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Pleistocene lagomorphs from Cathedral Cave, Nevada

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Faunal data from Cathedral Cave, Nevada, provide insight into biotic changes that occurred within the Great Basin prior to the latest Pleistocene. Taxonomic identifications of lagomorphs from Cathedral Cave were made using a morphological approach intended to minimize geographic and temporal assumptions. Although this approach to identification is conservative, the resultant data set is appropriate for inclusion in future analyses of regional biotic change. Lagomorphs recovered from the site include new regional records of two extinct taxa, *Aztlanolagus agilis* and *Brachylagus coloradoensis*. Other lagomorphs from Cathedral Cave include *Brachylagus idahoensis*, *Ochotona* sp., and *Sylvilagus* or *Lepus* sp. The presence of a posterorinternal reentrant fold on the p3 of some specimens of *Ochotona* sp. suggests that the range of variation present in the individual teeth of pikas needs to be described in further detail. In contrast to a previously established hypothesis of increasing enamel complexity in the p4 of *Aztlanolagus agilis*, evaluation of crenulation patterns of *Aztlanolagus agilis* from Cathedral Cave showed no distinct trends.

INTRODUCTION

A significant body of research on the fossil lagomorphs of the Great Basin is currently available in the literature, primarily as a result of efforts to understand mammalian biogeographic patterns in the region from the late Pleistocene to Recent. Several lagomorphs, including rabbits [*Sylvilagus nuttalli* (Nuttall's cottontail), *Lepus townsendii* (white-tailed jackrabbit)] and pikas [*Ochotona princeps* (North American pika)] were included in Brown's (1978) classic study on montane mammal biogeography in the Great Basin. As a result, subsequent research continued to emphasize the importance of Great Basin lagomorphs in biogeographic studies in the region (Mead et al. 1982, Thompson and Mead 1982, Mead 1987, Grayson 1993, Grayson and Livingston 1993, Hafner 1993, Mead and Spaulding 1995, Mead and Grady 1996, Grayson 2000a, 2000b, 2005, 2006). Here I present a systematic account of the lagomorphs from Cathedral Cave, Nevada, including the first Great Basin records for the extinct species *Aztlanolagus agilis* Russell and Harris and *Brachylagus coloradoensis* Ramos.

Cathedral Cave (CC) is located on a north-facing slope at the mouth of Smith Creek Canyon, Nevada, in the east-central Great Basin (Fig. 1). Preliminary fieldwork in 1989 tested the paleontological significance of the site (Bell 1990). Initial age estimates for portions of the excavated fauna were maximally between 15,000 ± 200 yr and 24,600 ± 2100 yr B.P. and were based on uranium-series analyses of a flowstone fragment attached to a small stalagmite and a whole bone fragment from different arbitrary excavation levels (Bell 1990). Subsequent analyses of the fauna and new research in the same region of the cave indicate an older age for the deposit (Bell 1995, Bell and Barnosky 2000, Bell et al. 2004b, Jass 2005, 2007). The most recent age data, based on uranium-series analyses of fine samples of *in situ* flowstone, place lower portions of the deposit in a maximum age range of 146.02 ± 2.584 ka to 151.2 ± 4.4 ka (Jass 2007). This age range places the fauna in a chronologically older context relative to other regional faunal assemblages. Specifically, faunal data from Cathedral Cave potentially provides insight into biotic changes that occurred within the Great Basin prior to the latest Pleistocene.

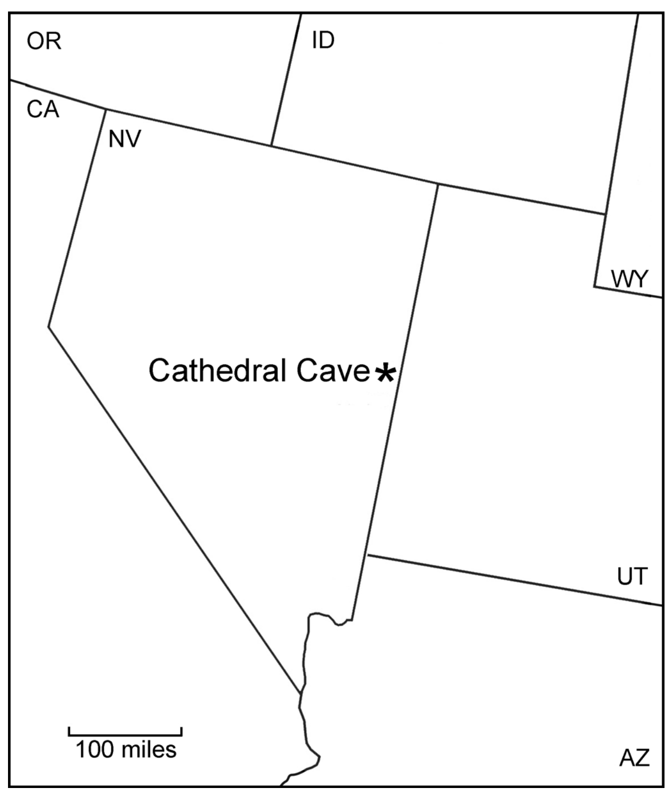

Figure 1. The geographic location of Cathedral Cave, NV.

