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The earliest North American record of the Antilocapridae (Artiodactyla, Mammalia)

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The Family Antilocapridae is considered to have first appeared in the Early Hemingfordian of western North America. Here we report a mandible of a merycodontine antilocaprid from the Late Arikareean Harrison Formation of eastern Wyoming. The mandible has three lower molars preserved and mandibular ramus features that allow it to be differentiated from other contemporaneous selenodont artiodactyl families, yet the lack of detailed understanding of intraspecific variation in *Paracosoryx* and *Merycodus* warrant caution in assigning this to a genus. This new material predates the previous first appearance of antilocaprids by approximately 3–4 million years and suggests that antilocaprid immigration from Eurasian ruminant stock occurred earlier than previously assumed and that caution should be exercised when using first appearances in broader analyses.

INTRODUCTION

The pronghorn Family Antilocapridae is considered wholly endemic to North America, though surely derived from a currently unknown Oligocene Eurasian stock (Davis 2007). The earliest previously recorded specimens of the Family Antilocapridae are those of *Paracosoryx* and *Merycodus* from the early Hemingfordian (~18Ma) (Janis and Manning 1998, Davis 2007). These early members were smaller than later antilocaprids and characterized by a suite of features, primarily cranial appendages, grouping them into the possibly paraphyletic subfamily Merycodontinae. The arrival of merycodontines in North America is considered to be one of the hallmarks of the onset of the Hemingfordian (Tedford et al. 2004), though questions still surround the origins of the family (Janis and Scott 1987). In July 1977, a University of Kansas field party in Wyoming collected a mandible that appears to be an antilocaprid, but was unexpectedly found near the Ellicott Ranch Local Fauna of the Harrison Formation of Latest Arikareean age (ca. 21 Ma) (Martin 1987). This is approximately three million years earlier than the previously known records of antilocaprids from North America (Tedford et al. 2004).

In this study, we describe this mandible, investigate its identity as a merycodontine antilocaprid and discuss its affinity with either of the known Hemingfordian merycodontines, *Merycodus* or *Paracosoryx*, using basic morphometrics of the lower postcanine dentition. This work, while preliminary, highlights the need for a thorough investigation of intra- and interspecific variation of antilocaprid dentitions and that many members of the subfamily Merycodontinae should be restudied and potentially revised.

Abbreviations: **KUVP**, University of Kansas Natural History Museum, Lawrence; **FMNH**, Field Museum of Natural History, Chicago, IL; **UCMP**, University of California Museum of Paleontology, Berkeley; **AMNH**, American Museum of Natural History, New York; **F:AM**, Frick Collection, American Museum of Natural History, New York.

GEOLOGICAL SETTING

KUVP 48020 is from KUVP locality Wy-115 in Sections 9 and 17, Township 31N, Range 60W, north of Van Tassel, Niobrara County, Wyoming, USA. The strata are identified as part of the lower portion of the Harrison Formation, a massive eolian sand. This lower portion where the specimen was found lies below the upper portion of the Harrison Formation. The upper portion of the Harrison Formation should not be mistaken for the "Upper Harrison Formation" which is now referred to as the Anderson Ranch Formation (Hunt 2002). The upper portion of the Harrison Formation is characterized by a heavily burrowed soil complex with interbedded eolian fine sands and preserves the Ellicott Ranch Local Fauna (see Fig. 1). This upper portion of the Harrison Formation containing the fossorial beaver, *Euhapsis*, was originally measured and dated as latest Arikareean, approximately 21Ma. This segment of the Arikareean is referred to as the Harrisonian by Yatkola (1978) and Martin (1980, 1987). The late Arikareean is characterized by the last occurrence of *Euhapsis* (Tedford et al. 2004). KUVP 48020 was found below the beds containing *Euhapsis* indicating this specimen must be at least late Arikareean in age or older. KUVP 48020 originates from the sandy facies just below this heavily burrowed layer, and is thus older than the Ellicott Ranch Local Fauna, although just how much older remains unknown.

