment of a right metacarpal (52139E) has a distinctive sulcus (su) with slight crests (not sharp) parallel to the sulcus and is

**Table 2.** Occlusal measurements of the maxillary dentition. *Ovis ammon*, *O. canadensis*, and *O. catclawensis* UT from Stokes and Conde (1961). *Ovis catclawensis* ID from Akersten et al. (2002). *Ovis shantungensis* from Matsumoto (1926). *Ovis zdanskyi* from Bohlin (1938). Abbreviations: L, length; W, width.

| Taxon | P2W | P2L | P3W | P3L | P4W | P4L | M1W | M1L | M2W | M2L |
|---|---|---|---|---|---|---|---|---|---|---|
| ***Sinocapra willdownsi*** | **8.0** | **8.1** | **8.1** | **8.5** | **-** | **7.6** | **12.3** | **13.5** | **11.3** | **15.3** |
| *Ovis zdanskyi* | - | - | - | 9.9 | - | 11.5 | - | 21.5 | - | 27.0 |
| *O. shantungensis* | 8.0 | 6.0 | 11.0 | 11.0 | 12.5 | 11.5 | 14.0 | 19.5 | 15.5 | 22.0 |
| *O. canadensis* | 7.5 | 8.0 | 10.0 | 10.0 | 11.0 | 10.0 | 13.0 | 17.0 | 14.0 | 21.0 |
| *O. catclawensis UT* | 7.7-8.5 | 8.0-9.0 | 10.5-11.0 | 9.0-10.0 | 11.5-12.0 | 9.5-10.0 | 14.0 | 17.5-18.0 | 12.5-15 | 22.0 |
| *O. catclawensis ID* | 8.5 | 8.8 | 11.3-11.5 | 7.2 | 11.9-12.1 | 11.2-12.6 | 15.2-15.6 | 16.0-17.2 | 15.3-17.4 | 20.3-24.6 |
| *O. dalli* | 7.7 | 7.8 | 8.0 | 9.1 | 9.6 | 10.5 | 12.6 | 18.3 | 12.4 | 19.6 |
| *O. ammon* | 8.0 | 9.5 | 11.0 | 11.0 | 12.0 | 11.0 | 16.0 | 17.0 | 17.0 | 25.0 |

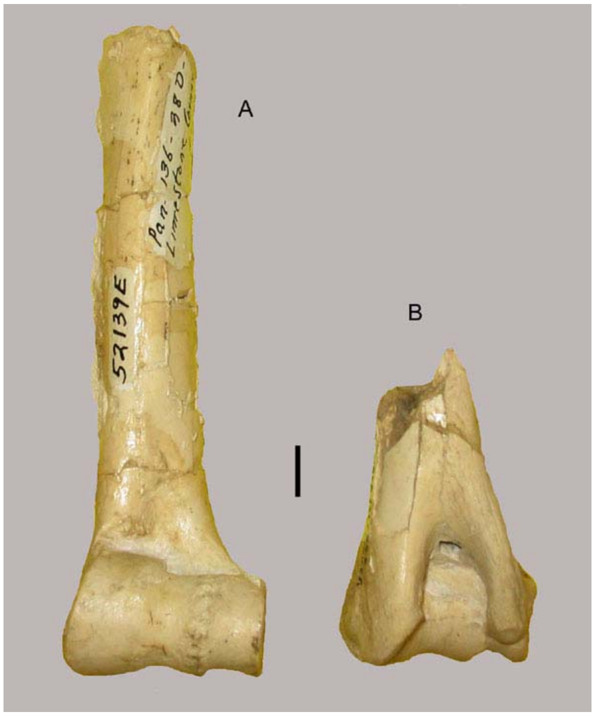

**Figure 7.** Humeri of *Sinocapra willdownsi* (62139E). **A**, Fragmental left humerus in dorsal view; **B**, fragmental right humerus in volar view. Scale bar equals 10 mm.

**Table 3.** Measurements of the left and right humeri of *Sinocapra willdownsi*. Methodology follows Scott (1985).

| | Left | Right |
|---|---|---|
| Greatest breadth of trochlea (H4) | 34.9 | 34.7 |
| Width of olecranone articular surface | 12.8 | 12.5 |

widely open (sagittal groove) at the distal epiphysis (Figure 9). Although the entire bone is not preserved, there is enough (approximately the distal third) preserved to indicate that the bone is from the right side and progressively widens from the diaphysis at the distal end, as occurs on a metacarpal and unlike the rapid expansion observed in metatarsals (see discussion below).

The width of the distal articular surface of the metacarpal of *Sinocapra willdownsi* and other caprine taxa are included in Table 4. The articular condyles of the first phalanges (verticilli of Köhler 1993) are high and sharply delineated, as seen in *Ovis*, *Oreamnos*, and other inhabitants of mountainous terrain.

**Discussion**: *Ovis* spp. and *Oreamnos* spp. do not have the prominent sulcus found on the metacarpal as seen in *Sinocapra willdownsi*. Living Caprini, 'Rupicaprini,' and Ovibovini have a superficial sulcus or none at all on the metacarpal. The measurements of the distal articular surface of various caprines indicate that the metacarpal of *S. willdownsi* is of about average size, compared to other living caprines (Table 4). The data presented for the metatarsal are similar (Figure 15).

### Phalanges

The first, second, and third (fragment) phalanges (52139E) appear to fit together and articulate precisely with the right metacarpal fragment, and therefore, they are assumed to be medial manus phalanges (third digit). An additional first phalanx is known but does not adequately articulate with either the right metacarpal or the right metatarsal and is therefore not described.

The first phalanx measures 47.1 mm long (greatest length between medial condyles) and 17.2 mm wide at the proximal end. The additional first phalanx measures 49.2 mm long and 16.8 mm wide at the proximal end. Interdigital ligament insertion ridges are short but prominent on both specimens (Figure 10B.1).