MATERIALS AND METHODS

The lagomorphs described here were collected during a new excavation conducted at Cathedral Cave in 2003. The excavation consisted of a 1.5 m x 2 m area of undisturbed sediments that were removed to a maximum depth of 110 cm below an arbitrary datum, or roughly 76 cm below the surface of the deposit. The excavation was stopped where large blocks of roof spall were interpreted as being situated directly on the bedrock floor of the cave. Excavation levels were hand dug using trowels and brushes in arbitrary 5-cm intervals except where natural sedimentary levels could be removed as distinct units. Unique horizontal (e.g., 1N 2E) and vertical (e.g., 45–50 cm below datum) provenience data were recorded for all excavated sediments and fossils.

Screen-washing of sediments was conducted at the Vertebrate Paleontology Laboratory of the Texas Natural Science Center and the Laboratory of Quaternary Paleontology at Northern Arizona University. All sediments were washed through nested pairs of screens (3.175 mm- and 0.7 mm-mesh). Washed sediments were air dried prior to being sorted for fossils. Additional details about the excavation and screen-washing methods employed in this study are presented elsewhere (Jass 2007).

The composite assemblage of 183 lagomorph fossils presented here represents 50 stratigraphic levels within the excavation. Specimens are housed at the Vertebrate Paleontology Laboratory of the Texas Memorial Museum (TMM) under locality number 43693, each with a unique specimen number (e.g., TMM 43693-1).

The majority of lagomorph specimens from Cathedral Cave consist of isolated teeth. Patterns of evolution and taxonomic identification in lagomorphs are usually based at least partially on changes in the enamel pattern of the p3 (e.g., White 1984, 1987, 1991a, 1991b). This study focuses on isolated p3s, dentaries that retain the p3, and a few edentulous dentaries that retain characteristics that allow for reliable taxonomic identification.

The lagomorph p3 is characterized by patterns of enamel-banded dentine that range from simple to complex, and cementum-filled re-entrant folds. The enamel folds in many leporid teeth appear wrinkled or crenulated and the degree of crenulation is sometimes used for identification, particularly for extinct taxa (Ramos 1999a). A binocular microscope with an ocular micrometer was used to examine the specimens and determine maximum occlusal length and width measurements.

SYSTEMATIC PALEONTOLOGY

The following summary of the lagomorphs from Cathedral Cave, Nevada, is based on results of the 2003 excavation. Taxonomy and classification above the species level follows McKenna and Bell (1997).

ORDER: LAGOMORPHA Brandt, 1855
FAMILY: OCHOTONIDAE Thomas, 1897
GENUS: *Ochotona* Link, 1795
Ochotona sp.

Referred Specimens—See Appendix 1.

Description—The p3s of *Ochotona* sp. from Cathedral Cave exhibit some variation in size (Fig. 2) and are characterized by the presence of at least three enamel reentrant folds (anterointernal, anteroexternal, and posteroexternal; Figs. 3a,b). The folds are simple and lack the crenulated enamel patterns seen in many leporid species. The degree to which enamel reentrant folds are developed varies in some specimens and depends on how far the enamel penetrates from the margin towards the midline of the tooth. Some specimens (e.g., TMM 43693-1857) display weak development (i.e., little or indistinct enamel penetration towards the midline) of the anterointernal reentrant, as in the '*Ochotona* sp. near Trout Cave form' from Porcupine Cave, Colorado (Mead et al. 2004). Several specimens retain at least some development of a fourth, posterointernal reentrant fold. A strongly developed posterointernal reentrant fold, in which there is distinct penetration of enamel towards the midline, is apparent in both occlusal and ventral views of specimen TMM 43693-1856 (Fig. 3c).

Ochotona dentaries lacking the p3 were identified on the basis of diminutive size and general shape similarity to those of modern pikas. Whenever possible, the shape of the m3 or m3 alveolus was evaluated because it is triangular in leporids, but anteroposteriorly short in ochotonids (Heaton 1985). Dentaries of *Ochotona* sp. from Cathedral Cave that preserve the m3 or m3 alveolus retain a flattened posterior margin that gives the tooth and alveolus a more rectangular appearance than those of leporids.