Radiometric dates of the type section of the Monroe Creek Formation of Nebraska containing *Euhapsis* have been dated as early Arikareean, approximately 28.3–27.5 Ma (Tedford et al. 2004). If the *Euhapsis*-bearing localities are all early Arikareean, then the upper portions of what was then known as the Harrison Formation when KUVP 48020 was collected is of the same age or older (Martin 1987). Alroy (2000) refers to the Harrisonian as encompassing dates of 24.8–23.5 Ma,

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though it remains unclear whether Martin (1987) and Alroy (2000) are referring to the same lithostratigraphic and/or biostratigraphic intervals. Nonetheless, this lower portion of the Harrison Formation from which KUVP 48020 was found is certainly older than the previously oldest first appearances of the antilocaprids (*Paracosoryx*) in the Anderson Ranch Formation (Hunt 2002).

SYSTEMATIC PALEONTOLOGY

ORDER: ARTIODACTYLA Owen 1848
SUBORDER RUMINANTIA Scopoli, 1777
INFRAORDER PECORA Linnæus, 1758
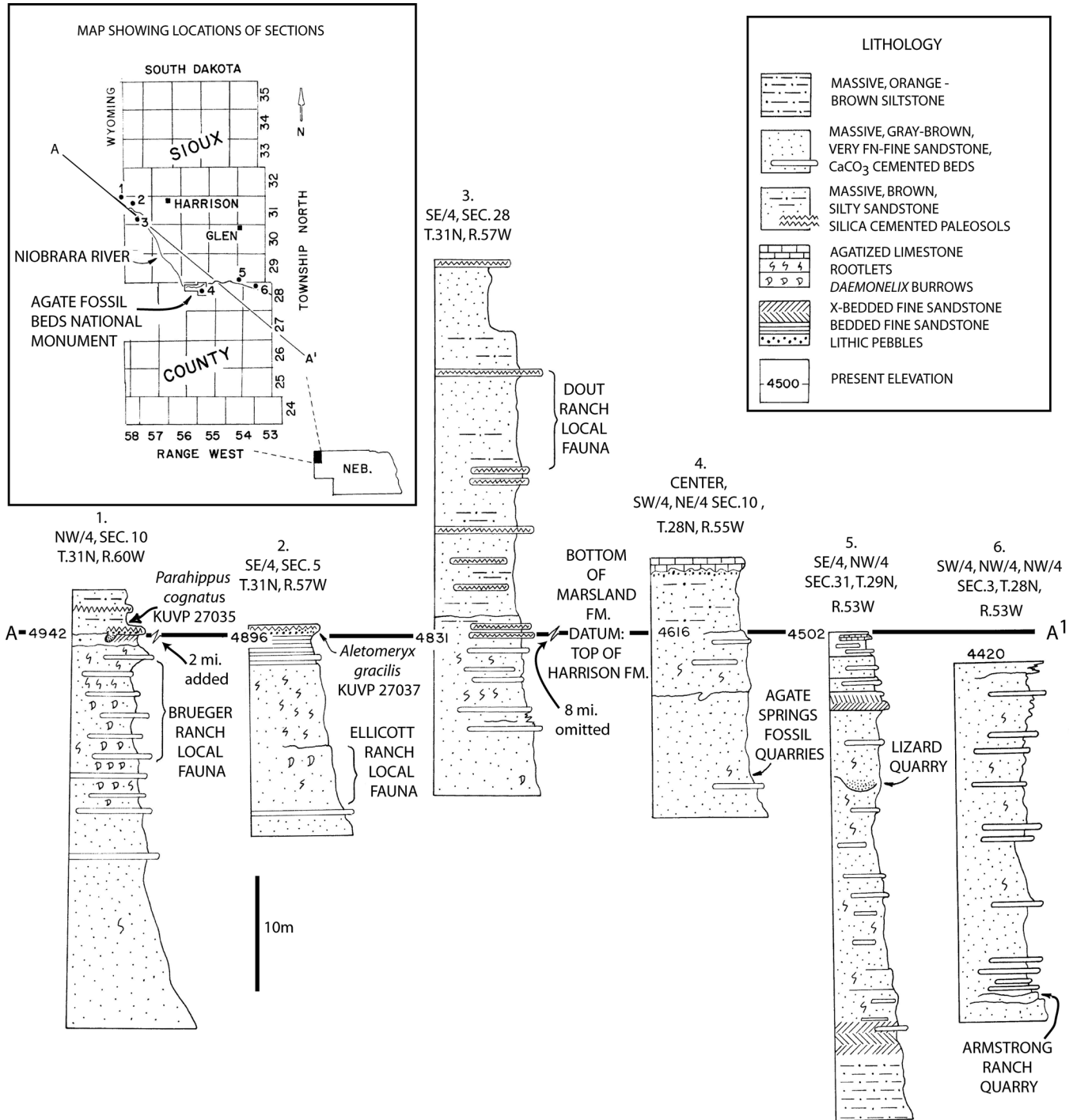FAMILY ANTILOCAPRIDAE Gray, 1866
GENUS: indeterminate

