

# BARSTOVIAN OCHOTONIDS FROM HEPBURN'S MESA, PARK COUNTY, MONTANA, WITH COMMENTS ON THE BIOGEOGRAPHY AND PHYLOGENY OF *OREOLAGUS*

BRIAN P. KRAATZ

ANTHONY D. BARNOSKY

*Department of Integrative Biology and Museum of Paleontology  
University of California, Berkeley*

## ABSTRACT

Few researchers have attempted rigorous cladistic analyses of fossil ochotonids (pikas), largely due to the paucity and morphological conservatism of the fossils. However, pikas were diverse and widespread during the Cenozoic, and we therefore explore the applicability of cladistic analysis utilizing dental characters, which comprise most of their fossil record. We used abundant Barstovian ochotonid specimens from Hepburn's Mesa, Montana, and previously described Miocene material to construct a phylogeny and explore congruencies among the phylogenetic, stratigraphic, and geographic occurrence of *Oreolagus* from the western United States. Maximum parsimony analysis was con-

ducted using 13 morphological characters. Stratigraphic and geographic occurrences of *Oreolagus* are generally congruent with the proposed hypothesis of phylogeny and seem to involve an early Hemingfordian first occurrence in the Great Plains, followed by later Hemingfordian and Barstovian radiations into and within the northern Rocky Mountain region, Oregon, and Nevada. Although this study is limited in scope, it illustrates that with further understanding of ontogenetic changes in occlusal morphologies of ochotonids, cladistic analysis is a viable method for reconstructing ochotonid phylogenies and exploring their biogeography.

## INTRODUCTION

In 1950 Malcolm C. McKenna and Dwight W. Taylor collected vertebrate fossils along the banks of the Yellowstone River north of Gardiner, Montana. Camel, equid, tortoise, and mylagaulid remains were recovered. Exhibiting the breadth and productivity that characterized his career, Malcolm quickly published one of his first papers in vertebrate paleontology on a mylagaulid skull from this locality while he finished his dissertation at the University of California, Berkeley (McKenna, 1955). About twenty-five years later, J. D. Love directed one of us (ADB) to the same locality, and more importantly, to contact Malcolm about the Rocky Mountain Miocene. Eventually that led to exploratory work by a crew from the University of Washington Burke Museum and the discovery of a rich screen-washing locality in the deposits Malcolm dubbed "Chalk Cliffs." Subsequently, field teams from The Carnegie Museum of Natural History collected many more specimens and set the exposures in magnetostratigraphic and biostratigraphic context (Barnosky and LaBar, 1989; Burbank and Barnosky, 1990). In light of Malcolm's discovery of this important locality, now known as Hepburn's Mesa, and his interest in pika-like mammals and the Rocky Mountain Miocene, we offer this paper.

Our purpose is to document the abundant ochotonids from Hepburn's Mesa, set them in a preliminary phylogenetic context, and use that information to explore some ideas concerning Miocene biogeography. We examine whether age and geographic distributions of this group are congruent with a phylogeny hypothesized by cladistic analysis.

### AGE, GEOLOGICAL, AND ENVIRONMENTAL SETTING

Hepburn's Mesa is located in the Yellowstone Valley, Montana, about 45 km south of Livingston (Fig. 1). Burbank and Barnosky (1990) determined that the fossil-bearing strata range in age from about 16.8 to about 13.7 Ma. The vast majority of the ochotonid material discussed in this report comes from Unit 16 of Burbank and Barnosky (1990), and has an estimated age of about 14.8 Ma in the early part of the late Barstovian. Barnosky and LaBar (1989) interpreted the environmental setting to represent nearshore facies of an intermittently saline lake, with regional topography more subdued than at present, and an arid or semiarid climate.

### RELEVANT BACKGROUND ON OCHOTONIDS

Modern ochotonids represent a small portion of the overall diversity found within Lagomorpha to-

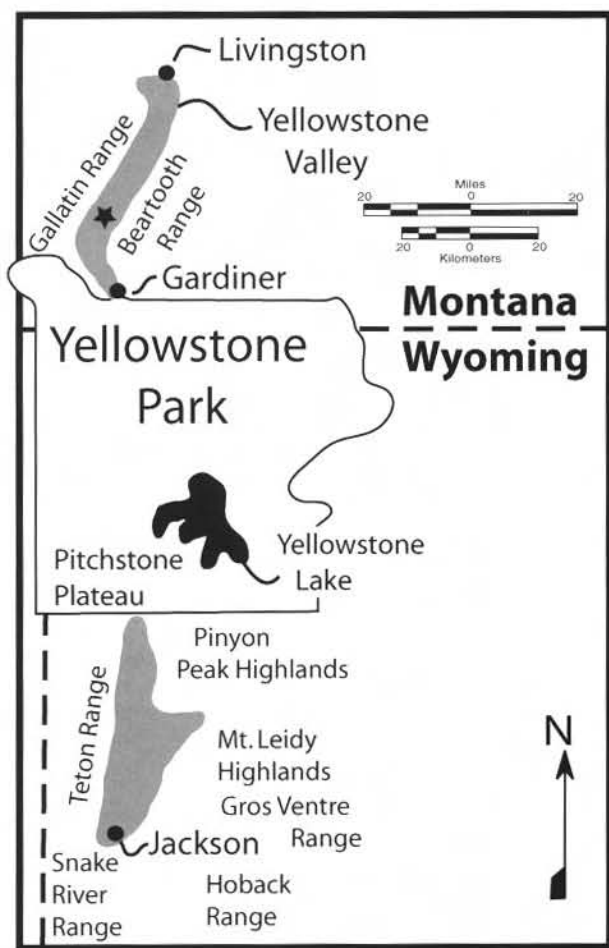


Fig. 1.—Map showing location of Hepburn's Mesa, indicated by star. For a detailed locality description see Barnosky and LaBar (1989).

day. The first appearance of the family Ochotonidae is in the early Oligocene of Mongolia—approximately 32–33 million years ago—represented by *Sinolagomys* from the Hsanda Gol formation (Kraatz, 2002). It is during this time that ochotonids are believed to have diverged from a more ancient leporid stock (i.e., hares and rabbits) (Dawson, 1965; Erbajeva, 1994). During the Miocene throughout much of the world, lagomorph faunas were dominated by ochotonids relative to leporids (Dawson, 1967). Extant ochotonids include only one genus and 27 species, all of which are found in Asia except for two species known from western North America (Nowak, 1999). In contrast to their limited distribution in modern faunas, ochotonids constitute a significant portion of small mammal diversity in many fossil localities throughout the Oligocene and Miocene.

Erbajeva (1994) conducted a phylogenetic study

of Ochotonidae (focusing on Asian taxa) but did not provide detailed discussion of phylogenetic characters or a rigorous cladistic analysis. In light of this, one goal of the present study is to determine the potential for cladistic analysis of ochotonids. Contributing to the lack of previous phylogenetic studies of the group is that the morphology of ochotonids is highly conserved and little morphological variation is seen through time, making the task of determining and evaluating characters difficult. In addition, the majority of fossil material known consists of isolated teeth. Dentaries or maxillae are known for only a few Tertiary taxa. Because of this few skull or post-cranial characters are recognized for most of the taxa within this family.

#### GEOGRAPHIC AND GEOLOGIC OCCURRENCES OF *OREOLAGUS*

*Oreolagus* is one of the earliest recorded ochotonids from North America. *Desmatolagus* has been reported from the early Oligocene and early or middle Miocene of North America and is sometimes referred to Ochotonidae (Dawson, 1965; Korth and Hageman, 1988; Munthe, 1988). In short, it is unclear whether this taxon should be considered an ochotonid, a leporid, or neither. For a discussion of the taxonomic implications of *Desmatolagus* the reader is referred to Burke (1936), Dawson (1965, 1967), and Sych (1975). Kellogg (1910) was the first to describe *Oreolagus* (although it was initially referred to *Palaeolagus*) and Dawson (1965) provided a thorough review of *Oreolagus* after additional species were described. Since publication of her paper, a significant amount of new fossil material has been found throughout the western United States. Most recently, five species have been recognized; *Oreolagus nevadensis* (Kellogg, 1910), *O. nebrascensis* (McGrew, 1941), *O. wallacei* (Dawson, 1965), *Oreolagus wilsoni* (Dawson, 1965), and *O. colteri* (Barnosky, 1986). Here we do not consider *O. colteri* a valid species (see below).

The first occurrence of *Oreolagus* is from the Hemingfordian of Colorado and Nebraska, represented by both *O. wilsoni* and *O. nebrascensis* (McGrew, 1941; Wilson, 1960; Dawson, 1965). Older *Oreolagus* material was reported from the late Oligocene Peterson Creek local fauna of Idaho (Nichols, 1976), but this material is not included in this study, as only a single lower cheek tooth is known and its assignment to *Oreolagus* is questionable. Younger Hemingfordian material is known from the Split Rock Formation of Wyoming; both Dawson (1965) and Munthe (1988) reported *O. ne-*

Table 1.—Geographic and biochronologic occurrence of *Oreolagus* taxa used in this study.