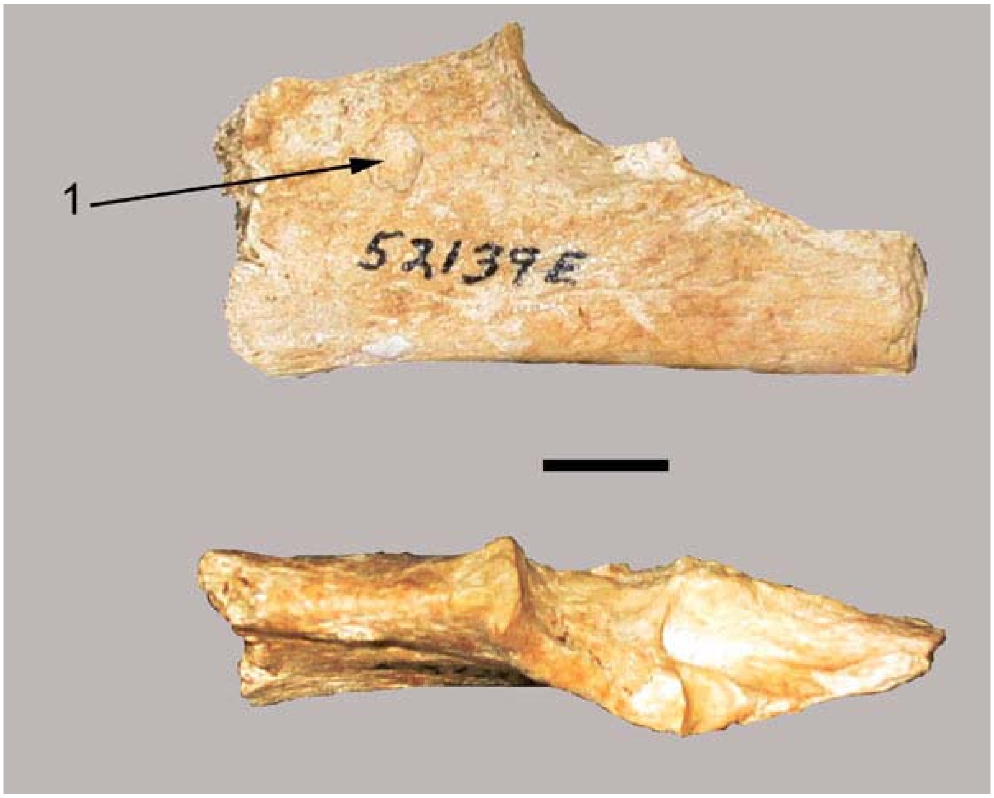

**Figure 8.** Fragment of the left ulna of *Sinocapra willdownsi* (52139E), exhibiting possible carnivore canine indentation (1).

The second phalanx is short and broad (27.6 mm long, following von den Driesch 1976), 13.9 mm wide at the proximal end. A postarticular plateau is lacking (Figure 10A.2), and the dorsal extensor protuberance (dexp) is elongate (Figure 10C). The insertion of the interdigital ligament is weak to almost absent (Figure 10C.3).

The third (distal) phalanx is fragmented, missing the distal half. A robust protuberance for the extensor tendon insertion (exp) is preserved (Figure 10D). A portion of the dorsal ridge is preserved distal to the extensor tendon insertion and appears to be at a more horizontal angle implying at least a slight convex appearance (typical of caprines, and not the highly slanted and straight ridge as in cervoids). The horizontal platform of the articular surface (hpe) is well established (Figure 10D).

**Discussion**: Although these phalanges are not taxonomically diagnostic, they do indicate that the joint was designed for tensor and flexor motion with a horizontal component that permits notable shock absorbency (see Leinders 1979; Köhler 1993). This implies that *Sinocapra willdownsi* was more of a mountainous and rocky terrain climber and not an animal adept at sustained, rapid locomotion on fairly level topography.

### Femur

Highly fragmented left and right femora (52319E) are known, but will not be discussed here.

### Navicular-cuboid

A complete right navicular-cuboid (52139E; central and fourth tarsal) is recovered. The comparative morphology used here is located in Figures 11 and 12. The patterns of the various articular facets and processes of the distal surface are within the realm of variation observed in modern *Ovis canadensis* and *O. dalli,* and therefore, are of little use to distinguish the new taxon. However, the articular facets and processes are distinctly unlike those found on cervoids and antilocaprids (see Lawrence 1951; Heintz 1970).

The plantar surface of 52139E contains the calcaneal articular facet (caf), a flange with its length truncated distally by the lateral groove of the tendon to the *musculus peroneus longus* (tmpl; Figures 11, 12). This groove on the lateral surface or its truncation by the tmpl is rarely observed in *Ovis*, *Ammotragus*, *Oreamnos americanus* (male and female), or the extinct *Oreamnos harringtoni*.

The medial process (mp; Figures 11B, 12B) on the anterior surface is a pronounced articular

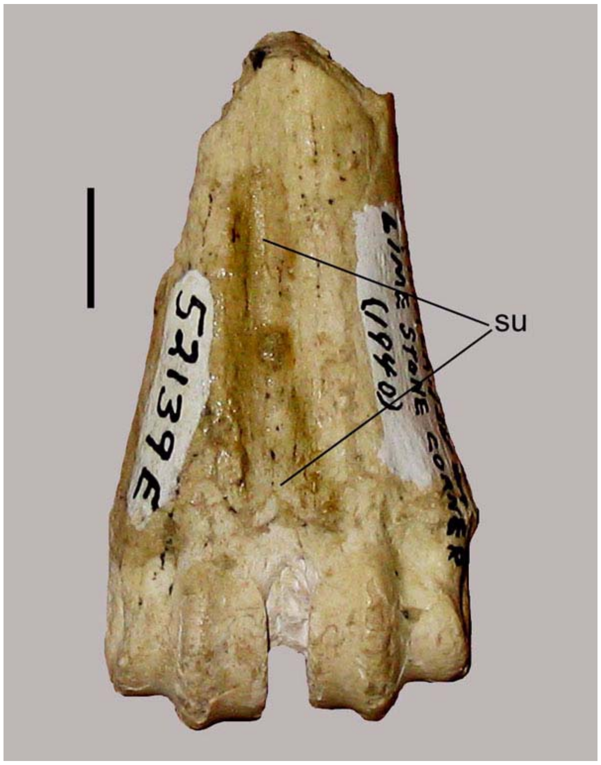

**Figure 9.** Right metacarpal of *Sinocapra willdownsi* (52139E) in dorsal view. Abbreviation: su, sulcus. Scale bar equals 10 mm.

**Table 4.** Width (mm) of the distal articular suface of the metacarpal from select caprines. Most of data of Mc4 from Scott (1985); *Oreamnos harringtoni* from Mead and Lawler (1994) and Jass et al. (2000). Arranged in increasing minimum size.

| Taxon | Range of Width |
|---|---|
| *Nemorhaedus goral* | 20.6-29.7 |
| *Ammotragus lervia* | 21.6-32.0 |
| *Ovis orientalis* | 21.9-29.2 |
| *O. musimon* | 23.1 |
| *Oreamnos harringtoni* | 23.7-39.2 |
| *Capricornis crispus* | 26.2-32.0 |
| *Capra falconeri* | 28.1 |
| *C. ibex* | 28.3-38.7 |
| *Pseudois nayaur* | 28.9-33.5 |
| ***Sinocapra willdownsi*** | **29.1** |
| *Ovis canadensis* | 29.1-34.6 |
| *O. dalli* | 29.3-33.2 |
| *Hemitragus jehmalahicus* | 29.8-32.4 |
| *Capra pyrenaica* | 32.4-33.8 |
| *Ovis ammon poli* | 32.9-39.2 |
| *O. ammon hodgsoni* | 33.9-38.9 |
| *O. ammon mongolica* | 34.4 |
| *Capra caucasica* | 36.2 |
| *Capricornis sumatraensis* | 37.2-41.7 |
| *Oreamnos americanus* | 43.1-43.2 |

process with distinct dorsal and plantar facets on *Sinocapra willdownsi* and on some specimens of *Oreamnos harringtoni* (GRCA 509044, 509160, 509273). This differs from the minute projections observed on *Ovis* spp. and *Oreamnos americanus*.