Figure 1. Stratigraphy of the Harrison Formation of the Niobrara Valley (drawn by D. A. Yatkola, previously unpublished). Note location of Ellicott Ranch Local fauna in Section 2.

Referred material—KUVP 48020, a partial left mandible.

Diagnosis—Moderately hypsodont selenodont lower molars with small ectostylids, but lacking other accessory features (such as metastylids found in later *Paracosoryx*). Length of m2 = 6.8 mm, width = 5.73 mm (N=1). The hypoconulid of the m3 has a sulcus on the posterolabial aspect, extending dorsoventrally for the entire exposed length.

Comments—The only antilocaprid yet known from the Arikareean. Taxonomic assignment is provisional pending revision of the Merycodontinae.

DESCRIPTION

Mandible and dentition

KUVP 48020 (Figs. 2–4) is a partial mandible with all three molars intact and fully erupted. Except for the broken distal root of the p4, the mandible anterior to the first molar is missing. The body of the mandible immediately below the teeth is complete and the inferior beginning of the ramus is preserved. Nothing remains of the angle of the mandible, the coronoid process or the mandibular condyle posteriorly, though the mandibular foramen is preserved. The depth of the mandible below the m2 = 11 mm. It steadily increases to 19mm at the level of the m3 hypoconulid, most likely to accommodate a more hypsodont m3. Other merycodontines, such as *Paracosoryx*, maintain a roughly uniform mandibular depth along these teeth, suggesting that this Arikareean merycodontine had slightly more hypsodont m3s or an enlarged site of attachment for the masseter and/or medial pterygoid muscles, or both.

The dentition is in an advanced, but not senescent stage of wear, with all dentine lakes connected, including that of the hypoconulid. The infundibulum of the m1 is nearly worn away, and if there was an infundibulum of the m3 hypoconulid, it is now missing. All that remains of the p4 is part of the distal root in the broken end of the mandibular body.

Unlike *Merycodus*, KUVP 48020 possesses ectostylids on the lower m1 and m2 (this region in the m3 is covered in calculus). Unlike *Paracosoryx*, it does not have any metastylids. An apomorphic feature of KUVP 48020 is the hypoconulid of the m3. A shallow vertical groove on its postero-labial edge makes the hypoconulid C-shaped in cross section (visible in occlusal view). Due to the advanced stage of wear, it is uncertain whether this hypoconulid was one solid cusp or a double posterior lobe. Because this shallow vertical groove is on the labial aspect, it differs from both conditions (open and closed) of the posterior lobe *sensu* Janis and Scott (1987). This posterolabial groove of the m3 hypoconulid is not reported in *Paracosoryx* or *Merycodus* (Janis and Manning 1998), and is not present in any specimens identified as such in the AMNH collections.