	Geographic occurrence	Stratigraphic occurrence
<i>Oreolagus nebrascensis</i>	Wyoming, Nebraska	Hemingfordian 1 & 2
<i>Oreolagus nevadensis</i>	Wyoming, Montana, and Nevada	Hemingfordian 2 and Barstovian 1
<i>Oreolagus wilsoni</i>	Colorado	Hemingfordian 2
<i>Oreolagus wallacei</i>	Oregon	Hemingfordian 2–Barstovian 1
<i>Desmatolagus gobiensis</i>	Mongolia, China	Early Oligocene
<i>Eurymylus laticeps</i>	China	Paleocene

*brascensis* from this area. However, the material we examined from Split Rock that was referred to *O. nebrascensis* by Munthe (1988) is attributable to *O. nevadensis*, and we also identified specimens of *O. nebrascensis*, indicating that both species are present at Split Rock. Kraatz (in progress) is redescribing the ochotonid material from the Split Rock localities.

The early Barstovian marks the first appearance of *O. wallacei* from Oregon (Wallace, 1946; Dawson, 1965; Tedford et al., in press). Dawson (1965) suggested that this fauna from Beatty Butte was equivalent to the Mascall, Sucker Creek, and Skull Spring local faunas, which Tedford et al. (2004), place in the early Barstovian. The early Barstovian also marks the occurrence of *Oreolagus* from Montana, and the continued occurrence of *O. nevadensis* (Sutton, 1977; Barnosky, 1986). *Oreolagus* material is also known from Saskatchewan, but that material is of poor quality and has not been identified beyond the generic level (Skwara, 1988). Figure 2 shows the geographic distribution of *Oreolagus* specimens referred to in this study from western

North America and Table 1 summarizes their biochronologic distributions.

Although Dawson (1965) commented on the implications of these distributions for the evolution of *Oreolagus*, suggesting that *Oreolagus* may have been derived from the Asian *Desmatolagus*, the substantial amount of material found and described since that publication warrants a reanalysis of biogeographic and temporal distribution of the genus. Some of this is provided here through: (1) description of new fossil *Oreolagus* material from the Hepburn's Mesa Formation; (2) reassessment of geographic and temporal distribution of the genus; and (3) cladistic analyses to obtain a hypothesis of phylogeny. The phylogenetic information is compared to the temporal and geographic data to draw inferences about the origins and paths of dispersal for this group.

#### LIST OF ABBREVIATIONS

CM—Carnegie Museum of Natural History.  
KUPV—University of Kansas Museum of Natural History. HM—Hepburn's Mesa.

## METHODS AND MATERIALS

Fossils from Hepburn's Mesa were correlated to detailed stratigraphic sections provided by Barnosky and LaBar (1989) and Burbank and Barnosky (1990). Most of the *Oreolagus* material was recovered from a screen-washing site designated CC-South Quarry (Unit 16). The rock from this extremely fossiliferous lens was broken into fist-sized chunks, soaked in water overnight, and then washed through a series of nested sieves with mesh sizes of 4, 8, 16, and 20 squares per inch (per 2.54 cm). Rocks that did not disaggregate during this procedure were taken back to the lab where they were frozen and thawed until they disintegrated enough to screen-wash. This procedure fragmented any jaws that may have been present, but the rocks were otherwise too indurated to effectively screen. Fossils were then picked from the dried matrix, mostly without the aid of magnification.

The following samples were considered representative of *Oreolagus* species mentioned in this paper. *Oreolagus nevadensis*—Hepburn's Mesa sample; examination of UCMP specimens from Split Rock; and published descriptions by Sutton (1977). *O. ne-*

*brascensis*—examination of specimens reported and published descriptions by Dawson (1965). *Oreolagus colteri*—examination of type and paratype material and descriptions by Barnosky (1986). *Oreolagus wilsoni*—examination of specimens reported by Wilson (1960) and published descriptions by Dawson (1965). *Oreolagus wallacei*—examination of specimens reported by Wallace (1946) and published descriptions by Dawson (1965).

Cladistic analyses were completed using maximum parsimony (MP) and the computer program PAUP\* 4.0b2a (Swofford, 1999). All characters were considered unordered and unweighted. MP topologies were obtained using exhaustive searches and bootstrap analysis was calculated for 2,000 replicates. Geographic and stratigraphic characters were utilized and traced onto the tree in MacClade (Maddison and Maddison, 1992). The stratigraphic data were created as a "stratigraphic character" type in MacClade. The geographic occurrences were optimized using ACCTRAN and DELTRAN as an unweighted and unordered standard character.

Table 2.—*Measurements of isolated teeth, Oreolagus nevadensis, Hepburn's Mesa Formation. Note all specimens are CM numbers. Column headings stand for AP, anteroposterior length; T, transverse width; TA, transverse width of anterior loph; TP, width of posterior loph; Hypostria, width which hypostria extends transversely across tooth; AP/T, anteroposterior length divided by transverse width; and H/T, width which hypostria extends across tooth divided by total width of tooth.*

Specimen	AP DP <sup>2</sup>	T			
64385	0.56	1.38			
64409	0.81	1.69			
64422	1.00	1.94			
64424	0.88	1.44			
64435	0.81	1.69			
66642	0.81	1.25			
66643	1.50	1.69			
mean	0.91	1.58			
	AP DP <sup>1</sup>	T			
63251	1.31	2.25			
63252	1.44	2.44			
63269	1.44	2.25			
63285	1.13	1.69			
64044	1.31	1.81			
64048	1.25	1.56			
64053	1.38	1.63			
64061	1.21	2.31			
64480	1.19	0.50			
64539	1.25	2.00			
66644	1.50	1.69			
mean	1.31	1.83			
	AP DP <sup>4</sup>	T			
63248	1.19	2.00			
63263	1.13	2.06			
63286	1.19	1.63			
64063	1.25	1.94			
64420	1.19	1.88			
64437	1.13	2.00			
64459	1.25	1.85			
64482	1.31	1.38			
64487	1.13	1.88			
64491	1.19	1.63			
64499	1.25	1.94			
64531	1.31	1.75			
mean	1.21	1.83			
	AP P <sup>2</sup>	T			
63290	1.00	1.13			
	AP P <sup>3</sup>	TA	T	AP/T	AL/T
63258	1.25	0.56	2.06	0.607	0.272
63268	1.38	0.75	1.94	0.711	0.387
63289	1.31	0.75	1.94	0.675	0.387
63374	1.25	0.75	2.00	0.625	0.375
63950	1.06	0.88	1.92	0.552	0.458
63957	1.19	0.75	1.94	0.613	0.387
64012	1.13	0.82	1.97	0.574	0.416
64056	1.19	0.69	1.60	0.744	0.431
64395	1.15	0.81	2.06	0.558	0.393
64492	1.25	0.75	1.82	0.687	0.412

Table 2.—*Continued.*

	AP P <sup>1</sup>	TA	T	AP/T	AL/T
64380	1.15	0.77	1.92	0.599	0.401
64509	1.19	0.81	2.19	0.543	0.370
64524	1.21	0.63	2.12	0.571	0.297
64535	1.38	0.88	2.19	0.630	0.402
66649	—	—	—	—	—
mean	1.22	0.75	1.98	0.620	0.385
	AP P <sup>4</sup>	Hypostria	T	AP/T	H/T
63243	1.63	0.81	2.38	0.685	0.340
63246	1.44	0.44	2.32	0.621	0.190
63257	1.38	0.69	2.25	0.613	0.307
63270	1.31	0.56	2.00	0.655	0.280
63273	1.15	0.77	2.08	0.553	0.370
63281	—	—	—	—	—
63284	1.38	0.87	2.38	0.580	0.366
63288	1.38	0.94	2.06	0.670	0.456
63293	1.31	—	—	—	—
63368	1.38	0.56	2.19	0.630	0.256
63371	1.38	0.88	2.25	0.613	0.391
63854	1.25	0.75	2.63	0.475	0.285
63952	1.56	0.69	2.31	0.675	0.299
64014	—	—	—	—	—
64016	—	—	—	—	—
64054	1.56	0.50	2.38	0.655	0.210
64059	1.38	0.69	2.38	0.580	0.290
64374	1.31	0.75	2.19	0.598	0.342
64377	1.44	—	2.56	0.563	—
64382	1.38	0.75	2.38	0.580	0.315
64383	1.38	0.95	2.25	0.613	0.422
64392	1.31	0.69	2.25	0.582	0.307
64484	1.56	0.50	1.63	0.957	0.307
64488	1.44	0.89	2.18	0.661	0.408
64500	1.31	0.69	1.69	0.775	0.408
64502	1.44	1.00	2.31	0.623	0.433
64504	1.31	0.74	2.00	0.655	0.370
64513	1.38	0.69	2.00	0.690	0.345
64514	1.31	0.44	2.13	0.615	0.207
64517	—	—	—	—	—
64523	1.31	0.38	2.19	0.598	0.174
64525	1.31	0.82	2.30	0.570	0.357
66639	1.26	0.56	2.05	0.615	0.273
66640	—	—	—	—	—
66641	—	—	—	—	—
mean	1.38	0.70	2.29	0.656	0.323
	AP M <sup>1</sup>	Hypostria	T	AP/T	H/T
63261	1.38	1.67	2.21	0.624	0.756
63266	1.50	1.92	2.31	0.649	0.831
63272	1.31	1.67	1.94	0.675	0.861
63274	1.28	1.62	2.02	0.634	0.802
63275	1.44	1.72	2.05	0.702	0.839
63278	1.38	1.74	2.19	0.630	0.795
63291	1.25	1.64	2.00	0.625	0.820
63292	1.25	1.45	1.69	0.740	0.858
63294	1.33	1.79	2.05	0.649	0.873
63295	1.38	1.59	2.05	0.673	0.776
63375	1.25	1.62	2.05	0.610	0.790
63409	1.19	1.13	—	—	—

Table 2.—Continued.