Discussion—Two species of pika, *O. collaris* and *O. princeps* inhabit North America today. *Ochotona collaris* is geographically restricted to portions of Alaska and northwestern Canada, while *O. princeps* inhabits portions of southwestern Canada and the western United States (Wilson and Ruff

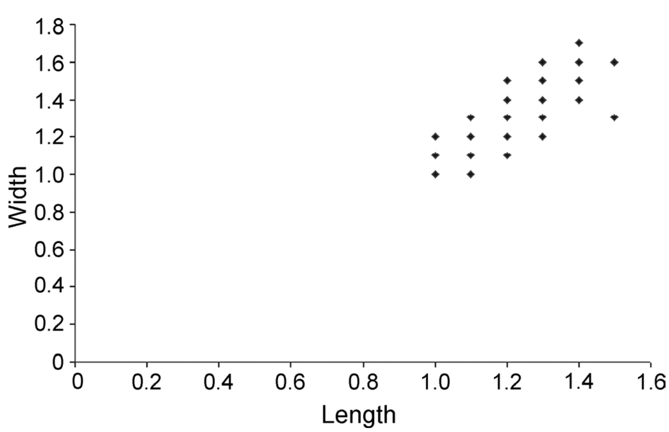

Figure 2. Scatter plot of length versus width in specimens of *Ochotona* sp. (n=74) from Cathedral Cave, NV. Measurements were taken to nearest 0.1 mm using an ocular micrometer. See Appendix 1 for individual specimen data.

1999). Fossil specimens, mainly attributed to *O. princeps*, are known from eastern and western portions of the United States and Canada (Mead 1987). Two extinct species of pika are also known from North America. *Ochotona spanglei* occurs in the late Miocene-early Pliocene of Oregon (Shotwell 1956), and the larger *O. whartoni* was found in the Pleistocene of Alaska and Canada (Guthrie and Matthews 1971, Mead and Grady 1996). Other morphological variants are recognized in the fossil record but their taxonomic status is uncertain (Mead et al. 2004).

The average length of the p3 in Cathedral Cave specimens is 1.23 mm (n = 75; SD = 0.11; range = 1.0–1.5) and the average width is 1.32 mm (n = 74; SD = 0.16; range = 1.0–1.7). Although there are size differences among individual specimens, the scatterplot of measurements for the p3 (i.e., length versus width; Fig. 2) is not clearly bi- or polymodal. This might suggest the presence of a single species exhibiting intraspecific variation at Cathedral Cave. However, Mead and Grady (1996) presented scatterplots (length versus width) of the m1 and P3 in extant and fossil pikas that show species "clusters". If this result can be extrapolated to the p3s from Cathedral Cave, several species might be represented by the size range found here.

The amount of variation occurring in quantitative and qualitative morphologic characters of the p3 in fossil and extant pikas needs further study. There is some indication that morphological variants occur in the fossil record (e.g., Mead and Grady 1996, Mead et al. 2004), but the taxonomic level at which that variation is expressed remains uncertain. It is possible that most, if not all, of the specimens from Cathedral Cave are *Ochotona princeps*; however, the presence of a few unique morphological variants suggests that other species might be represented in the fauna. Because our understanding of morphologic variation in the individual teeth of *Ochotona* is rudimentary, assigning the specimens from Cathedral Cave to *O. princeps* would, by default, be partially based on the assumption that fossil *Ochotona* occurring within or near the modern range of *O. princeps* are that species. As noted elsewhere, assumptions about geography during the identification process may lead to circularity in subsequent hypotheses concerning regional faunal dynamics (e.g., biogeography; Bell et al. 2004a). Therefore, I restricted my identifications to *Ochotona* sp. but provide an illustration of a specimen (TMM 43693-1856) with a morphotype that might be outside of the natural range of variation in the p3 of *O. princeps* (Fig. 3c).

TMM 43693-1856 has a well-developed postero-internal fold that is unique among North American pikas examined in this study. Erbajeva's (1994) review of the phylogeny and evolution of ochotonids includes an illustration of a p3 of *Ochotona antiqua* that exhibits four reentrant folds as in TMM 43693-1856. *Ochotona antiqua* is known only from late Miocene-early Pliocene deposits in the Old World (Erbajeva 1994). I am hesitant to assign TMM 43693-1856 to any particular species prior to a thorough review of variation in the p3 of New and Old World species of *Ochotona*. The occurrence of this p3 morphology in Cathedral Cave specimens could represent a new species or a new record of an Old World species, or it may fall within the natural, but as yet undocumented, range of variation exhibited by extant North American pikas.