Comparisons

Differentiating this mandible from other Late Arikareean artiodactyls of similar size is difficult, particularly because many taxa within this size range lack both cranial appendages
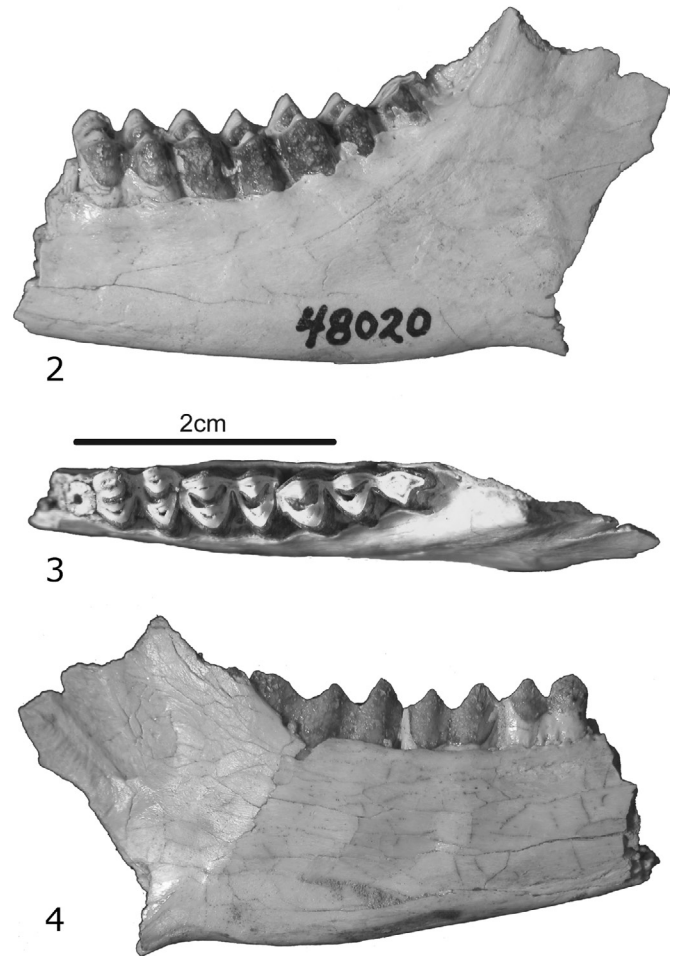
Figures 2–4. KUVP 48020. **2.** left labial view. **3.** occlusal (dorsal) view. **4.** right lingual view.

and well-diagnosed dental characteristics. Future studies of intraspecific variation from large samples of these relatively smaller artiodactyls may better clarify their range of variation. The combination of dental characteristics and mandibular depth preserved in KUVP 48020 is not found in other contemporaneous selenodont artiodactyl groups, including gelocids, leptomerycids, hypertragulids, moschids and camelids.

The Family Gelocidae is typically characterized by an anterior cingulum on the lower molars (Janis and Scott 1987) and brachydont lower molars (Métais and Vislobokova 2007). Like KUVP 48020, gelocids lack metastylids, although this is where the similarities end. Gelocids have only a remnant of a paraconid present, crowded metaconids and entoconids and a trace of the *Dorcatherium* fold (Métais and Vislobokova 2007). *Pseudoceras*, the only known North American gelocid (Frick 1937, Webb and Perrigo 1984), differs from KUVP 48020 in having a posteriorly directed metaconid and a hypoconid enclosing a narrow fossettid (Métais and Vislobokova 2007).

Leptomerycids are perhaps the best candidate outside of merycodontines for the placement of KUVP 48020 based

primarily on size and the lack of distinctive lower molar characters, although their mandibular ramus depth is much less. *Pronodens* is larger than KUVP 48020 with broader lower molars (molar width holotype m2 = 7.2 mm) (Koerner 1940, Métais and Vislobokova 2007).

The hypertragulids, including *Hypertragulus* and *Nanotragulus*, share one feature with KUVP 48020: an enlarged masseteric fossa and mandibular angle (Frick 1937). Though the mandibular angle is not preserved in KUVP 48020, the posterior portion of the inferior rim of the mandibular ramus preserves the ventral projection of the most anterior part of an enlarged masseteric fossa. This ventral projection can be seen in *Hypertragulus* as well, though it should be noted that hypertragulids (including the holotype of *Hypertragulus*, AMNH 6815) otherwise differ from KUVP 48020 in having brachydont lower molars with a shallow mandibular ramus depth. Also, *Hypertragulus* has prominent anterior cingula as well as accessory cuspids, unlike KUVP 48020 (Vislobokova 1998, Webb 1998, Métais and Vislobokova 2007).