	AP M <sup>1</sup>	Hypostria	T	AP/T	H/T
63830	1.31	1.79	2.00	0.655	0.895
63841	1.38	1.54	2.05	0.673	0.751
63844	1.31	1.46	1.92	0.682	0.760
63848	1.38	1.48	1.67	0.826	0.886
63855	1.38	1.51	1.87	0.738	0.807
63880	—	—	—	—	—
63947	1.31	1.67	2.10	0.624	0.795
64015	1.44	—	2.05	0.702	—
64057	1.31	1.77	2.03	0.645	0.872
64065	1.25	1.55	2.05	0.610	0.756
64378	1.44	—	—	—	—
64379	1.38	1.69	2.18	0.633	0.775
64389	1.56	2.00	2.44	0.639	0.820
64411	1.31	—	—	—	—
64414	—	—	—	—	—
64423	—	—	—	—	—
64434	—	—	—	—	—
64441	1.38	1.67	2.06	0.670	0.811
64481	1.31	1.72	2.26	0.580	0.761
64486	1.38	1.46	1.72	0.802	0.849
64501	—	—	—	—	—
64503	1.44	1.85	2.25	0.640	0.822
64508	1.56	1.69	2.25	0.693	0.751
64516	1.25	1.54	2.05	0.610	0.751
64519	1.13	1.74	2.25	0.502	0.773
64521	1.50	1.92	2.31	0.649	0.831
64528	—	—	—	—	—
64529	1.44	1.69	2.00	0.720	0.845
64534	1.31	1.67	2.05	0.639	0.815
64540	1.38	1.67	2.06	0.670	0.811
66645	—	—	—	—	—
66646	1.31	1.63	1.92	0.682	0.849
66647	1.25	—	—	—	—
66648	1.38	1.54	1.79	0.771	0.860
66650	—	—	—	—	—
mean	1.39	1.65	2.05	0.665	0.790
	AP M <sup>2</sup>	T	AP/T		
63242	0.81	2.06	0.393		
63245	0.94	1.75	0.537		
63262	0.81	1.94	0.418		
63868	0.94	2.06	0.456		
63949	1.00	2.19	0.457		
64019	0.81	—	—		
64030	0.81	—	—		
64066	0.75	1.63	0.460		
64387	0.88	—	—		
64429	0.81	—	—		
64496	0.75	1.75	0.429		
64526	0.81	2.06	0.393		
mean	0.84	1.93	0.443		
	AP DP <sup>1</sup>	TA	TP		
63369	1.76	0.69	1.43		
64055	—	—	1.71		
64381	2.56	1.38	1.92		
64425	—	—	—		
64430	—	—	—		

Table 2.—Continued.

	AP DP <sup>2</sup>	TA	TP
64483	1.77	0.83	1.18
64490	1.94	0.92	1.13
64498	—	—	1.15
66652	2.51	1.08	1.56
66653	2.17	1.28	1.64
66654	—	0.82	—
66655	2.13	1.19	1.25
mean	2.12	1.02	1.44
	AP DP <sup>3</sup>	TA	TP
63280	1.69	1.06	1.06
64384	1.44	1.00	—
64413	1.50	1.19	1.38
64433	—	—	—
mean	1.54	1.08	1.22
	AP P <sub>2</sub>	TA	TP
64071	—	—	—
64371	0.69	—	—
64412	1.06	0.38	0.77
64418	—	—	—
64436	0.79	0.58	1.00
64489	—	—	—
64495	1.00	0.89	1.15
64527	1.00	0.50	1.50
64541	0.90	0.38	1.18
64544	1.00	1.60	—
mean	0.92	0.72	1.12
	AP P <sub>2</sub> , M <sub>1</sub> , or M <sub>2</sub>	TA	TP
63241	1.63	1.63	1.50
63254	1.69	1.50	1.44
63255	1.56	1.38	1.44
63256	1.81	1.69	1.44
63259	1.69	1.63	1.69
63260	1.56	1.63	1.63
63265	1.50	1.44	1.31
63271	1.69	1.63	1.63
63276	1.50	1.44	—
63277	1.69	1.56	1.44
63279	1.50	1.25	1.06
63282	1.81	1.44	1.69
63283	1.69	1.50	1.50
63287	1.69	1.50	1.50
63373	1.75	1.44	1.50
63837	1.50	1.38	1.38
63842	1.63	1.50	1.75
63860	1.69	1.50	1.38
63876	1.69	1.56	1.69
63943	1.69	1.56	1.44
63944	1.69	1.56	1.56
63951	1.63	1.50	1.63
63953	1.81	1.56	1.50
63958	1.69	1.63	1.63
63960	—	—	—
64011	1.69	1.56	1.50
64017	1.50	1.38	1.44
64058	1.75	1.63	1.68



Table 2.—Continued.

	AP P <sub>4</sub> , M <sub>1</sub> , or M <sub>2</sub>	TA	TP
64062	1.75	1.38	1.31
64064	1.69	1.81	1.56
64067	1.56	1.25	1.56
64373	1.69	1.38	1.44
64375	1.50	1.69	—
64376	1.81	1.38	1.63
64386	1.75	1.69	—
64388	1.81	1.38	1.63
64391	—	—	—
64393	1.56	1.50	1.38
64394	1.63	1.50	1.63
64432	—	—	—
64485	1.69	1.38	1.63
64506	—	—	—
64511	1.88	1.75	1.69
64512	1.69	1.69	1.81
64515	1.88	1.63	1.56
64518	1.63	1.44	1.19
64520	1.38	1.38	1.31
64522	1.63	1.56	1.63
64530	1.81	1.75	1.56
64532	1.41	1.44	1.28
64533	1.75	1.00	1.25
64538	1.63	1.69	—
64542	1.63	1.13	1.06
66651	1.56	1.38	1.56
mean	1.66	1.50	1.50

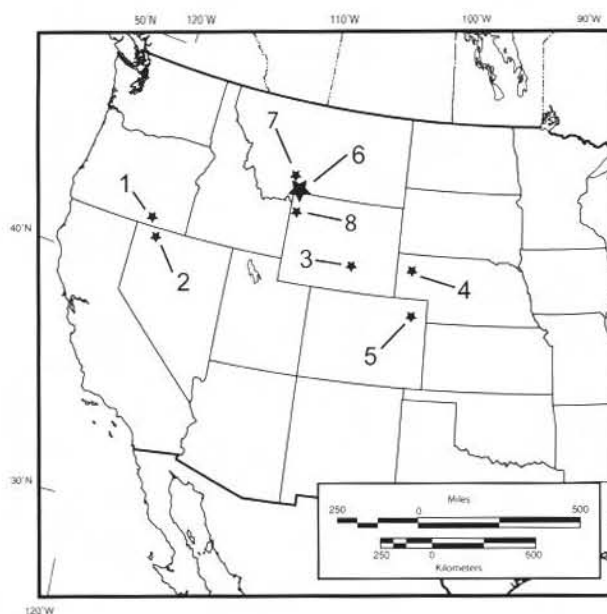


Fig. 2.—Location of Miocene fossil localities that have yielded species of *Oreolagus* and were used in this study. Numbers denote the following areas; (1) Beatty Butte, Oregon, (2) Virgin Valley, Nevada, (3) Split Rock, Wyoming, (4) Marsland, Nebraska, (5) Quarry A, Colorado, and (6) Hepburn's Mesa, Montana; (7) Anceney, Montana; and (8) Jackson Hole, Wyoming. Note that not all occurrences of *Oreolagus* are listed here (e.g. *Oreolagus* sp. from several localities).

## SYSTEMATIC PALEONTOLOGY

Order Lagomorpha Brandt, 1855

Family Ochotonidae Thomas, 1897

Genus *Oreolagus* Dice, 1917

*Oreolagus nevadensis* (Kellogg, 1910)

Table 2

Figure 3, A–I

*Localities*.—1935 CC South.

*Age*.—early Late Barstovian.

*Referred Specimens*.—Maxilla with P<sup>3</sup>–M<sup>1</sup>, CM 63372, CM 63376, Dentary with M<sup>1-2</sup>, CM 61203, Dentary with M<sub>1-2</sub>, CM 61202, Dentary with M<sub>1-2</sub>, CM 61201, Dentary with M<sub>1</sub>, CM 61204, Dentary, CM 61200, Partial dentaries, CM 61205, CM 63376, DP<sup>2</sup>, CM 64385, 64409, 64422, 64424, 64435, 66642, 66643, DP<sup>3</sup>, CM 63251, 63252, 63269, 63285, 64044, 64048, 64053, 64061, 64480, 64539, 66644, DP<sup>4</sup>, CM 63248, 63263, 63286, 64063, 64420, 64437, 64459, 64482, 64487, 64491, 64499, 64531, P<sup>2</sup>, CM 63290, P<sup>3</sup>, CM 63258, 63268, 63289, 63374, 63950, 63957, 64012, 64056, 64380, 64395, 64492, 64509, 64524, 64535, 66649, P<sup>4</sup>, CM 63243, 63246, 63257, 63270, 63273, 63281,