The navicular-cuboid of *Sinocapra willdownsi* is square in shape as in *Ovis* spp., whereas it is medio-laterally wider in *Oreamnos* spp. (with its wider foot for mountain climbing). This width on *Oreamnos* comes from the lateral expansion of the antero-external metatarsal facet (amf) and the postero-external metatarsal facet (pmf) along with their adjacent ligament attachments (Figure 12A). Widening of the *Oreamnos* navicular-cuboid situates the pmf near the middle of the plantar surface, as viewed posteriorly, whereas in *Sinocapra willdownsi* and *Ovis* spp. this process is at the lateral-plantar border of the bone (Figure 11.2). The widening within *Oreamnos* spp. is also caused by the medial widening of the internal astragal articular facet, a character not found in *Sinocapra willdownsi* or in *Ovis* spp. This character indicates that the foot of *Sinocapra willdownsi* was not as wide and sturdy as that of the mountain goats, but is comparable with the mountain sheep.

The insertion of the tendon on the plantar side (Figure 11.1) is centrally located on *Sinocapra willdownsi*, yet continues as a groove proximally. No such groove is observed in *Ovis* spp. or *Oreamnos* spp.

The attachment area for the long medial ligament, the plantar ligament, and the long lateral ligament is robust and extensive on *Oreamnos* spp. and *Ovis* spp., yet is minute on *Sinocapra willdownsi* (Figure 11.3). Various muscles attach to these ligaments with tendons. Although the ligaments restrict the amount of absolute movement at the joint, the tendons and muscles attaching on the plantar side permit various flexor and tensor motions of the foot and digits (see Sisson and Grossman, 1938 and subsequent editions).

The internal process (ip) of the internal astragal articular facet (iaaf) permits the attachment of a number of tendons on the plantar and medial sides (Figures 11B, 12B). This process also allows for the formation of a groove that accommodates passing the tendon of the tibialis posterior. It is in this groove that a ligament attaches (in part the tarso-metatarsal ligament). In *Ovis*, the ligament attachment blends in with the form of the groove. The anterior end of the groove contains a large bony lump for this ligament attachment, simi-

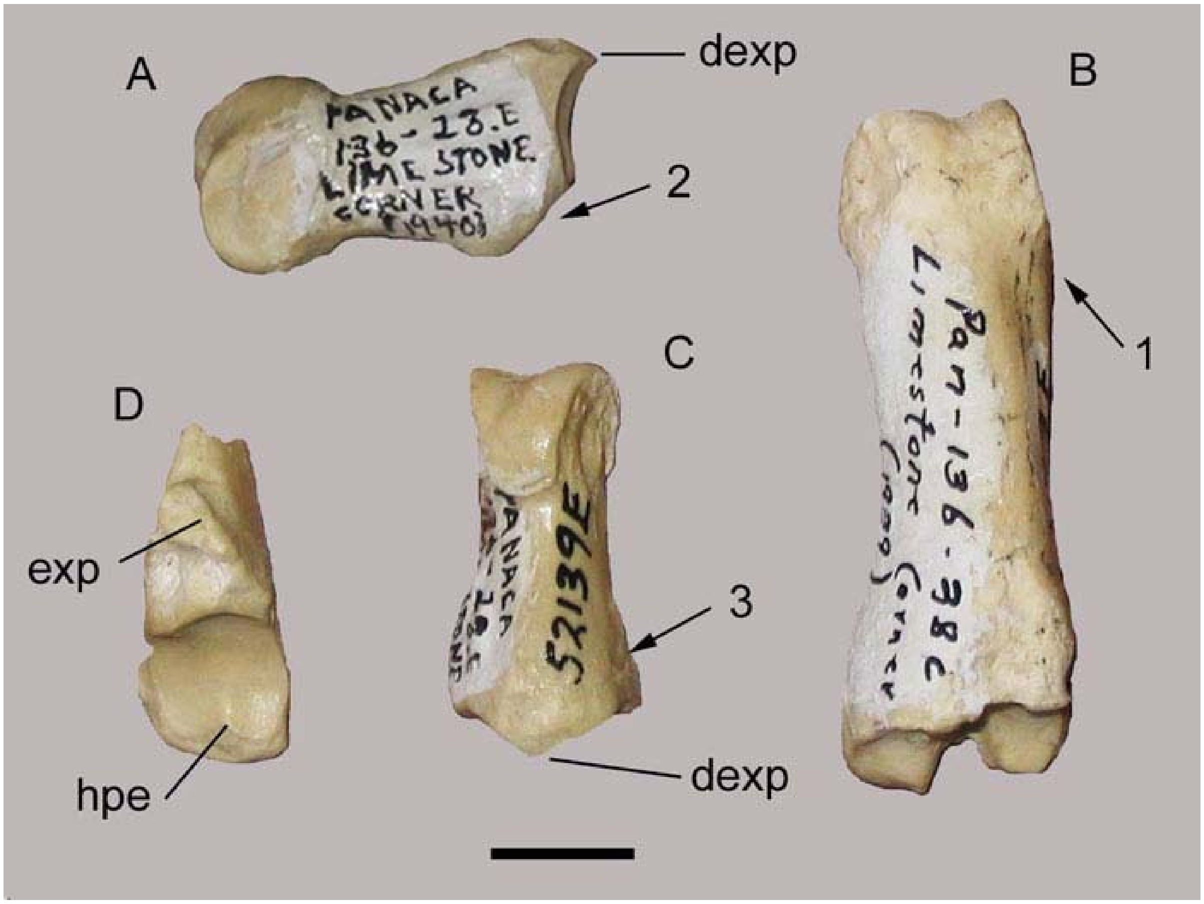

**Figure 10.** Medial manus phalanges of *Sinocapra willdownsi* (52139E). **A**, second phalanx medial view; **B**, first phalanx dorsal view; **C**, second phalanx (=A) dorsal view; **D**, fragment third phalanx in dorsal view. Abbreviations: dexp, dorsal extensor protuberance; exp, extensor protuberance; hpe, horizontal posterior extension of articular surface. **1**, insertion area of interdigital ligament; **2**, lack of a postarticulare plateau; **3**, location area of interdigital ligaments, insertion is weak to wanting (see text). Scale bar equals 10 mm.

lar to, but not as massive as, that found on *Oreamnos*.

**Discussion**: The navicular-cuboid 52319E is similar in size and shape to that found on *Ovis* and dissimilar to that of *Oreamnos*. Although similar to that of *Ovis*, differences indicate a different animal and one that, although an inhabitant of mountainous terrain, was not as adept to this habitat as *Ovis* spp. and *Oreamnos americanus* are today.

### Metatarsal

The right metatarsal (52139E) is nearly complete (Figure 13). A sulcus (su) occurs on the dorsal surface and proceeds from proximal to distal epiphyses, distinct most of its length, prominent and open the distal third with crests on both sides of the sulcus, and widely open (sagittal groove) at the distal epiphysis (Figure 13A), a character typical of bovids but not cervoids (Heintz 1970; Leinders 1979; Köhler 1993). This sulcus is wide and shallow to almost non-existent on *Ovis* spp. and *Oreamnos* spp. The goat-like caprines (*Capra*, *Hemitragus*) possess a slightly more distinct sulcus at the distal end than do the sheep-like caprines (*Ovis*; along with the ovibovines and 'rupicaprines'). The volar or plantar surface (posterior of Heintz 1970) has almost no trace of a groove except near the epiphyses (Figure 13B), similar to that observed on *Ovis* spp. and *Oreamnos* spp.