The only members of the Moschidae that immigrated to North America were the Blastomerycinae, which consist of six genera (Prothero 2007). Unlike gelocids and KUVP 48020, moschid lower molars have metastylids like *Paracosoryx*. Unlike moschids, antilocaprid metaconid crests (including that of *Paracosoryx* and KUVP 48020) are not anteriorly directed to meet the paraconid crest (Webb 1998).

KUVP 48020 can be differentiated from camelids in general because it lacks the labial ribs and entostylids of the postcanine dentition that are considered characteristic of the Camelidae. Of the stenomylines, *Stenomylus* is the only known Arikareean taxon, and although its molars are also hypsodont, the m3s of stenomyline camels are characteristically extremely elongated anteroposteriorly (Honey et al. 1998), which KUVP 48020 is not. The protolabine camelid *Michenia* is known from this time period, but is differentiated from KUVP 48020 by its more slender mandibular ramus and larger teeth (length of m2 = 16–24.8 mm) (Frick and Taylor 1971, Honey et al. 1998).

Lastly, KUVP 48020 is differentiated from the contemporary ruminant, *Delahomeryx*, on the basis of molar morphology. The dentition of *Delahomeryx* is larger than KUVP 48020 (*Delahomeryx* m2 length 14.4 mm). The entoconid overlaps the hypoconulid and the protocone has unusual intercolumnar tubercles (Stevens et al. 1969), unlike KUVP 48020.

DISCUSSION

Postcanine dental variation in *Merycodus* and *Paracosoryx*

Despite how distinctive KUVP 48020 is from other small artiodactyls of its time, how can we be sure of its identity as an antilocaprid? The length of the m2 (6.8 mm) in KUVP 48020 is distinctly smaller than the average length of m2 (9.4 mm) for the early merycodontine antilocaprid *Merycodus* and larger than the average length of m2 (4.6 mm) for the equally early merycodontine, *Paracosoryx* (Janis and Manning

1998). Unfortunately, little is known regarding intraspecific variation in antilocaprids. Because the generic assignments of several key species of merycodontines remain unclear, we compare measurements of the postcanine dentition (Table 1) of KUVP 48020 with some of the earliest examples of the merycodontines: *Merycodus* and *Paracosoryx,* including the probable *nomen dubium*, *Merycodus prodromus* Cook 1934 (from the Latest Arikareean of Sioux Co., Nebraska); *Merycodus minimus* Frick 1937 (from Cuyamungue, New Mexico); *Merycodus minor* Frick 1937 (from Tesuque, New Mexico) and *Paracosoryx wilsoni* Frick 1937 (from the Late Hemingfordian of Sioux Co., Nebraska). *Merycodus prodromus* is only known from a pair of damaged upper molars that are not presently diagnostic for any single genus of merycodontine, and may represent another artiodactyl group entirely. *Merycodus minimus* and *Merycodus minor*, originally described as *?Submeryceros minimus* and *?Submeryceros minor* by Frick (1937), were still considered morphologically distinct as *Submeryceros* by Voorhies (1990) and Storer (1975) based on their horn morphologies. Janis and Manning (1998) and Davis (2007) considered *Submeryceros* a junior synonym of *Merycodus* and we follow their assignment until further analyses of these taxa are undertaken.

Without extensive studies of intraspecific variation and subsequent revisions of merycodontines, we can only compare our new specimen with the Hemingfordian merycodontines. A comparison of the length and width of the lower second molar in these taxa with KUVP 48020 fits well within the cloud of points generated for specimens of *Merycodus*, but outside the cloud of points comprised of specimens of *Para-*
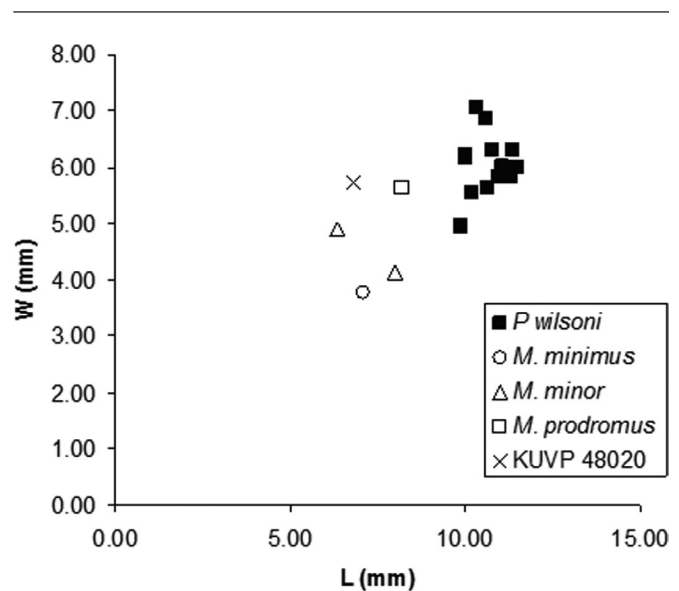