63284, 63288, 63293, 63368, 63371, 63854, 63952, 64014, 64016, 64054, 64059, 64374, 64377, 64382, 64383, 64392, 64484, 64488, 64500, 64502, 64504, 64513, 64514, 64517, 64523, 64525, 66639, 66640, 66641, M<sup>1</sup>, CM 63261, 63266, 63272, 63274, 63275, 63278, 63291, 63292, 63294, 63295, 63375, 63409, 63830, 63841, 63844, 63848, 63855, 63880, 63947, 64015, 64057, 64065, 64378, 64379, 64389, 64411, 64414, 64423, 64434, 64441, 64481, 64486, 64501, 64503, 64508, 64516, 64519, 64521, 64528, 64529, 64534, 64540, 66645, 66646, 66647, 66648, 66650, M<sup>2</sup>, CM 63242, 63245, 63262, 63868, 63949, 64019, 64030, 64066, 64387, 64429, 64496, 64526, DP<sub>3</sub>, CM 63369, 64055, 64381, 64425, 64430, 64483, 64490, 64498, 66652, 66653, DP<sub>4</sub>, CM 63280, 64384, 64413, 64433, P<sub>3</sub>, CM 64071, 64371, 64412, 64418, 64436, 64489, 64495, 64527, 64541, 64544, P<sub>4</sub>, M<sub>1</sub>, or M<sub>2</sub>, CM 63241, 63254, 63255, 63256, 63259, 63260, 63265, 63271, 63276, 63277, 63279, 63282, 63283, 63287, 63373, 63837, 63842, 63860, 63876, 63943, 63944, 63951, 63953, 63958, 63960, 64011, 64017, 64058, 64062, 64064,

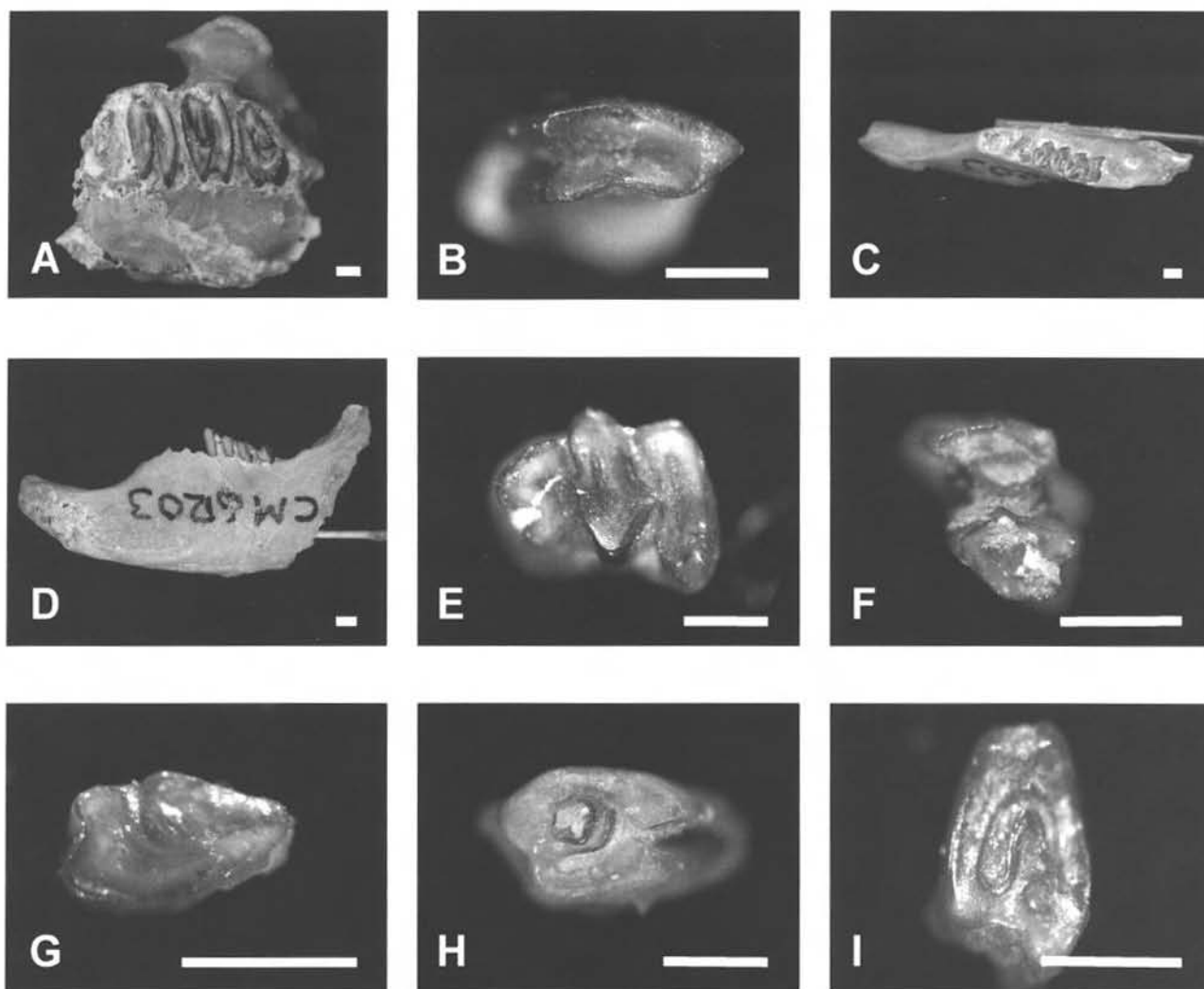


Fig. 3.—Digital images of *O. nevadensis* specimens from Hepburn's Mesa. A. CM 63372, right upper jaw with P<sup>3</sup>–M<sup>1</sup>, occlusal view, lateral at top. B. CM 64526, left M<sup>2</sup>, occlusal view, lingual to right, posterior at top. C. CM 61203, right lower jaw with M<sub>1-2</sub>, occlusal view, labial at top. D. Same as C, lingual view, dorsal at top. E. CM 66652, DP<sub>3</sub>, occlusal view, anterior to left. F. CM 63280 left DP<sub>4</sub>, occlusal view, posterior at top. G. CM 64409, left DP<sub>2</sub>, occlusal view, lingual to left, anterior at top. H. CM 64044 DP<sub>3</sub>, occlusal view, lingual to right, posterior at top. I. CM 63263, DP<sub>4</sub>, occlusal view, posterior to right, labial at top.

64067, 64373, 64375, 64376, 64386, 64388, 64391, 64393, 64394, 64432, 64485, 64506, 64511, 64512, 64515, 64518, 64520, 64522, 64530, 64532, 64533, 64538, 64542, 66651.

**Description and Comparison.**—Specimens from HM are generally similar to specimens of *Oreolagus nevadensis* described by Sutton (1977) from the Ancney Local Fauna. Two maxillary fragments were recovered from HM, CM 63372 and CM 63376, both containing P<sup>3</sup>–M<sup>1</sup>. CM 63372 is broken along the posterior side of the alveoli of M<sup>2</sup> and the posterior portion of the alveoli for the P<sup>2</sup> (Fig. 3A). CM 63376 is broken along the anterior side of the alveoli for P<sup>3</sup> and between M<sup>1</sup> and M<sup>2</sup>. In both specimens, the contact between the zygoma and the maxillary tuberosity terminates between P<sup>3</sup> and P<sup>4</sup>. The position of the premolar foramen differs slightly from that of *O. nevadensis* from Ancney. The foramen is preserved only in CM 63372 and is aligned be-

tween the anterior and posterior lochs of P<sup>3</sup>. The premolar foramen occurs in line with the posterior loph of P<sup>3</sup> in the Ancney specimens and with the anterior loph of P<sup>3</sup> in *O. wilsoni* and *O. nebrascensis* (Dawson, 1965). Due to breakage in maxillae it is not known whether M<sup>3</sup> has been lost in the HM specimens.

The upper cheekteeth from HM closely match those of other *Oreolagus*; characters include a basined M<sup>2</sup> and rootless upper teeth. Fifteen P<sup>3</sup>s were recovered. In all of these specimens the anterior loph is less than one-half the width of the posterior loph, which is similar to the condition found in *O. nevadensis* and *O. wallacei* (Table 2). In contrast, the anterior loph extends more than one-half the width of posterior loph in specimens of *O. wilsoni* and *O. nebrascensis*. The P<sup>3</sup>s from HM also have a J-shaped crescentic valley that opens anteriorly and is persistent along the entire columnar length of the tooth. All of the length measurements of P<sup>3</sup>s from HM are less than that reported for *O. wilsoni* by Dawson (1965:6 KUVF 10303, AP=1.5) and fall

within a similar range to that reported for *O. nevadensis* by Sutton (1977).

Thirty-five  $P^4$ s and 47  $M^1$ s were collected from HM.  $P^4$  is distinguishable from  $M^1$  based on the presence of a J-shaped crescentic valley in the former and its absence in the latter. This condition is similar to that found in *O. wallacei* and *O. nevadensis*, where a crescentic valley is not present in  $M^1$ . In *O. wilsoni* and *O. nebrascensis* the  $M^1$  has a crescentic valley. In  $P^4$  from HM the lingual hypostria terminates lingual to the crescentic valley and does not extend more than one-half the width of the tooth.  $M^1$  is similar in size and shape to  $P^4$  except for the lack of a crescentic valley and the extension of the hypostria labially in the  $M^1$ . In these teeth the hypostria extends between  $\frac{3}{4}$  and  $\frac{9}{10}$  the width of the tooth.  $M^2$  has not been reported previously for *O. nevadensis*. Twelve  $M^2$ s are included in the HM specimens. As in other species of *Oreolagus* the  $M^2$  is slightly reduced relative to the  $M^1$  and forms a transversely elongated, basined column (Fig. 3B). A distinct lingual fold is present in the HM specimens.