The distal end flares abruptly with a broad 'V' from the epiphysis to the intertrochlear notch (in) on 52139E. The connections of the lateral extensor tendon (lext) and the medial extensor tendon (mext) are prominent on *Sinocapra willdownsi* (Figure 13A). This character set is not significant in *Ovis* spp. but is robust in *Oreamnos* spp.

The posterior sub-facet of the navicular-cuboid facet (psfncf) is completely abraded, and it cannot be determined if this facet was raised or level with the rest of the naviculo-cuboid facet (Figures 13B.1 and 14.2). The posteromedial projection (pp; Figure 14) is prominent and has a hooked-

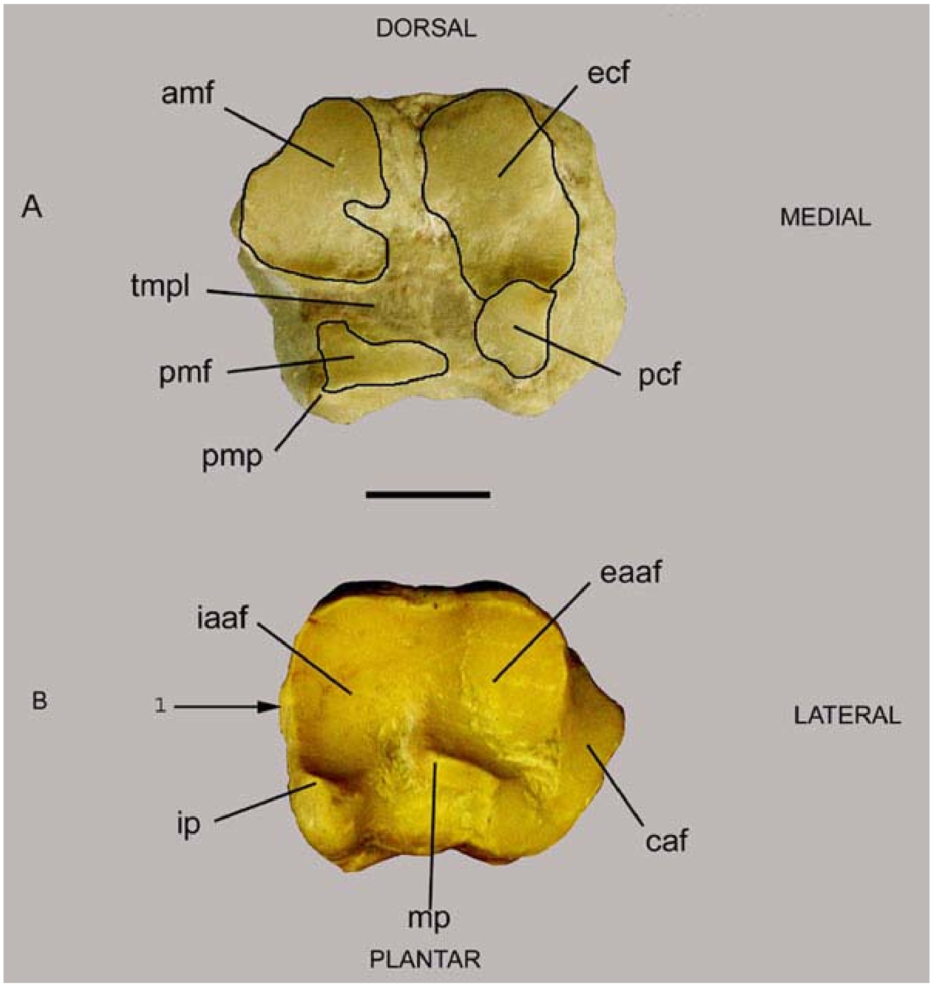

**Figure 11.** Right navicular-cuboid of *Sinocapra willdownsi* (52139E). **A**, distal view and **B**, proximal view. Abbreviations: ecf, entocuneiform facet (anterior cuneal facet; 2nd. and 3rd. tarsal); amf, antero-external metatarsal facet; caf, calcaneal articular facet; eaaf, external astragal articular facet; iaaf, internal astragal articular facet; ip, internal process; mp, medial process; pcf, posterior cuneal facet (1st. tarsal); pmf, postero-external metatarsal facet; pmp, postero-external metatarsal process; tmpl, groove for tendon to musculus peroneus longus. **1**, medio-lateral width, see text. Scale bar equals 10 mm.

appearance on 52139E. However, this is due to abrasion and to the deep fossa below. Due to the abraded state of the fossil, this character (= character 93 of Gentry 1992) cannot be used. The articular condyles for the first phalanges (verticilli of Köhler 1993) are high and sharply delineated, as found with *Ovis*, *Oreamnos*, and other mountainous terrain inhabitants (Figure 13).

The metatarsal is neither excessively long nor short, nor narrow or wide, when compared with other caprines (Table 5). To observe its size relative to other caprines, we made a comparison between the overall length and the width of metatarsals, at the distal end. Figure 15 illustrates this comparison among the various caprines. The length/distal width ratio of *Sinocapra willdownsi* is analogous to those of some *Capra ibex* and *Pseudois nayaur*, and not all that dissimilar with some *Ammotragus lervia* and *Ovis orientalis*. These similarities, although not helpful with the identification of the specimen, do indicate that *S. willdownsi* had a relatively short and wide foot, one very capable of mountain terrain. The size of the metatarsal on *S. willdownsi* indicates that the individual described here was not a large or heavy animal.

## DISCUSSION

Data presented indicate that the Panaca caprine, *Sinocapra willdownsi*, is not a member of any living genus within the Caprini and most closely resembles the extinct caprine, *S. minor* of China. The holotype of *Sinocapra willdownsi* is shown to be an adult female of this relatively small genus within the Caprini that had small, straight,