Figure 5. Bivariate plot of second lower molar dimensions for a sample of Arikareean and Hemingfordian merycodontines. Note that the measurements of *Merycodus prodromus* are based on the upper molars of the holotype and included to assess potential similarity (presuming upper and lower molars are approximately equal in length for occlusal reasons).

Table 1. Specimens of early Merycodontinae used in this study. Taxonomic assignments are provisional until revisions of the subfamily can be made. Abbreviations: m, molar; hyl, hypoconulid. *= possibly inaccurate because of fossil deformation or breakage.

Cat. #	Genus	Species	Locality	m2 L	m2 W	m3 L	m3 W	hyl L	hyl W
KUVP 48020	n. gen.?	n. sp.?	Near Van Tassel, WY	6.80	5.73	12.45	5.15	4.65	3.8
AMNH 31748	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	10.21	5.56	13.07	4.75	3.22	3.21
AMNH 1247	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	11.36	6.30	16.61	5.73	4.25	3.59
AMNH 32007	*Paracosoryx*	*wilsoni*	Long quarry, Antelope Draw, NE	11.31	5.84	13.89	5.75	3.66	3.94
AMNH 32010	*Paracosoryx*	*wilsoni*	Long quarry, Antelope Draw, NE	9.98	6.21	13.60	6.08	3.62	3.53
AMNH 31745	*Paracosoryx*	*wilsoni*	Long quarry, Antelope Draw, NE	10.62	6.86	14.70	5.84	4.01	3.77
AMNH 32008	*Paracosoryx*	*wilsoni*	Long quarry, Antelope Draw, NE	11.48	5.98	13.82	5.40	?	?
AMNH 51539	*Paracosoryx*	*wilsoni*	Long quarry, Antelope Draw, NE	10.32	7.05	13.93	6.05	4.07	3.92
AMNH 31743	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	10.78	6.29	13.51	5.73	3.46	3.68
AMNH 31746	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	10.01	6.16	14.00	6.03	3.19	4.10
AMNH 51554	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	11.07	6.01	15.05	5.46	4.07	3.70
AMNH 32007	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	10.67	5.62	14.59	4.62	3.47	2.95
AMNH 32005	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	10.95	5.83	13.13	4.80	2.85	3.24
AMNH 32006	*Paracosoryx*	*wilsoni*	Sheep Creek Fm., Sioux Co., NE	9.89	4.93	14.13	4.36	2.67	3.05
AMNH 30991	*Merycodus*	*minimus*	Cuyamungue, NM	7.08	3.76	9.02	3.46	2.20	2.19
AMNH 51827	*Merycodus*	*minor*	Tesuque, NM	6.37	4.88	10.47	4.35	3.14	2.58
AMNH 30987	*Merycodus*	*minor*	Tesuque, NM	8.01	4.13	9.97	2.54*	2.23*	2.15*

cosoryx wilsoni (Fig. 5). Though morphometrically similar to *Merycodus*, the dental characteristics and age of KUVP 48020 suggest it is a new taxon.

Problems with "horns" and hypsodonty

One difficulty with regard to the identification and subsequent phylogenetic analyses of these early ruminants is that taxa are commonly described from specimens with preserved horns or dentition, but rarely both. This situation creates the problem of organ taxa, more commonly encountered in paleobotany. Taxa diagnosed solely by cranial appendage characters, such as *Ramoceros*, are especially problematic; its phylogenetic character data places it in an unstable position within the early merycodontines (Janis and Manning 1998). Data on postcrania may help to sort this out (Davis 2007). In the case of *Merycodus*, numerous cranial and postcranial specimens have been collected and described (Matthew 1904, Frick 1937).