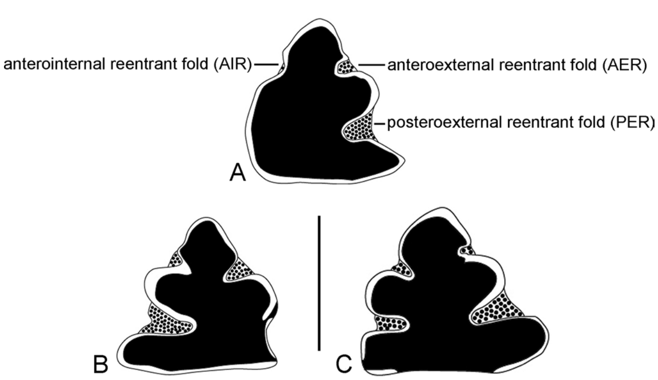

Figure 3. The p3 of *Ochotona* from Cathedral Cave. **A**. Occlusal pattern and terminology discussed in text; **B**. Left p3 (TMM 43693-1814) of *Ochotona* sp. from Cathedral Cave; **C**. Right p3 of *Ochotona* sp. exhibiting a fourth reentrant fold (TMM 43693-1856). Scale bar equals 1 mm.

FAMILY: LEPORIDAE Fischer de Waldheim, 1817

GENUS: *Aztlanolagus* Russell and Harris, 1986

Type species: *Aztlanolagus agilis* Russell and Harris, 1986

Aztlanolagus agilis Russell and Harris, 1986

Referred Specimens—See Appendix 1.

Description—The p3s of *Aztlanolagus agilis* are characterized by the presence of five reentrant folds (Fig. 4a; Russell and Harris 1986). No extant North American leporid retains this pattern, and among fossil taxa only *Nekrolagus* is similar (Russell and Harris 1986). All specimens identified as *A. agilis* exhibit a strongly developed anterointernal fold and a well-developed posterointernal fold (Fig. 4b) or lake. The presence of a strongly developed anterointernal fold on the p3 distinguishes *A. agilis* from *Nekrolagus*, in which the fold is less developed or absent (Russell and Harris 1986). The degree of crenulation within individual folds varies among individual specimens from Cathedral Cave. Table 1 summarizes the number of major crenulations in the anteroexternal reentrant, along the posterior wall of the posterointernal reentrant, and along the posterior wall of the posteroexternal reentrant. For specimens of *A. agilis* from Cathedral Cave, the p3 average length is 2.40 mm (n = 25; SD = 0.23; range = 1.7–2.8) and average width is 2.29 mm (n = 25; SD = 0.34; range = 1.2–2.8). These are slightly larger than average measurements recorded by Winkler and Tomida (1988) for other localities in the southwestern United States.

Discussion—*Aztlanolagus* is known from Blancan to late Rancholabrean deposits in the western United States and Mexico. Records other than Cathedral Cave come from

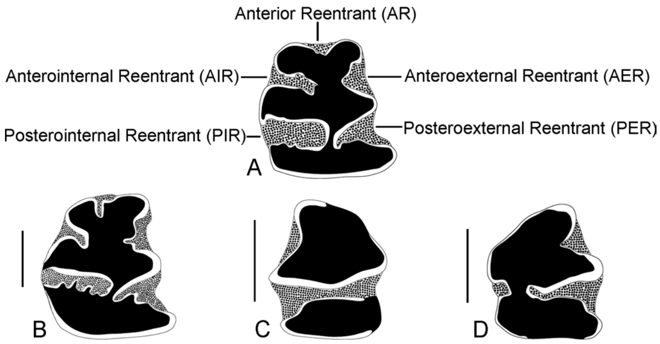

Figure 4. Leporid teeth from Cathedral Cave. **A**. Enamel pattern and terminology for the p3; **B**. Right p3 of *Aztlanolagus agilis* (TMM 43693-1750) from Cathedral Cave; **C**. Left p3 of *Brachylagus idahoensis* (TMM 43693-1777) from Cathedral Cave; **D**. Right p3 of *Brachylagus coloradoensis* (TMM 43693-1774) from Cathedral Cave. Scale bars equal 1 mm.

localities within Porcupine Cave, CO (Barnosky and Hopkins 2004, Baxter 2004), and localities in northern Mexico, New Mexico, Arizona, and Texas (Russell and Harris 1986, Winkler and Tomida 1988). Although Winkler and Tomida (1988) tentatively referred all specimens that they examined to *A. agilis,* Baxter (2004) reported Porcupine Cave specimens as *Aztlanolagus* spp. because of variation in tooth size and crenulation patterns.

Aztlanolagus might be synonymous with *Pliopentalagus*, an extinct leporid known mostly from China that has five reentrant folds on the p3 (Tomida and Jin 2002, 2004). However, until the argument for synonymy is formalized, *Aztlanolagus* should be retained. Taxonomic issues notwithstanding, the disappearance of *A. agilis* is one of the few known late Quaternary small mammal extinctions in continental North America.