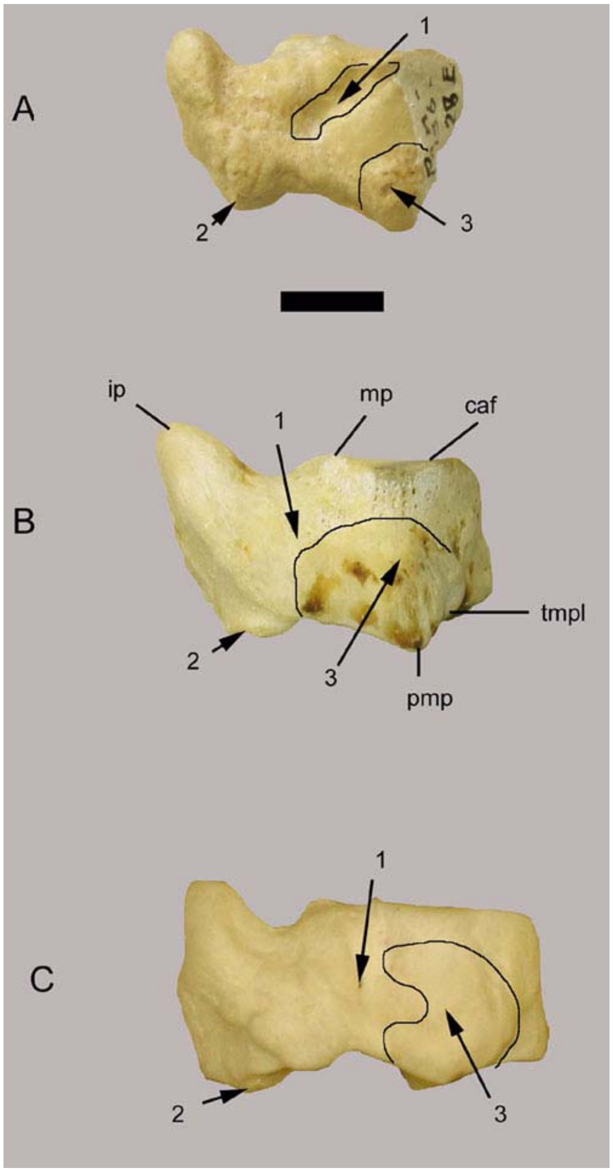

**Figure 12.** Plantar view of navicular-cuboid. **A**, *Sinocapra willdownsi* (52139E); **B**, *Ovis canadensis* (male, NAU QSP 2781); **C**, *Oreamnos americanus* (female, NAU QSP 2797). Abbreviations: caf, calcaneal articular facet; mp, medial process; pmp, postero-external metatarsal process; tmpl, groove for tendon to musculus peroneus longus. **1**, ligament insertion and groove; **2**, distalmost medial projection as viewed from plantar aspect, see text; 3, attachment area of the lantar ligament. Scale bar equals 10 mm.

non-diverging, horn cores lacking torsion, and therefore, likely had simple horn sheaths. The metacarpal and metatarsal measurements of *Sinocapra willdownsi* indicate that the size of the metapodials is about average among the living caprines, and appears most similar in dimensions to *Capra ibex*, *Pseudois nayaur*, and *Ammotragus lervia* (Table 4, Figure 15).

**Figure 13.** Right metatarsal of *Sinocapra willdownsi* (52139E). **A**, dorsal view; **B** volar (plantar) view (anterior and posterior respectively of Heintz, 1970). Abbreviations: in, intertrochlear notch; lext, lateral extensor tendon insertion; mext, medial extensor tendon insertion; su, sulcus. 1, reconstruction of the presumed eroded location of psfncf, posterior subfacet of navicular-cuboid facet. Scale bar equals 10 mm.

The argument that the type and referred specimens of *Sinocapra minor* represent male individuals, is based primarily on the width of the pedicle base of the horn cores. These horn cores imply that *S. minor* had fairly robust but comparatively short, straight, non-diverging, non-torsioned horn sheaths (unlike those observed in the living caprines; see Figure 5). The horn cores of *S. minor* and *S. willdownsi* are similar in construction and unlike those of any living caprine. The data and this comparison also imply that *Sinocapra* exhibited little if any sexual dimorphism.

At this time little is understood about the description and characterization of *S. minor* from China. Comparisons between the two species of *Sinocapra* are complicated in that the only bones recovered in common between them are the horn cores, with the Chinese species determined here

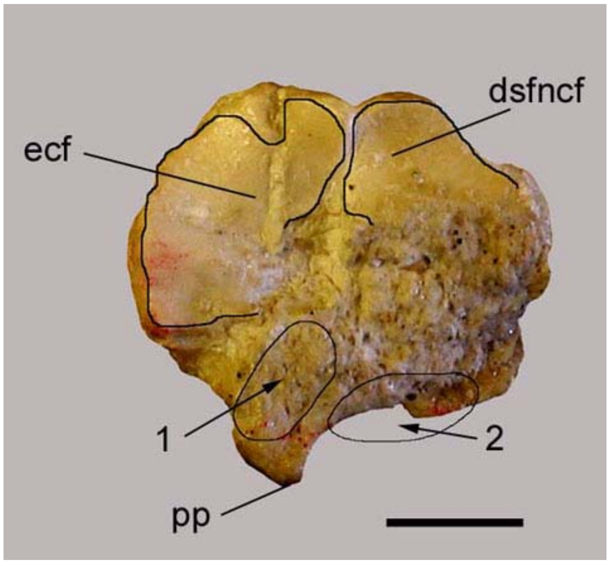

**Figure 14.** Proximal end of right metatarsal of *Sinocapra willdownsi* (52139E). Abbreviations: ecf, entocuneiform facet (3rd. tarsal); dsfncf, dorsal subfacet of navicular-cuboid facet; pp, posteromedial projection. **1**, presumed eroded location of (first tarsal); **2**, presumed eroded location of psfncf, posterior subfacet of navicular-cuboid facet.

to be a male and the North American form a female. The slight size differences between them may be due to a minor sexual dimorphism within the genus, an unusual phenomenon within the Caprini yet common among the 'Rupicaprini.'

*Sinocapra willdownsi* lived at least in the Intermountain Region of western North America between approximately 4.95 to 4.50 Ma. *Sinocapra minor* from the Mazegou Formation, Yushe Basin, China, represents a younger caprine that dates to the late Pliocene Yushean land mammal age (Teilhard and Piveteau 1930; Teilhard and Trassaert 1938; Chen 1991; Flynn et al. 1991; Tedford et al. 1991). The locality YS78 falls in magnetic chron C2An3n, about 3.5 Ma. Despite the few specimens of *S. minor* the different morphology, age difference of at least one million years, and isolated geography (China versus North American) permit separate species designation. This is not ideal but challenges the recovery of more caprines of Pliocene age in both northeastern Asia and northwestern North America. The differences between the two forms become greater if all specimens are considered the same sex. This would imply that *S. willdownsi* was smaller, and that the younger Yushe caprine developed into a larger taxon by the late Pliocene.