Likewise, hypsodonty is a poor feature to characterize early ruminants, as it is apparent that it has been independently derived multiple times among morphologically similar groups (Janis and Scott 1987). Nonetheless, the characteristics used to identify merycodontines are principally the plesiomorphic characters of moderate hypsodonty and cranial appendages formed by a pedicle and a horn core bordered in between by a rim of rough bone (known as a burr). In addition to these

plesiomorphies, several apomorphies are used to identify some of the more derived merycodontines, including the loss of dental characteristics such as metastylids and ectostylids. These are only found in some early merycodontines such as *Merycodus*, *Paracosoryx* and KUVP 48020. These diagnostic dental characters are all potentially problematic in specimen identification and future phylogenetic analysis.

Paracosoryx and *Merycodus* are in desperate need of review and revision. As Janis and Manning (1998) point out, many of the species described for the genus subsequent to the type species, *P. wilsoni*, may belong to other genera from more derived portions of the phylogeny. Moreover, the whole of the Merycodontinae needs to be revisited with respect to characters that are not cranial appendages. Once dental and other characters are clarified, it should be more reasonable to assess the validity of these taxa and gauge what their Eurasian ancestors may be.

Biostratigraphy and divergence dates

Coming from the Harrison Formation (Late Arikareean, 21–23 Ma), KUVP 48020 extends the range of the Antilocapridae. The previously oldest known antilocaprids are *Merycodus* and *Paracosoryx*, both from formations that are Early Hemingfordian in age or younger (Hunt 2002, Tedford et al. 2004). The first appearance of antilocaprids has been used as an indicator of the beginning of the Hemingfordian land mammal age, although *Paracosoryx* has been reported from the latest Arikareean Anderson Ranch Formation (Tedford et al. 2004). We believe this report to be in error, as no material definitively diagnostic for *Paracosoryx* was published in the reference cited therein (Hunt 2002) or to date. Hunt (2002, p. 33) postulates that "hypertragulids made their last appearance in the Upper Harrison as the genus *Nanotragulus*, possibly replaced by the first occurrence of merycodont antilocaprids in the Runningwater Formation", and then claims that the first occurrence of merycodontines was an Early Hemingfordian fauna in the Runningwater Formation.

However, as noted by Hunt (2002, p. 35): "The contrasting styles of sedimentation indicated by Upper Harrison and Runningwater rocks suggest that a number of first and last appearances are probably correlated with environmental preferences of these mammals, and do not actually reflect their 'extinction' or 'sudden' origin in the North American midcontinent. As such, the evident turnover in amphicyonid species at the Arikareean-Hemingfordian boundary may be at least influenced, and possibly determined, by the shift in depositional environments taking place at this time in the central Great Plains." We could not agree more. The concept underlying the North American Land Mammal Ages was never intended to form an absolute basis for determing dates for strata or the animals found in them (Wood et al. 1941). It should not be surprising that some fauna only previously known from the Runningwater and Anderson Ranch Formations would be found in slightly older rocks reflecting the appropriate environment for those faunal con-

stituents. Even though antilocaprids were previously only known from Hemingfordian and younger ages, our evidence suggests that their first appearance should not be used as a defining criterion for the Hemingfordian land mammal age. The existence of an antilocaprid in the Late Arikareean of Wyoming strengthens the argument that first appearances are diachronous (Alroy 1998). Although not listed as an "index taxon," antilocaprids are vagile enough that they should be widespread more quickly than smaller mammals with smaller ranges, begging the question: why are they diachronous in distribution as well? Perhaps, as Hunt (2002) reasons, appearances, including first appearances, may reflect environmental preferences more than origination events. Studies by Prothero et. al. (2008) have supported the opposite conclusion, that discrepancies of appearance dates were the result of stochastic sampling of diffusive immigration. It remains uncertain which situation is more prevalent, and further tests of contemporaneous well-sampled sequences are required to help clarify this dilemma. When first and last appearances are used in broader analyses, limits of the fossil record and our understanding of paleoecology are evident and require further study.

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