The records of *Aztlanolagus agilis* from Cathedral Cave presented here represent its first known occurrence in the Great Basin. The only other specimen known from the Great Basin is unnumbered in bulk material from Smith Creek Cave, Nevada, housed at the Nevada State Museum (Jass *personal observation*).

GENUS: *Brachylagus* Miller, 1900

Type species: *Lepus idahoensis* Merriam, 1891

Brachylagus idahoensis (Merriam, 1891)

Referred Specimens—See Appendix 1.

Description—Three specimens of *Brachylagus idahoensis* were identified from Cathedral Cave (Fig. 4c). Two of the specimens retain simple anteroexternal reentrants and the trigonid and talonid are either completely (TMM 43693-1777), or nearly (TMM 43693-1776), separated by cementum. The extension of the anteroexternal folds across the tooth is characteristic of *B. idahoensis* (Ramos 1999b). Length and width of the p3s were: (TMM 43693-1777) - l = 1.8 mm, w = 1.6 mm; (43693-1776) - l = 1.8 mm, w = 1.8 mm.

A third p3 specimen (TMM 43693-1775) with a damaged occlusal surface that was also identified as *Brachylagus idahoensis* is unique. In ventral view, it has a posteroexternal reentrant that extends across two-thirds of the tooth, but exhibits an enamel lake in the position of a posterointernal reentrant. Because the joining of the posteroexternal reentrant with the enamel lake would result in a morphology more similar to *B. idahoensis* than *B. coloradoensis* (see below), the specimen is identified as the former. Further review of variation in the p3 enamel patterns of *B. idahoensis* is needed.

Discussion— *Brachylagus* is distinguished from most extant and fossil North American leporids by the lack of an anterior reentrant on the p3 (Kurtén and Anderson 1980, Ramos 1999a). The extinct genus *Hypolagus* is similar in some qualitative aspects to an extinct form of *Brachylagus* (*B. coloradoensis*) but is larger in size (Ramos 1999b). Until recently, the genus *Brachylagus* was considered monotypic, with *B. idahoensis* as the only recognized species (Ramos 1999b).

Fossils of *Brachylagus idahoensis* are known only from the western United States and most fall within or near the present distribution of the species (Kurtén and Anderson 1980). Exceptions are the records from Isleta Cave No. 2 and Sheep Camp Shelter in New Mexico (Harris 1993). The occurrence of *B. idahoensis* at Cathedral Cave was previously noted by Ramos (1999b).

Brachylagus coloradoensis Ramos 1999

Referred Specimens—See Appendix 1.

Description—The two specimens identified as *Brachylagus coloradoensis* are similar to *B. idahoensis*, but both have a weakly developed posterointernal reentrant and a posteroexternal reentrant that extends only between one-third and two-thirds across the tooth (Fig. 4d). As such, these specimens are consistent with those identified as *B. coloradoensis* from Porcupine Cave (Ramos, 1999b).

Discussion—Prior to this report, *B. coloradoensis* was known only from several localities of Irvingtonian or unknown age within Porcupine Cave (Ramos 1999b, Barnosky 2004, Barnosky and Hopkins 2004, Baxter, 2004; age assignments from Barnosky et al. 2004). Its occurrence in Cathedral Cave extends both its geographic and chronologic ranges.

GENUS: *Sylvilagus* Gray 1867 or *Lepus* Linnaeus 1758

Sylvilagus or *Lepus* sp.

Referred Specimens—See Appendix 1.

Description—Specimens identified as *Sylvilagus* or *Lepus* sp. are characterized by the presence of three (anterior, anteroexternal, and posteroexternal) reentrant folds on the p3. The presence of the anterior fold distinguishes these specimens from *Ochotona*, which also typically retains three reentrant folds on the p3. In most specimens the anterior and anteroexternal reentrants are simple with little crenulation, while the posteroexternal reentrant fold may or may not exhibit crenulations. Length and width of the p3s are listed in Appendix 1 and were graphed on a scatter plot used to evaluate if distinct size groupings exist (Fig. 5).

Discussion—*Sylvilagus audubonii*, *S. nuttalli*, *Lepus californicus*, and *L. townsendii* all have modern ranges that include the region surrounding Cathedral Cave. One, all, or none of these taxa may be represented in Cathedral Cave. Previous authors noted that there is considerable difficulty in the identification of *Lepus* versus *Sylvilagus* (e.g., Kurtén and Anderson 1980) and that size overlap occurs (Dalquest and Schultz 1992, Ramos 1999a). Because it would be necessary to invoke either geographic or evolutionary assumptions (i.e., constant size in the past relative to the modern) to separate these genera, no attempt was made to differentiate *Lepus* and *Sylvilagus* from Cathedral Cave (see discussion below).