**Table 5.** Measurements of the right metatarsal of *Sinocapra willdownsi* (52139E). Measurements (in mm) follow von den Driesch (1976).

| | |
|---|---|
| Greatest length | 161.8 |
| Minimum depth diaphysis | 12.5 |
| Minimum breadth diaphysis | 12.0 |
| Proximal breadth | 26.1 |
| Proximal depth | 25.1 |
| Distal breadth | 29.5 |
| Distal depth | 20.4 |

## Habitat

Köhler (1993) determined that many morphological characters observed on various skeletal elements within the bovidae are of more ecological or paleocological use than of phylogenetic value. Köhler (1993) divided the bovids into occupants of three habitats: (A) humid-wooded, (B) dry, more open, and (C) mountainous terrain. Inhabitants of B and C are more similar to each other than they are to A. In the Köhler classification, the morphological characters observed on the metacarpal and metatarsal of *Sinocapra willdownsi* suggest that the Panaca caprine does not belong to an existing genus of Caprinae, and that it likely was not an inhabitant of open, mountainous terrain such as is inhabited by *Ovis*, *Oreamnos*, and most other caprines (not including *Nemorhaedus* or *Capricornis*). The phalanges indicate that, like many other caprines, *Sinocapra willdownsi* was more of a mountain climber than a deep forest, flat-land inhabitant. The length-width of the metatarsal and the width of the metacarpal indicate that the Panaca caprine had medium stature. Its feet were not as wide as those of the best cliff-climbers (*Oreamnos*) or as long (stilted) and wide as the wild sheep (*Ovis ammon*, *O. canadensis*, *O. catclawensis*). The distal articulations of the metacarpal and metatarsal suggest this same conclusion. The length of the extensor tendon insertions on the proximal end of the metatarsal is similar to those of a mountainous inhabitant, although the rugosity of these attachment areas is more similar to those found in forested habitats (Köhler 1993). The width of the distal end of the metacarpal and the presence of a distinct and somewhat narrow sulcus and sagittal groove on both metapodials is more diagnostic to a woodland habitat than to wide-open terrain (Köhler 1993). *Sinocapra willdownsi* would seem to fit into the Köhler classification (1993, p. 74) of "Ubiquitouus Type A/B" – a group of bovids situated between the clearly wooded and the clearly open habitat.

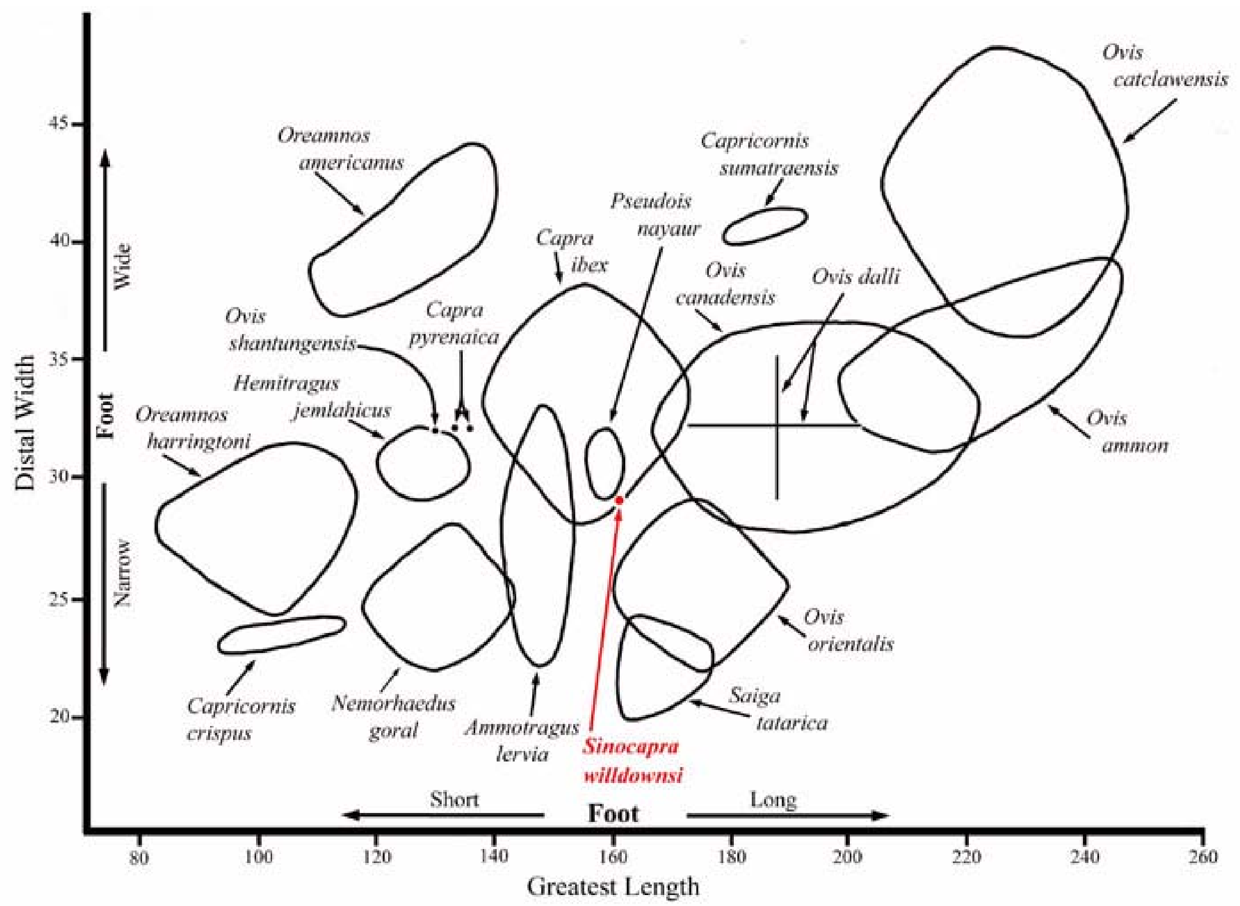

**Figure 15.** Greatest length and width measurements of metatarsals from a number of modern and extinct caprines. Data from Scott (1985), Mead and Lawler (1994), and Jass et al. (2000).

## Systematics and Evolution

Chen (1991) considered *Sinocapra minor* more closely related to the 'goat' (*Capra*) lineage within Caprini rather than to the 'ovine' (sheep, *Ovis*) linage. However, the Yushe *Sinocapra* horn cores clearly lack torsion and a transverse ridge (keel), as does *S. willdownsi*, typical characters within members of the 'goat' lineage. Therefore, we are of the opinion that *Sinocapra* exhibits more ovine characters and most likely lies within or adjacent to *Ovis* ancestry.

*Ovis* makes its first appearance in the Chinese fossil record at approximately 2.42 Ma (*Ovis shantungensis*; Matsumoto 1926), and first appears in Europe during an unspecified time within the middle Pleistocene (Crégut-Bonnoure 1992). The earliest *Ovis* in North America is from El Golfo, Sonora, Mexico (Shaw 1981), and possibly dates to 1.2 Ma (Irvingtonian NALMA). This mandibular specimen and its age assignment are in need of detailed appraisal. *Ovis* sp. is also reported from Porcupine Cave, Colorado, dating to approximately 0.6 Ma (Mead and Taylor 2004).

Given the known fossil record and biostratigraphic position of *Sinocapra*, *Ovis*, and *Capra*, it appears possible that *Sinocapra* was the progenitor of *Ovis* and possibly *Capra*, or, at least a sister taxon. *Sinocapra* clearly occurs at least one million years earlier in North America than either *Ovis* or *Capra* occur in Europe (Crégut-Bonnoure 1992). *Ovis shantungensis* and *S. minor* apparently coexisted in China (Teilhard and Trassaert 1938). No evidence indicates that the caprines evolved in North America, so the occurrence of *Sinocapra* at Panaca indicates an earlier immigration event, possibly at about the time of the Mahui-Gaozhuang hiatus after 6.0 Ma (Flynn et al. 1991; Tedford et al. 1991). If this is correct, then an early form of *Sinocapra* should have existed in China. It is also possible that an unknown and undescribed progenitor form of early caprine evolved in Asia, migrated to North America during the Hemphillian (as did *Neotragocerus*), and *Sinocapra* actually evolved on this continent. A subsequent immigration event during the Pliocene could have brought *Sinocapra* to Asia from North America.