Five partial lower jaws were recovered from HM. CM 61200 contains the alveoli for  $P_3$ – $M_1$ . CM 61201 contains two teeth that appear to be  $M_1$ – $M_2$  based on the strong curvature of posterior tooth. Another jaw containing  $M_1$ – $M_2$  is broken anterior to  $M_1$  (CM 61202). CM 61203 and CM 61204 are the most complete jaws and show much of the diastema and the alveoli for all of the teeth (Fig. 3C and D). Both contain  $M_1$  and CM 61203 also contains  $M_2$ . None of the available jaws retain  $P_3$  or  $P_4$ . The lower jaws show slight variation in the position of the anterior mental foramen. The foramen is present below  $P_3$  in the Ancney specimens, but occurs below the anterior border of  $P_3$  or slightly anterior to  $P_3$  in the HM specimens. The position of the posterior mental foramen varies from below the middle of  $M_1$  to below the talonid of  $M_1$ .

$P_3$ s from HM are small and simple, somewhat compressed anteroposteriorly, and contain a single prominent cement-filled labial groove. No lingual or anterior fold or groove is present.

Fifty-four individual  $P_4$ s,  $M_1$ s, and  $M_2$ s were recovered. All have at least a slight anterior protrusion from the trigonid and are indistinguishable from one another.

The complete deciduous dentition is represented in the HM sample. The 46 deciduous teeth recovered included 12  $DP_{3s}$ , 4  $DP_{4s}$ , 7  $DP^2s$ , 11  $DP^3s$ , and 12  $DP^4s$  (Fig. 3E–I). Comparison of these teeth to those of other species of *Oreolagus* is difficult because the occlusal morphologies change significantly with wear.  $DP_{3s}$  from the HM population exhibit three transverse lophs that increase in width from anterior to posterior (Fig. 3E). As in *Oreolagus* from Jackson Hole, a single groove is bordered by two lophs on the anterior surface of tooth.  $DP_4$  is morphologically similar to that of  $P_4$ ; however, the deciduous teeth are strongly double rooted (Fig. 3F).  $DP_4$  has an anterior protrusion from the trigonid that is similar to that seen in  $P_4$ – $M_2$ .  $DP^{2-4}$  represented within the HM population vary significantly due to wear and are difficult to distinguish.

**Discussion.**—The Hepburn's Mesa specimens are referable to *Oreolagus nevadensis*. They are also similar to *O. wallacei* and *Oreolagus* of Jackson Hole in that the anterior loph of  $P^3$  is less than one-half the width of the posterior loph. In *O. nebrascensis* and *O. wilsoni*, the anterior loph of  $P^3$  is more than one-half the width of the posterior loph. The  $M^1$  of HM specimens do not contain a crescentic valley. This crescent valley is also absent in *O. wallacei*; however, the HM population is distinguishable from *O. wallacei* by position of the premolar foramen and a smaller  $P^3$  in the HM specimens. The premolar foramen appears between  $P^3$  and  $P^4$  in *O. wallacei* and between the anterior and posterior lophs of  $P^3$  in *O. nevadensis* from HM.

## PHYLOGENETIC ANALYSIS

### SELECTION OF OUTGROUPS

No previous cladistic studies have been conducted on *Oreolagus*, and consequently no outgroup has been suggested. We chose two taxa as outgroups. *Eurymylus laticeps* from the Paleocene of China was chosen mainly because it is one of the earliest known lagomorphs. We also selected an outgroup that likely had a more recent common ancestry with *Oreolagus*, the early Oligocene *Desmatolagus gobiensis*. Dawson (1965) suggested that *D. gobiensis* taxon may be on the line of ancestry to *Oreolagus* (Dawson, 1965).

### SELECTION OF TAXA

All five previously described species of *Oreolagus* were considered as possible terminal taxa. These are the most common ochotonids known from the early Miocene of western North America. Large samples of *O. nevadensis*, *O. wallacei*, and

*O. nebrascensis* were studied. Specimens of *O. wilsoni* were not available, so the character analysis for this taxon was completed using detailed published descriptions and illustrations (especially Dawson, 1965). The type and paratype of what Barnosky (1986) defined as *O. colteri* were examined.

Specimens were first assembled and then studied without regard to previous taxonomic assignment. Most of the taxa fell out nicely as operational taxonomic units (OTUs). During reanalysis of *O. colteri* it became evident that this species is invalid. The sample of isolated teeth of *Oreolagus* from Jackson Hole contains representatives of at least two different genera, likely *Oreolagus* and *Hesperolagomys*. Unfortunately none of the material that is attributable to *Oreolagus* from Jackson Hole can be placed within an existing or a new species with confidence. For this reason, *O. colteri* has been left out of the present analysis. Further work on the



Table 3.—Character matrix listing species and scored character states. Missing information is designated as a question mark. See text for descriptions and discussion of characters.

	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Eurymylus laticeps</i>	0	0	?	?	0	0	0	0	0	0	0	0	?
<i>Desmatolagus gobiensis</i>	1	0	1	0	3	0	1	0	0	0	0	0	?
<i>Oreolagus wilsoni</i>	1	2	1	0	1	1	1	0	0	1	1	1	1
<i>Oreolagus wallacei</i>	2	2	0	0	3	1	1	1	1	1	1	1	?
<i>Oreolagus nevadensis</i>	2	2	0	0	2	1	0	1	0	1	1	1	0
<i>Oreolagus nebrascensis</i>	1	1	1	0	1	2	1	1	0	1	1	1	1

Jackson Hole material is currently underway by B. P. Kraatz and Andrea Bair.

#### SELECTION OF CHARACTERS

Twenty-two morphological characters were initially identified. After further analysis nine of these characters were eliminated, either because the characters were found not to be discrete among the species or because variation was substantial within several of the species (e.g., position of the anterior and posterior mental foramina). This left thirteen morphologic characters to utilize, nine of which were phylogenetically informative with respect to the ingroup. As no previous study had conducted cladistic analysis of this group, many of the characters were gleaned from prior descriptions of *Oreolagus*. All of the characters were restricted to those of the upper and lower tooth rows or to the adjacent palate, maxilla, and dentary because only these elements are common in fossil material. Several characters that relate to variation in size have been discussed in previous descriptions of *Oreolagus* (Dawson, 1965; Barnosky, 1986); only one of these was used to establish that size was not improperly weighted. The character states for each taxon are listed in Table 3. Following is a detailed description of the morphologic characters used in this study.

(1) Anteroloph of  $P^3$ .—In most ochotonids the upper premolars and molars are bilophodont. The anterior loph of the  $P^3$  is often greatly shortened transversely relative to the posterior loph. Previous authors have used the degree to which the anterior loph is shortened relative to the posterior loph to distinguish among species. States included in this character are: (0) anterior loph of  $P^3$  at least equal in width to posterior loph; (1) anterior loph greater than or equal to one half the width of posterior loph,

but shorter than the posterior loph; or (2) anterior loph less than one half the width of posterior loph. Note that although the range of these states approaches one another in potential value, the character was gap-coded based on the discrete values seen among species.

(2) Point of origin of the lower incisor.—This character state was determined by which tooth the posterior end of the lower incisor was located underneath. The states for this character are as follows: (0) lower incisor originates below  $M_2$  or posterior to that position; (1) incisor originates below middle of  $M_1$  or  $M_1$  talonid; or (3) incisor originates below trigonid of  $M_1$  or anterior to that position.

(3) Crescentic valley of  $M^1$ .—Presence of a crescentic valley on  $M^1$  connecting the anterior and posterior lophs: (0) absent; or (1) present.

(4) Crescentic valley of  $P^4$ .—Presence of a crescentic valley on  $P^4$  connecting the anterior and posterior portions of the tooth: (0) absent; or (1) present.

(5) Position of premolar foramen.—The premolar foramen, if present, varies in position on the palate: (0) absent; (1) opposite the anterior loph of  $P^3$ ; (2) opposite the posterior loph or the middle of  $P^3$ ; or (3) opposite a point between  $P^3$  and  $P^4$ .

(6) Contact between the maxillary tuberosity and the zygoma.—The following character states were assigned according to whether the tuberosity contacts the zygoma at a line opposite the (0) anterior loph of the  $P^3$ , (1) in between  $P^3$  and  $P^4$  or (2) anterior loph of the  $M^1$ .

(7) Anterior-posterior length of  $P_4$ – $M_2$ .—Few lower jaws of *Oreolagus* are known. However, states for this character were gap-coded for the values: (0) less than 5.2 mm; or (1) greater than 5.2 mm.

(8)  $M^1$  hypostria.—Length in which the hypostria extends across the  $M1$  was coded as follows; (0)  $\frac{2}{5}$ – $\frac{3}{5}$  total width of the tooth; or (1)  $\frac{3}{4}$ – $\frac{4}{5}$  total width of tooth.

(9) Anteroposterior compression of  $P_4$  (AP/T).—Anteroposterior length divided by transverse width of  $P_4$ , coded as: (0) greater than 0.53; or (1) less than 0.53.

(10)  $M^3$ .—Presence of  $M^3$ , (0) present; or (1) absent.

(11)  $M^2$  basined.—Like  $P^4$  and  $M^1$ ,  $M^2$  has a hy-

postria in some taxa. In others the  $M^2$  is basined. The character has been coded as follows: (0) not basined; or (1) basined.