DISCUSSION

Bell's (1990) report on lagomorphs from Cathedral Cave included *Ochotona princeps*, *Brachylagus idahoensis* (as *Sylvilagus idahoensis*), *Sylvilagus* sp., and *Lepus* sp. The 2003 excavation resulted in the recognition of a more diverse lagomorph assemblage that includes new records of *B. coloradoensis* and *Aztlanolagus agilis*. The record of *A. agilis* is particularly notable because it consists of a reasonable sample size (n = 25) that might be used to further evaluate the variation in crenulation patterns of this taxon. Older specimens of *A. agilis* appear to have less-complex crenulation patterns than do more recent specimens (Winkler and Tomida 1988). My attempt to quantitatively evaluate crenulation patterns of the p3 in *A. agilis* from Cathedral Cave by counting the number and distinctness of major crenulations failed to show a pattern of increasing complexity from lower to upper excavated levels (Table 1). This does not negate the possibility of such a pattern over a broader time scale, but does provide a measure by which specimens from other localities might be compared. Nevertheless, the occurrence of *A. agilis* at Cathedral Cave provides an important record for understanding Pleistocene lagomorph diversity in the Great Basin and western North America.

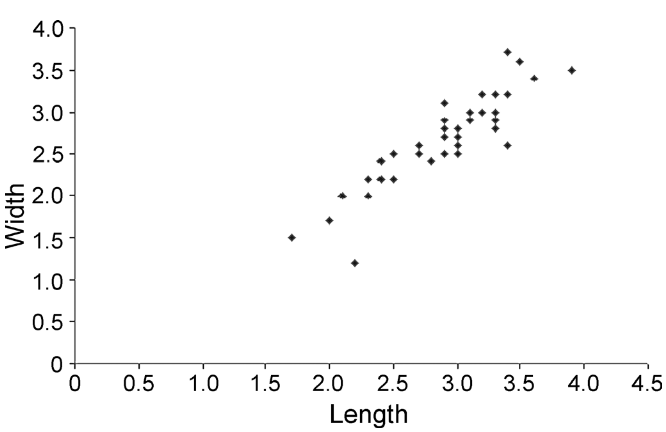

Figure 5. Scatter plot of length versus width in specimens identified as *Sylvilagus* or *Lepus* sp. (n = 42) from Cathedral Cave, NV. Measurements were taken to nearest 0.1 mm using an ocular micrometer. See Appendix 1 for individual specimen data.

Fossil lagomorphs have had a prominent role in paleontological research in the Great Basin since the 1970s when Brown (1971, 1978) published his classic research on montane mammal biogeography. Those studies helped initiate a number of research projects on Great Basin lagomorphs (e.g., Grayson 1977, Mead 1987, Hafner 1993, Mead and Spaulding 1995, Osterhaudt 1999), and continue to influence research on lagomorphs of the region (e.g., Grayson 2005). Great Basin lagomorph fossils are ideal for such studies because they are common constituents of many Pleistocene and Holocene vertebrate assemblages (e.g., Heaton 1985).

The taxonomic approach taken here is more conservative than those of prior studies of Great Basin lagomorphs so that taxa are identified based exclusively upon morphological criteria and, in turn, excluded from regional-scale biogeographic and evolutionary assumptions. Minimal use of geography as either an implicit or explicit character in the fossil identification process results in identifications that are more appropriate for broad biogeographic analyses (e.g., Bell et al. 2004a). The use of modern geographic range data to restrict possible identifications only to those species currently inhabiting or in close proximity to the Great Basin (e.g., *Ochotona princeps*, *Sylvilagus audubonii*, *S. nuttalli*, *Lepus californicus*, and *L. townsendii*) would foster circularity in biogeographic interpretations of the region. At present, there is not enough primary data on morphologic variation in the p3 to substantiate species-level identifications of pika (*Ochotona* sp.) and some leporids (*Sylvilagus* or *Lepus* sp.). Similarly, the invocation of size alone as a criterion for distinguishing species or genera (e.g., *Lepus* vs. *Sylvilagus*) assumes a pattern of stasis in body size relative to modern populations, where such an assumption may not be appropriate. For example, it is possible that certain species of *Sylvilagus* were larger 130,000 years ago and more comparable in size to extant *Lepus*. In the absence of other independent characters, the size of a particular taxon might simply reflect ecophenotypic variation. The identification of other lagomorph faunas and re-evaluation of previously described faunas under comparable, conservative identification criteria are needed to better understand how this mode of identification influences our understanding of broad biotic change in the Great Basin.