Whether *Sinocapra* evolved in Asia from a yet-to-be-realized ancestor in the late Miocene and immigrated to North America, or evolved in North America, later to immigrate to Asia, it seems evident that *S. willdownsi* is the oldest representative of the genus and is North American. *Sinocapra willdownsi* appears to be the earliest member of the Caprini in North America and one of the earliest bovids in the New World; *Ovis*, *Oreamnos*, and the ovibovines all arrived sometime during the middle Pleistocene (Irvingtonian).

Various researchers presume *Neotragocerus* to be a 'rupicaprine.' We question this assumption and suggest that *Neotragocerus* is not a member of that tribe; it clearly is not a member of the Caprini. These hypotheses indicate the need for additional detailed study of the bovids of northeastern Asia and North America. It seems clear that much of the history of the caprine bovids of North America remains to be discovered, a history that was richer and more diverse than previously understood.

## ACKNOWLEDGMENTS

This article is dedicated to the life and scientific achievements of William R. Downs, III, who helped all of paleontology through his extensive field and laboratory activities and by freely providing translations of Chinese papers to all who needed them. We appreciate the help of and discussions with W.A. Akersten, J. Barry, C.J. Bell, N. Czaplewski, D. Diveley, W. Downs, R. Fisher, V. Geist, A. Gentry, C.N. Jass, E.H. Lindsay, J. Meng, C. Norris, C.A. Repenning, C. Shaw, R. Tedford, and R. White. Thanks to reviews by L.J. Flynn and L.L. Jacobs, this paper was improved significantly. We thank D. Dyer (University of Montana) and R. White (International Wildlife Museum) for the loan of comparative skeletons. We thank L. Flynn and personnel of the Institute of Paleoanthropology and Paleontology, Chinese Academy of Science, Beijing for obtaining a cast of *Sinocapra*. We appreciate the permission of G. Schaller to use the line drawing of living caprines from his book *Mountain Monarchs* (University of Chicago Press). We thank S. Swift and M. Carpenter for providing the line drawings.

## REFERENCES

Akersten, W.A., Miller, S.J., and Repenning, C.A. 2002. The Booth Canyon Local Fauna, a depauperate mammalian assemblage from the Late Pleistocene of eastern Bonneville County, Idaho, p. 101-130. In Akersten, W.A., Thompson, M.E., Meldrum, D.J., Rapp, R.A., and McDonald, H.G. (eds.), And Whereas…Papers on the Vertebrate Paleontology of Idaho Honoring John A. White, Volume 2. *Idaho Museum of Natural History Occasional paper 37*.

Bartley, J.M., Axen, G.J., Taylor, W.J., and Fryxell, J.E. 1988. Cenozoic tectonics of a transect through eastern Nevada near 38° N latitude, p. 1-20. In Weide, D.L. and Faber, M.L. (eds.), *The Extended Land, Field Trip Guidebook*. Geological Society of America Cordilleran Section Meeting, Tucson.

Bohlin, B. 1937. Eine tertiäre säugetier-fauna aus Tsaidam. Paleontologia Sinica, Series C, 14, Reports from the Scientific Expedition to the North-Western Provinces of China under Leadership of Dr. Sven Hedin. *The Sino-Swedish Expedition. VI. Vertebrate Paleontology*, 1:1-111, 9 plates.

Bohlin, B. 1938. Einige jungtertiäre und Pleistozäne cavicornier aus nord-China. *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, *Series* 4, 11:1-54 + 12 plates.

Chen, G. 1991. A new genus of Caprini (Bovidae, Artiodactyla) from upper Pliocene of Yushe, Shansi. *Vertebrata PalAsiatica* 29:230-239.

Cowan, I.M. 1940. Distribution and variation in the native sheep of North America. *American Midland Naturalist*, 24:505-580.

Crégut-Bonnoure, E. 1992. Dynamics of bovid migration in western Europe during the middle and late Pleistocene. *Forschungsinstitut Senckenberg, Sonderdruck aus CFS-Courier*, 153:177-185.

Flynn, L.J. 1997. Late Neogene mammalian events in North China, pp. 183-192. In Aguilar, J.-P., Legendre, S., and Michaux, J. (eds.), *Actes du Congrès BiochroM'97*, Mémoires et Travaux EPHE, Institut Montpellier, 21, Montpellier, France.

Flynn, L.J., Tedford, R.H. and Qui, Z. 1991. Enrichment and stability in the Pliocene mammalian fauna of North China. *Paleobiology*, 17:246-265.

Gatesy, J., Amato, G., Vrba , E.,. Schaller, G., and DeSalle, R. 1997. A cladistic analysis of mitochondrial ribosomal DNA from the Bovidae. *Molecular Phylogenetics and Evolution*, 7:303-319.

Geist, V. 1971. *Mountain Sheep: A Study in Behavior and Evolution*. University of Chicago Press, Chicago.

Gentry, A.W. 1971. The earliest goats and other antelopes from the Samos *Hipparion* Fauna. *Bulletin of the British Museum (Natural History), Geology*, 20(6):229-296 + 6 plates.

Gentry, A.W. 1992. The subfamilies and tribes of the family Bovidae. *Mammal Review*, 22:1-32.

Gentry, A.W. 2000. The Ruminant radiation, p. 11-25. In Vrba, E.S. and Schaller, G.B. (eds.), *Antelopes, Deer, and Relatives. Fossil Record, Behavioral Ecology, Systematics, and Conservation*. Yale University Press, New Haven.

Gentry, A.W. and Heizmann, E.P. 1996. Miocene ruminants of the central and eastern Tethys and Paratethys, p. 378-391. In Bernor, R.L., Fahlbusch, V., and Mittmann, H.-W. (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York.

Gray, J.E. 1821. *On the natural arrangement of vertebrate mammals*. London Medical Repository 15(1): 296-310.

Grubb, P. 1993. Order Artiodactyla, p. 377-414. In Wilson, D.E. and Reeder, D.M. (eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference*. 2nd. Edition. Smithsonian Institution Press, Washington.

Grubb, P. 2001. Review of family-group names of living bovids. *Journal of Mammalogy*, 82:374-388.

Heintz, E. 1970. Les cervidés Villafranchiens de France et D'Espagne. Paris, *Mémoires du Muséum National D'Histoire Naturelle. Série C, Sciences de la Terre*, 22.

Jass, C.N., Mead, J.I., and Logan, L.E. 2000. Harrington's extinct mountain goat (*Oreamnos harringtoni* Stock 1936) from Muskox Cave, New Mexico. *Texas Journal of Science*, 52:121-132.

Köhler, M. 1987. Boviden des türkischen Miozän (Känozoikum und Braunkohlen der Türkei. 28). *Paleontologia i Evolució*, 21:133-246.