(12) Upper cheek teeth roots.—Based on whether the upper teeth were completely hypsodont and unrooted or rooted; (0) rooted; or (1) unrooted.

(13) Anterior portion of  $DP_3$ .—Coded as whether the anterior portion of the  $DP_3$  is characterized by: (0) a medial groove bordered by two lobes; or (1) a medial lobe bordered by two grooves.

## RESULTS AND DISCUSSION

Maximum parsimony produced two most parsimonious trees of length 18 steps (Fig. 4). As the bootstrap values suggest, strong support exists for the monophyly of *Oreolagus* (at least with respect to the outgroups chosen here). However, this should be considered tentative until analyses can be conducted that include additional taxa. In the present analysis, the *Oreolagus* clade is relatively stable and does not collapse until parsimony is relaxed by 4 steps. The position of *O. nebrascensis* and *O. wilsoni* is relatively unstable. In both of the most parsimonious trees, *O. nevadensis* and *O. wallacei* were united. The close relationship of these two species is also suggested by the high bootstrap value (90) for this clade. For comparative purposes UPGMA and Neighbor Joining trees were created that showed the same topology as the maximum parsimony trees. Figure 5 shows trees in which the geographic occurrences of taxa were inserted as an unordered character, traced, and optimized in both DELTRAN and ACCTRAN. This figure also shows a stratigraphic character traced onto the tree.

As suggested by the decay indices and bootstrap values in the maximum parsimony trees, it is clear that the topology within the *Oreolagus* clade is unstable—although the unification of *O. nevadensis* and *O. wallacei* is more stable than other portions of the tree. The stratigraphic data are generally congruent with the maximum parsimony trees. Figure 6 shows the temporal distribution of taxa mapped onto the strict consensus tree and indicates that the earlier branching taxa appear earlier in the fossil record than the later branching taxa.

The geographic distribution of *Oreolagus*, however, is less congruent with the maximum parsimony trees, except at the terminal branches. The clade of *O. nevadensis* and *O. wallacei* seems to fit a biogeographic hypothesis in which the clade was

first present in the eastern Rocky Mountains (*O. nevadensis*) and subsequently expanded southwestward and westward into Nevada and Oregon, respectively. This pattern gains support with the presence of *O. nevadensis* that we recognized in the Split Rock Formation of Wyoming, which is earlier than previously recognized for the species. Stepping down the cladogram, the data also are consistent with the hypothesis that *Oreolagus* from the early Hemingfordian of the western Great Plains (*O. wilsoni* and possibly Marsland species) provided populations that dispersed northwestward to eventually give rise to the late Hemingfordian Rocky Mountain taxa. More data from a network of sites that provide better geographic and stratigraphic coverage are desirable to test these ideas, which at present should be regarded only as working hypotheses rather than firm conclusions. Figure 7 shows the MP topology overlain on the geographic distribution of *Oreolagus*.

The origin of the entire *Oreolagus* clade is much less clear. This problem is due largely to the limited taxonomic sampling in this analysis. Tree A in Figure 5 shows the geographic distributions mapped onto one of the most parsimonious trees. Both DELTRAN and ACCTRAN settings mapped the same on this tree. The equivocal portion of the other most parsimonious tree (Fig. 5B) is traced as Asiatic until the *O. wilsoni* branch when the character is optimized using DELTRAN. Because *O. nebrascensis* is found in both Nebraska (based on a questionable description from Marsland, Nebraska) and Wyoming it is difficult to hypothesize about the geographic origin of this group because this taxon, along with *O. wilsoni*, is the earliest branching. It should be noted that one of the most parsimonious trees does not resolve whether an *O. wilsoni*–*O. nebrascensis* clade or an *O. wallacei*–*O. nevadensis* clade branches earlier. It seems generally apparent

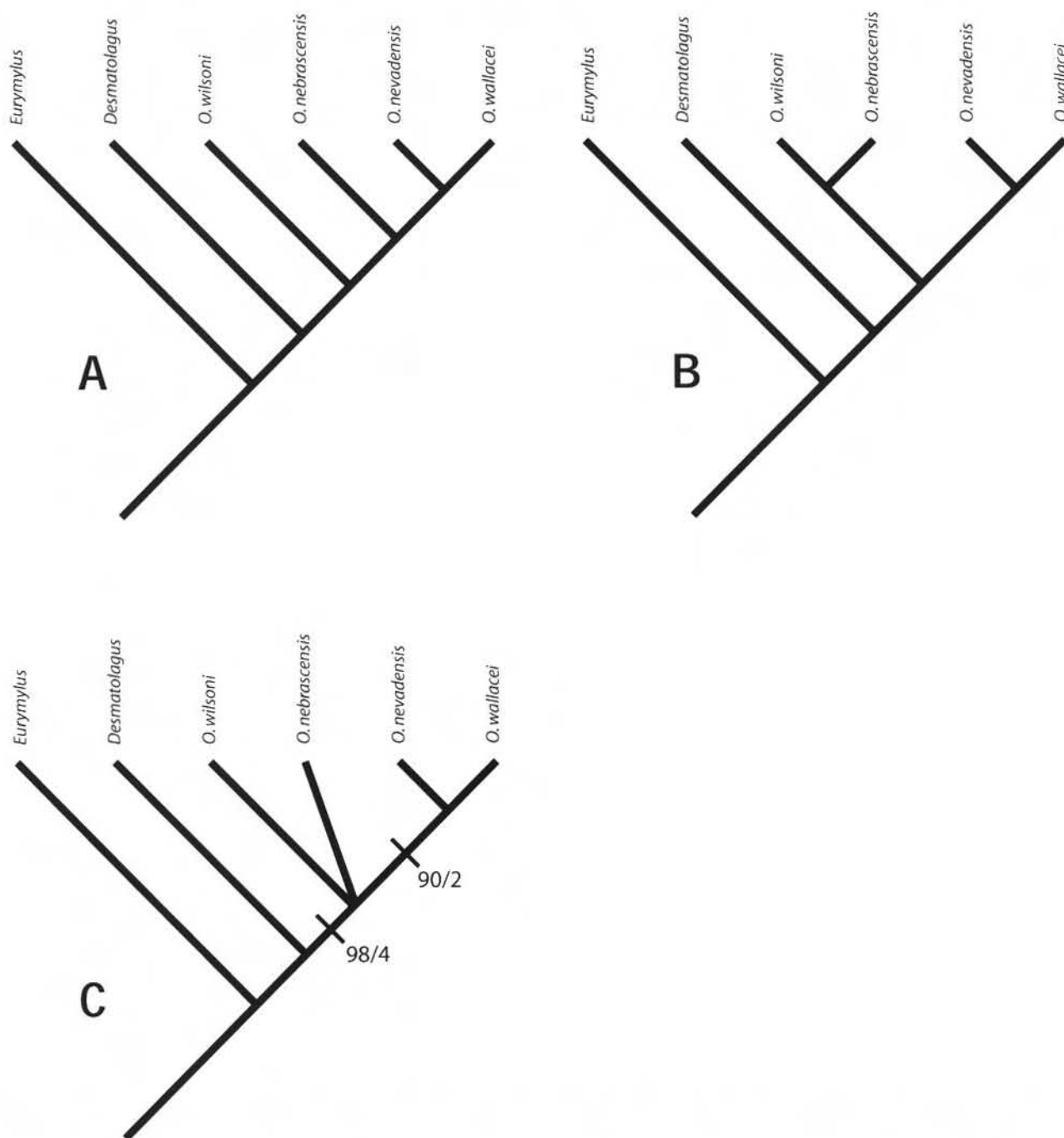
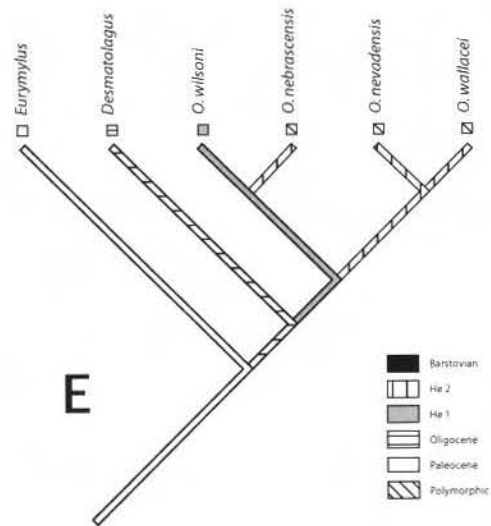
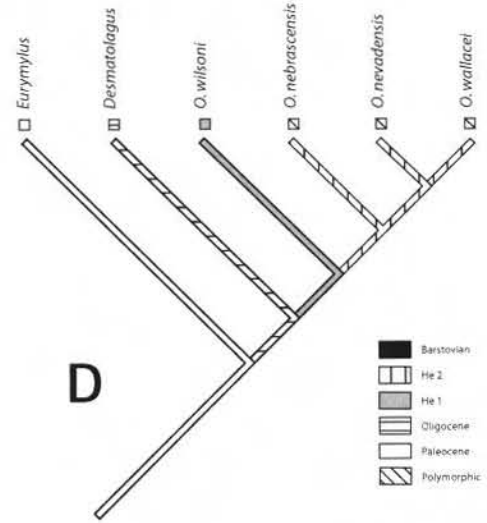
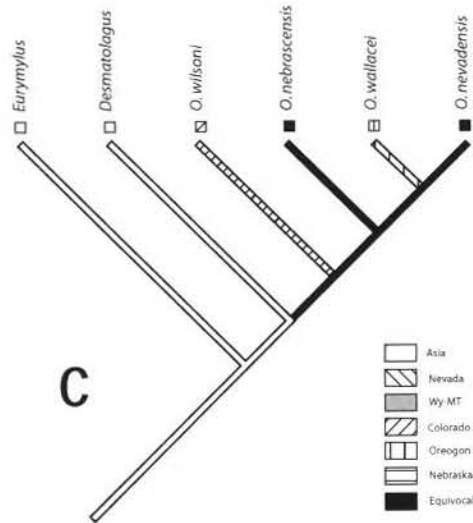
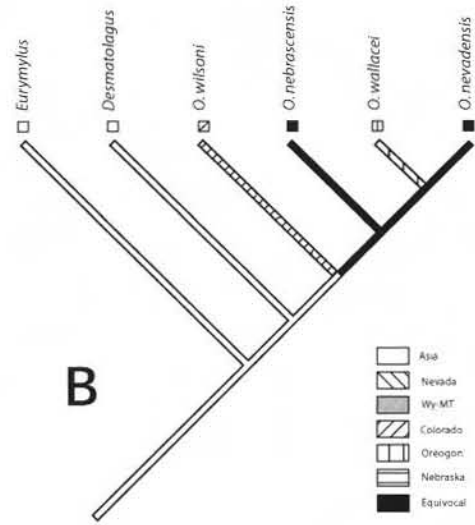
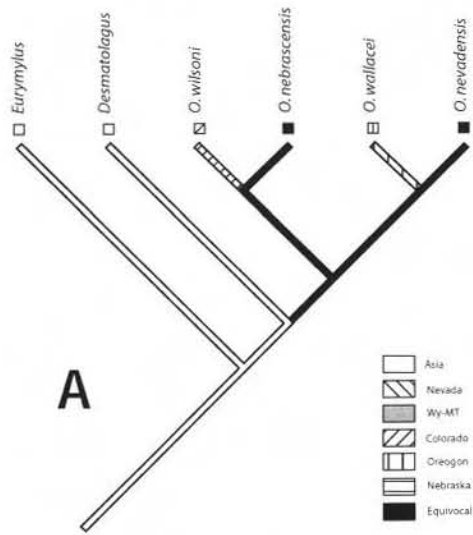