In summary, Cathedral Cave preserves the first Great Basin records of the extinct species *Aztlanolagus agilis* and *Brachylagus coloradoensis*. By virtue of their presence at Cathedral Cave, the records of these taxa in the Great Basin are limited to time periods preceding the last glacial episode, possibly as old as 146.02 ± 2.584 ka to 151.2 ± 4.4 ka. Other records from Cathedral Cave include *Ochotona* sp., *B. idahoensis*, and *Sylvilagus* or *Lepus* sp. Additional work focusing on variation in the p3 of lagomorphs is needed to determine if there are morphologic characters that support species-level identifications for taxa conservatively identified here as *Ochotona* sp. and *Sylvilagus* or *Lepus* sp. Future work

Table 1. Variation in the number of major crenulations on the anteroexternal reentrant (AER), posterior wall of the posterointernal reentrant (PW-PIR), and posterior wall of the posteroexternal reentrant (PW-PER) in the p3 of *Aztlanolagus agilis* from Cathedral Cave, Nevada, by excavated level. (?) = minimum number of major crenulations. Dash (-) = data could not be evaluated. Specimen No. = unique specimen number for locality TMM 43693 (i.e., TMM 43693-1748 is the full number for the first specimen listed below).

Specimen No.	Excavated Level	AER	PW-PIR	PW-PER
1748	2N 3E 40-45 cmbd	0	1	0
1749	2N 3E 40-45 cmbd	0	2(?)	0
1750	1N 3E Cemented Level	2	4	2
1751	1N 3E 43.5-55 cmbd; below Cemented Level	–	2	2
1752	1N 3E 43.5-55 cmbd; below Cemented Level	0	4	3
1753	2N 2-3E 45-60 cmbd	0	2	2
1754	2N 2-3E 45-60 cmbd	–	–	–
1755	2N 2-3E 45-60 cmbd	0	2	2
1756	1N 2E 55-60 cmbd	–	2(?)	3
1757	1N 2E 60-65 cmbd	1	2	0
1758	2N 2-3E 60-65 cmbd	2	3	2
1759	2N 2-3E 60-65 cmbd	–	3	2
1760	1N 2E 65-70 cmbd	0	0	1
1761	1N 2E 65-70 cmbd	0	1	0
1486	1N 3E 65-70 cmbd	2	4	3
1762	2N 2-3E 65-70 cmbd	2	2	1
1763	2N 2-3E 65-70 cmbd	0	4	3
1764	2N 2-3E 70-75 cmbd	0	2	0
1765	2N 2-3E 70-75 cmbd	0	2	0
1766	1N 2-3E 75-80 cmbd	0	1	1
1767	2N 2-3E 75-80 cmbd	0	2	2
1768	2N 2-3E 80-85 cmbd	2	4	–
1769	1N 2-3E 85-90 cmbd	1	0	1
1770	1-2N 2-3E 87-102 cmbd; below pedasteled rocks	1	1	1
1771	2N 2-3E 90-95 cmbd	1	2	1
1772	2N 2-3E 90-95 cmbd	1	0	1

will examine how data on lagomorphs from Cathedral Cave relate to broad patterns of biotic change in the region (e.g., montane island biogeography).

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APPENDIX 1

Identified specimens of lagomorphs collected during the 2003 excavation at Cathedral Cave, Nevada, by taxon and provenience. Measurements of length (*l*) and width (*w*) of the third premolar (p3) are presented in millimeters to the nearest 0.1 mm. The column headed by the number symbol (#) contains unique specimen numbers associated with Cathedral Cave locality number TMM 43693 (i.e., TMM 43693-1748 is the full number for the first specimen listed below).