Köhler, M. 1993. Skeleton and habitat of recent and fossil ruminants. Münchner Geowissenschaftliche Abhandlungen. Reihe A. Geologie und Paläontologie 25:1-88. München.

Kurtén, B. and Anderson, E. 1980. *Pleistocene Mammals of North America*. Columbia University Press, New York.

Lawrence, B. 1951. Post-cranial skeletal characters of deer, pronghorn, and sheep-goat with notes on *Bos* and *Bison*. Harvard University, *Papers of the Peabody Museum of American Archaeology and Ethnology*, 35:7-43.

Leinders, J.J.M. 1979. On the osteology and function of the digits of some ruminants and their bearing on taxonomy. *Zeitschrift für Säugetierkunde*, 44:305-319.

Lindsay, E., Mou, Y., Downs, W., Pederson, J., Kelly, T.S., Henry, C., and Trexler, J. 2002. Recognition of the Hemphillian/Blancan boundary in Nevada. *Journal of Vertebrate Paleontology*, 22:429-442.

Matsumoto, H. 1926. On a new fossil race of bighorn sheep from Shantung, China. *Science Reports of the Tôhoku Imperial University, Second Series (Geology)*, 10:39-41 + 2 plates.

Matthew, W.D. and Cook, H.J. 1909. A Pliocene fauna from western Nebraska. *Bulletin of the American Museum of Natural History*, 26:361-414.

Mead, J.I. and Lawler, M.C. 1994. Skull, mandible, and metapodials of the extinct Harrington's mountain goat (*Oreamnos harringtoni*). *Journal of Vertebrate Paleontology,* 14:562-576.

Mead, J.I. and Taylor, L.H. 2004. Pleistocene (Irvingtonian) Artiodactyla from Porcupine Cave, p. 280-292. In Barnosky, A.D. (ed.), *Biodiversity Response to Climate Change in the Middle Pleistocene: The Porcupine Cave Fauna from Colorado*. University of California Press, Berkeley.

Merriam, C.H. 1918. New Mammalia form the Idaho Formation. *University of California Publications, Geology*, 10:523-530.

Mou, Y. 1997. A new arvicoline species (Rodentia: Cricetidae) from the Pliocene Panaca Formation, southeast Nevada. *Journal of Vertebrate Paleontology*, 17:376-383.

Owen, R. 1848. Description of teeth and portions of jaws of two extinct anthracotheroid quadrupeds (Hyopotamus vectianus and H. bovinus) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight. *Quarterly Journal of Geological Society of London,* 4: 104-141.

Pederson, J., Smith, G., and Pazzaglia, F. 1999. Comparing the modern, Quaternary, and Neogene records of climate-controlled hillslope sedimentation in southeast Nevada. *Geological Society of America Bulletin*, 113:305-319.

Phoenix, D.A. 1948. Geology and ground water on the Meadow Valley Wash drainage area, Nevada, above the vicinity of Caliente, Nevada. Office of State Engineer, *Water Resources Bulletin*, 7:1-117.

Pilgrim, G.E. 1939. The fossil Bovidae of India. *Memoirs of the Geological Survey of India. Palaeontologia Indica*, 26, *Memoir* 1.

Repenning, C.A, 1987. Biochronology of the microtine rodents of the United States, p. 236-268. In Woodburne, M.O. (ed.), *Cenozoic Mammals of North America*. University of California Press, Berkeley.

Schaller, G.B. 1980. *Stones of Silence: Journeys in the Himalaya.* Viking Press, New York.

Schaller, G.B. 1977. *Mountain Monarchs: Wild Sheep and Goats of the Himalaya*. University of Chicago Press, Chicago.

Scopoli, Giovanni Antonio. 1777. *Introductio ad historiam naturalem sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae.* Prague. 506 pp.

Scott, K.M. 1985. Allometric trends and locomotor adaptations in the Bovidae. *Bulletin of the American Museum of Natural History*, 179:197-288.

Shaw, C.A. 1981. *The middle Pleistocene El Golfo local fauna from northwestern Sonora, Mexico.* Unpublished Master of Science Thesis, California State University, Long Beach, California.

Simpson, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*, 85:1-350.

Sisson, S. and Grossman, J.D. 1938. *The Anatomy of the Domestic Animals*. W.B. Saunders Company, Philadelphia.

Solounias, N., Barry, J.C., Bernor, R.L., Lindsay, E.H., and Raza, S.M. 1995. The oldest bovid from the Siwaliks, Pakistan. *Journal of Vertebrate Paleontology*, 15:806-814.

Stock, C. 1921. Later Cenozoic mammalian remains from the Meadow Valley region, southeastern Nevada. *American Journal of Science*, *Fifth Series* 2(18):250-264.

Stokes, W.L. and Conde, K.C. 1961. Pleistocene bighorn sheep form the Great Basin. *Journal of Paleontology*, 35:598-609.

Tedford, R.H., Flynn, L.J., Zhanxiang, Q., Opdyke, N.D., and Downs, W.R. 1991. Yushe Basin, China; paleomagetically calibrated mammalian biostratigrphic standard for the late Neogene of eastern Asia. *Journal of Vertebrate Paleontology*, 11:519-526.

Tedford, R.H., Albright, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt, R.M., et al. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (Late Oligocene through Early Pliocene Epochs), p. 169-231. In Woodburne, M.O. (ed.), *Late Cretaceous and Cenozoic Mammals of North America: Biostratigraphy and Geochronology*. Columbia University Press, New York.

Teilhard de Chardin, P. and Piveteau, J. 1930. Les Mammifères fossiles de Nihowan (Chine). *Annales de Paleontologie*, 19:1-134.

Teilhard de Chardin, P. and Trassaert, M. 1938. Cavicornia of South-Eastern Asia. *Palaeontologia Sinica, New Series C*, 6:1-104.

Valdez, R. 1982. *The Wild Sheep of the World*. Wild Sheep and Goat International, Mesilla, New Mexico.

von den Driesch, A. 1976. A guide to the measurement of animal bones from archaeological sites. Harvard University, *Peabody Museum of Archaeology and Ethnology, Peabody Museum Bulletin* 1.

Vrba, E.S. and Schaller, G.B. 2000. Phylogeny of Bovidae based on behavior, glands, skulls, and postcrania, p. 203-222. In Vrba, E.S. and Schaller, G.B. (eds.), *Antelopes, Deer, and Relatives. Fossil Record, Behavioral Ecology, Systematics, and Conservation*. Yale University Press, New Haven.

White, J.A. 1987. The Archaeolagine (Mammalia: Lagomorpha of North America, excluding *Archaeolagus* and *Panolax*. *Journal of Vertebrate Paleontology*, 7:425-450.

White, J.A. 1991. North American Leporinae (Mammalia: Lagomorpha) from late Miocene (Clarendonian) to latest Pliocene (Blancan). *Journal of Vertebrate Paleontology*, 11:67-89.

Woodburne, M.O. and Swisher, C.C. 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. *Geochronology Time Scales and Global Stratigraphic Correlation, SEPM Special Publication* 54:335-364.