Fig. 4.—Trees A and B are maximum parsimony trees (length 18). Tree C is the semi-strict consensus of the most parsimonious trees and shows bootstrap values and decay indices.

that the early origin of the *Oreolagus* clade appeared within the Great Plains and subsequent populations dispersed into the Rocky Mountains and more western areas of North America.

Although the maximum parsimony trees (Fig. 4) constructed in this study were mostly congruent with the biostratigraphic data associated with fos-

sils of *Oreolagus*, it is clear that additional characters are needed to obtain a more robust tree—this is one of the most important facts revealed by this study. Several of our initial characters were discarded because they were determined not to be discrete and/or independent. However, some of these may prove useful when ontogenetic variation



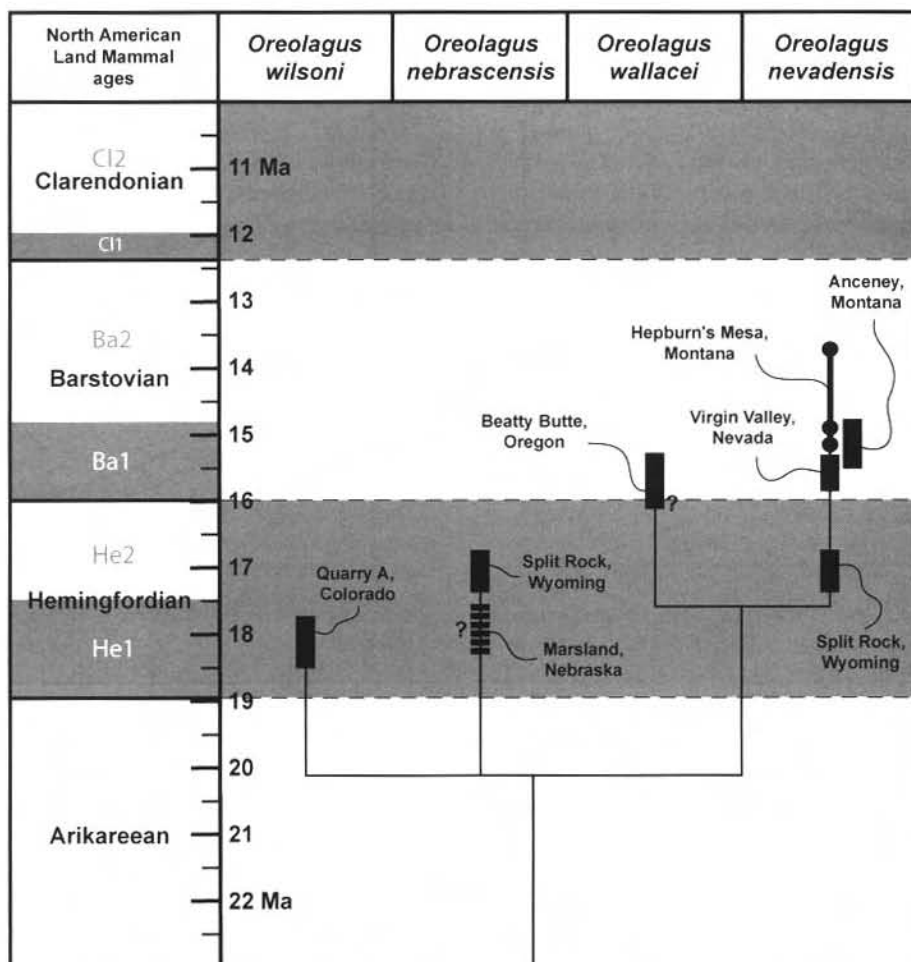


Fig. 6.—Maximum parsimony tree with stratigraphic occurrence mapped. Timescale and stratigraphic correlations of Tedford et al. (in press) were used. Note that black bars do not necessarily indicate geologic range; rather an estimate of locality age. For the Hepburn's Mesa area, large black circles indicate specific localities where *O. nevadensis* was recovered, while the bar represents this taxon's inferred range from these occurrences.

is clarified within the species. *Oreolagus* teeth are ever growing, which results in an occlusal morphology that changes throughout the life of the animal and makes it difficult to determine whether variations in occlusal morphology are due to phylogenetic or ontogenetic change. In a study of *Desmatolagus* from the Oligocene of Mongolia, Sych (1975) synonymized 15 named species into a single species because previous researchers had named different species based on different oc-

clusal wear stages of the same taxon. An example of such an ontogenetically variable character in *Oreolagus* may be the lingual fold on the anterior loph of  $P_3$ . Although this fold is invariably absent from *O. nevadensis*, it is usually, but not always, present in *O. wilsoni* and *O. nebrascensis* (Barnosky, 1986). Such characters may prove to be phylogenetically useful if workers code them based on whether the lingual fold is present in early stages of wear.

Fig. 5.—Tree A shows geographic occurrences traced as a character onto one of the most parsimonious trees and optimized using both ACCTRAN and DELTRAN (giving the same result) settings. Trees B and C show the same character traced onto the other most parsimonious tree using DELTRAN and ACCRAN settings, respectively. Trees D and E show a traced stratigraphic character mapped onto each of the most parsimonious trees.



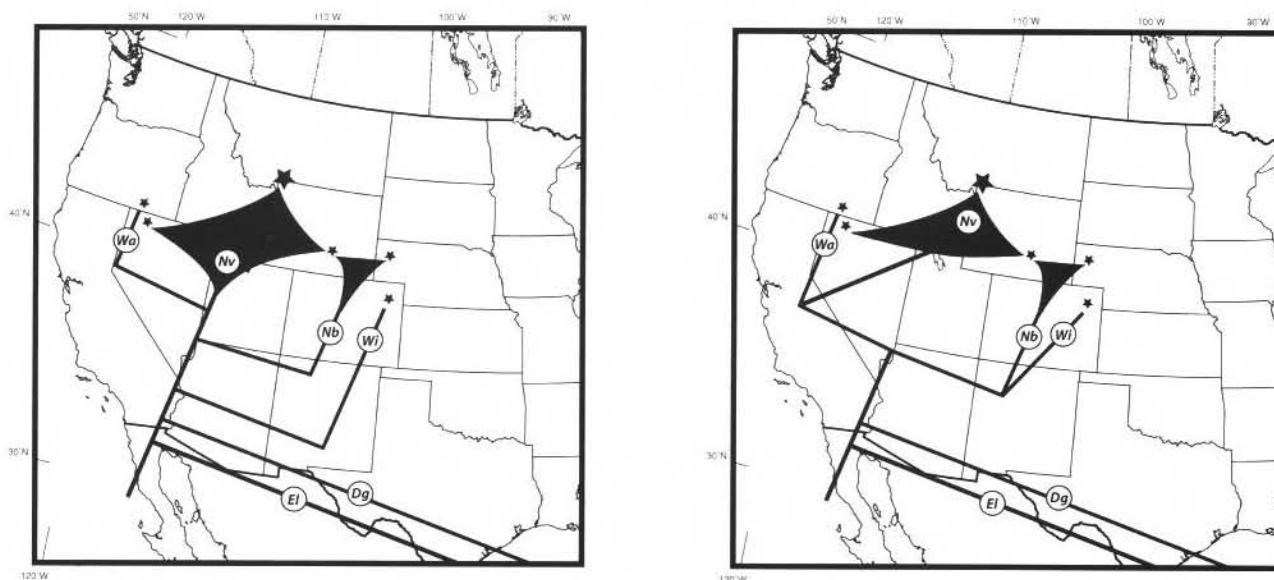


Fig. 7.—Maximum parsimony tree fitted to geographic occurrences of fossils. (Wa) notes *Oreolagus wallacei*, (Nv) *O. nevadensis*, (Nb) *O. nebrascensis*, (Wi) *O. wilsoni*, (Dg) *Desmatolagus gobiensis*, and (El) *Eurymylus laticeps*. Broad black areas on distal branches represent the occurrence of species at several different geographic areas and do not reflect a change in diversity or phylogenetic divergence.

## CONCLUSIONS

This study documents an exceptionally large sample of *Oreolagus nevadensis* from Hepburn's Mesa, and shows that cladistic analysis can be successfully applied to ochotonids. Our analysis indicates that *Oreolagus* is monophyletic with respect to the outgroups used here, but monophyly should be tested further by including more North American samples as they are discovered. Several other ochotonid genera appear in the late Miocene and would be important additions to future cladistic studies. Strong agreement exists between biostratigraphic distribution of *Oreolagus* species and the evolutionary relationships suggested by our analysis. Combined with the geographic distribution of the species, the data are consistent with a latest Hemingfordian or early Barstovian dispersal of *Oreolagus* from Wyoming and Montana westward to Nevada and Oregon, and possibly a slightly earlier (early to mid-Hemingfordian) dispersal of Great Plains *Oreolagus* into the Rocky Mountains regions. As evidenced by the presence of *Oreolagus* in Montana and Wyoming throughout the Barstovian, it is clear that some populations remained in the Rocky Mountain area. The data presented here do little, however, to clarify where the ultimate geographic origin of this group might have been. The network

of sites is still sparse; thus, additional fieldwork is needed to uncover new ochotonid-bearing deposits in key areas, which is essential to test the working hypotheses we provide here. Also, further studies of the wear stages of ochotonid occlusal morphologies must be conducted to better determine the validity of new characters.

Overall, the fossil record of *Oreolagus* has improved greatly since Dawson (1965) thoroughly reviewed the genus, especially with the increased sampling of *O. nevadensis* via new specimens from Anceney, Montana and the material described here from Hepburn's Mesa. This added material provides understanding of the range of variation within currently recognized species, and shows that *O. wallacei* and *O. nevadensis* are most closely related to one another. The analysis we present here suggests that *O. wilsoni* and *O. nebrascensis* exhibit more "primitive" characters than other species, but it is unclear whether they are more closely related to one another than to other species, or if they both simply represent early branches of the *Oreolagus* clade.

Also noteworthy is the recognition that (1) "*O. colteri*" from Jackson Hole is not a valid species, and instead represents a mixture of *Oreolagus* specimens which cannot be identified to species and

*Hesperolagomys* teeth; and (2) that both *O. nevadensis* and *O. nebrascensis* are present at Split Rock. Further work on *Oreolagus* from these two localities is underway and will be published elsewhere.

As Dawson (1965) recognized, modern North American pikas are restricted to high altitude mountainous habitats (Nowak, 1999), whereas Miocene species were widely distributed through the western half of the United States. The Hepburn's Mesa occurrence demonstrates that Barstovian pikas lived in environments analogous to the desert floor of to-

day's Great Basin, inasmuch as the fossils were recovered from nearshore saline lake deposits.

Our study represents only an initial attempt to conduct cladistic and biogeographic analysis on *Oreolagus*, but nevertheless generates useful hypotheses about the evolution and dispersal of the group within the western United States. Continued application of these techniques, as more specimens become available, holds the promise of more robust phylogenetic and biogeographic interpretations.

## ACKNOWLEDGMENTS

ADB extends a personal note of thanks to Malcolm for taking an interest when I was a wayward graduate student and setting an example of how to do science and live life. BPK thanks Malcolm for introducing me to vertebrate paleontology, showing me my first pikas, and taking this "waiter" under his wing while demonstrating how accessible knowledge can be. For these things and much help along the way—thank you.

Discussions with Andrea Bair greatly helped the manuscript, especially in regard to the validity of *Oreolagus* material previously described from Jackson Hole. Two anonymous reviewers

improved the manuscript through careful technical reviews. Material for this study was generously lent to the authors from the following institutions, Carnegie Museum of Natural History, Los Angeles County Museum of Natural History, The University of Wyoming, and the American Museum of Natural History. Angela Caldwell curated and helped to measure many of the specimens used in this study. NSF Grant EAR-99009353 supported this research. This is University of California Museum of Paleontology Contribution number 1783.

## LITERATURE CITED

- BARNOSKY, A. D. 1986. Arikarean, Hemingfordian, and Barstovian mammals from the Miocene Colter Formation, Jackson Hole, Teton County, Wyoming. *Bulletin of Carnegie Museum of Natural History*, 26:1–69.
- BARNOSKY, A. D., AND LABAR, W. J. 1989. Mid-Miocene (Barstovian) environmental and tectonic setting near Yellowstone Park, Wyoming and Montana. *Bulletin Geological Society of America*, 101:1448–1456.
- BURBANK, D., W., AND BARNOSKY, A. D. 1990. The magneto-chronology of Barstovian mammals in southwestern Montana and implications for the initiation of Neogene crustal extension in the northern Rocky Mountains. *Bulletin Geological Society of America*, 102:1093–1104.
- BURKE, J. J. 1936. *Ardynomys* and *Desmatolagus* in the North American Oligocene. *Annals of the Carnegie Museum*, 25: 135–154.
- DAWSON, M. R. 1965. *Oreolagus* and other Lagomorpha (Mammalia) from the Miocene of Colorado, Wyoming, and Oregon. *University of Colorado Studies: Series in Earth Sciences*, 1:1–36.
- . 1967. Lagomorph history and the stratigraphic record. *University of Kansas Department of Geology Special Publication*, 2:286–316.
- DICE, L. R. 1917. Systematic position of several American Tertiary lagomorphs. *University of California Publications, Bulletin of the Department of Geology*, 10:179–183.
- ERBAJEVA, M. A. 1994. Phylogeny and evolution of Ochotonidae with emphasis on Asian ochotonids., Pp. 1–13, in *Rodent and Lagomorph Families of Asian Origins and Diversification* (Tomida, Y., Li, C. K., and Setoguchi, eds.). National Science Museum Monographs No. 8.
- KELLOGG, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. *University of California Publication, Bulletin of the Department of Geology*, 5:421–437.
- KORTH, W. W. AND HAGEMAN, J. 1988. Lagomorphs (Mammalia) from the Oligocene (Orellan and Whitneyan) Brule Formation, Nebraska. *Transactions of the Nebraska Academy of Sciences*, 16:141–152.
- KRAATZ, B. P. 2002. New fossil lagomorph material from the Hsanda Gol Formation, Valley of the Lakes, Mongolia. *Journal of Vertebrate Paleontology*, 22:76A.
- MADDISON, W. P., AND MADDISON, D. R. 1992. *MacClade: Analysis of Phylogeny and Character Evolution*, version 3.0. Sunderland, MA: Sinaur Associates.
- MCGREW, P. O. 1941. A Miocene lagomorph. *Geological Series of the Field Museum of Natural History*, 8:37–41.
- McKENNA, M. C. 1955. A new species of mylagaulid from the Chalk Cliffs local fauna, Montana. *Journal of the Washington Academy of Sciences*, 45:107–110.
- MUNTHE, J. 1988. Miocene mammals from the Split Rock area, Granite Mountains Basin, Central Wyoming. *University of California Publications: Geological Sciences*, 126:1–135.
- NICHOLS, R. 1976. Early Miocene mammals from the Lemhi Valley of Idaho. *Tebiwa*, 18:9–33.
- NOWAK, R. M. 1999. *Walker's Mammals of the World*. Sixth edition. The Johns Hopkins University Press, Baltimore, Maryland.
- SKWARA, T. 1988. Mammals of the Topham Local Fauna: early Miocene (Hemingfordian), Cypress Hills Formation, Saskatchewan. *Saskatchewan Parks, Recreation and Culture Natural History Contributions*, 9:1–169.

- SUTTON, J. 1977. Mammals of the Anceney Local Fauna (Late Miocene) of Montana. Unpublished Ph.D. Dissert., Texas Tech University, Lubbock, Texas.
- SWOFFORD, D. L. 1999. *PAUP\* Phylogenetic Analysis Using Parsimony (and Other Methods), Version 4.0b*. Sunderland, MA, Sinauer.
- SYCH, L. 1975. Lagomorpha from the Oligocene of Mongolia. *Palaeontologia Polonica*, 33:183–200.
- TEDFORD, R. H., ALBRIGHT, L. B. III., BARNOSKY, A. D., FERUSQUIA, I. V., HUNT, R. J. JR., STORER, J., SWISHER, C. C. III., WEBB, S. D., AND WHISTLER, D. P. 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs), North America. Pp. 169–231 in *Late Cretaceous and Cenozoic Mammals of North America: Geochronology and Biostratigraphy* (M. O. Woodburne, ed.). Columbia University Press, New York.
- WALLACE, R. E. 1946. A Miocene mammalian fauna from Beatty Buttes, Oregon. *Carnegie Institution of Washington Contributions to Paleontology*, publication 551:113–134.
- WILSON, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. *The University of Kansas Paleontological Contributions*, 7:1–131.