#	TAXON	SIDE	ELEMENT	*l*	*w*	PROVENIENCE
1748	*Aztlanolagus agilis*	L	p3	2.1	2.1	2N 3E 40-45 cmbd
1749	*Aztlanolagus agilis*	R	p3	2.4	2.7	2N 3E 40-45 cmbd
1750	*Aztlanolagus agilis*	R	p3	2.6	2.5	1N 3E Cemented Level
1751	*Aztlanolagus agilis*	L	p3	2.6	2.3	1N 3E 43.5-55 cmbd; below Cemented Level
1752	*Aztlanolagus agilis*	L	p3	2.6	2.4	1N 3E 43.5-55 cmbd; below Cemented Level
1753	*Aztlanolagus agilis*	L	p3	2.5	2.1	2N 2-3E 45-60 cmbd
1754	*Aztlanolagus agilis*	R	p3	—	—	2N 2-3E 45-60 cmbd
1755	*Aztlanolagus agilis*	R	p3	2.3	2.3	2N 2-3E 45-60 cmbd
1756	*Aztlanolagus agilis*	L	p3	2.1	1.2	1N 2E 55-60 cmbd
1757	*Aztlanolagus agilis*	L	p3	2.6	2.4	1N 2E 60-65 cmbd
1758	*Aztlanolagus agilis*	L	p3	2.6	2.5	2N 2-3E 60-65 cmbd
1759	*Aztlanolagus agilis*	R	p3	2.8	2.6	2N 2-3E 60-65 cmbd
1760	*Aztlanolagus agilis*	L	p3	2.3	2.1	1N 2E 65-70 cmbd
1761	*Aztlanolagus agilis*	L	p3	2.2	2.1	1N 2E 65-70 cmbd
1486	*Aztlanolagus agilis*	R	p3	2.5	2.8	1N 3E 65-70 cmbd
1762	*Aztlanolagus agilis*	R	p3	2.2	2.0	2N 2-3E 65-70 cmbd
1763	*Aztlanolagus agilis*	L	p3	2.5	2.3	2N 2-3E 65-70 cmbd
1764	*Aztlanolagus agilis*	L	p3	2.6	2.5	2N 2-3E 70-75 cmbd
1765	*Aztlanolagus agilis*	L	p3	2.4	2.3	2N 2-3E 70-75 cmbd
1766	*Aztlanolagus agilis*	R	p3	1.7	1.7	1N 2-3E 75-80 cmbd
1767	*Aztlanolagus agilis*	R	p3	2.5	2.5	2N 2-3E 75-80 cmbd
1768	*Aztlanolagus agilis*	L	p3	2.5	2.1	2N 2-3E 80-85 cmbd
1769	*Aztlanolagus agilis*	L	p3	2.2	2.1	1N 2-3E 85-90 cmbd
1770	*Aztlanolagus agilis*	R	p3	2.5	2.5	1-2N 2-3E 87-102 cmbd; below pedestaled rocks

#	TAXON	SIDE	ELEMENT	*l*	*w*	PROVENIENCE
1771	*Aztlanolagus agilis*	R	p3	2.5	2.6	2N 2-3E 90-95 cmbd
1772	*Aztlanolagus agilis*	R	p3	2.3	2.5	2N 2-3E 90-95 cmbd
1773	*Brachylagus coloradoensis*	L	dentary with p3-p4	1.6	1.6	1N 2E 65-70 cmbd
1774	*Brachylagus coloradoensis*	R	p3	1.8	1.8	2N 2-3E 80-85 cmbd
1775	*Brachylagus idahoensis*	L	p3	1.4	1.2	1N 2E 25-30 cmbd
1776	*Brachylagus idahoensis*	R	p3	1.8	1.8	2N 2-3E 45-60 cmbd
1777	*Brachylagus idahoensis*	L	p3	1.8	1.6	2N 2-3E 75-80 cmbd
1778	Leporidae	R	p3	–	–	1N 3E 30-35 cmbd
1779	Leporidae	R	p3	–	–	2N 2E E Half Cemented Level
1780	Leporidae	R	p3	2.0	–	1N 2-3E 70-75 cmbd
1781	*Ochotona* sp.	L	p3	1.2	1.2	1N 3E 45-70 cmbd; Wall Collapse
1782	*Ochotona* sp.	R	p3	1.2	1.5	1N 3E 45-70 cmbd; Wall Collapse
1783	*Ochotona* sp.	R	p3	–	–	1N 3E 45-70 cmbd; Wall Collapse
1784	*Ochotona* sp.	L	p3	1.1	1.2	1N 3E 45-70 cmbd; Wall Collapse
1785	*Ochotona* sp.	R	p3	–	–	1N 2E 30-35 cmbd
1786	*Ochotona* sp.	R	p3	1.2	1.3	1N 3E 35-40 cmbd
1787	*Ochotona* sp.	L	p3	1.1	1.2	1N 2E 40-45 cmbd
1788	*Ochotona* sp.	L	p3	1.1	1.0	1N 2E 40-45 cmbd
1789	*Ochotona* sp.	R	p3	1.3	1.5	1N 3E 40-45 cmbd
1790	*Ochotona* sp.	L	p3	1.5	1.6	2N 3E 40-45 cmbd
1791	*Ochotona* sp.	R	p3	–	–	2N 3E 40-45 cmbd
1792	*Ochotona* sp.	L	p3	1.4	1.6	1N 3E Cemented Level
1793	*Ochotona* sp.	R	p3	1.4	1.7	1N 3E Cemented Level
1794	*Ochotona* sp.	R	p3	1.3	1.4	1N 3E Cemented Level
1795	*Ochotona* sp.	R	p3	1.3	1.3	1N 3E Cemented Level
1796	*Ochotona* sp.	L	p3	1.5	–	2N 2E E Half Cemented Level
1797	*Ochotona* sp.	R	p3	1.2	1.1	1N 3E 43.5-55 cmbd; below Cemented Level
1798	*Ochotona* sp.	R	p3	1.3	1.4	1N 3E 43.5-55 cmbd; below Cemented Level
1799	*Ochotona* sp.	R	dentary with m1-m3	–	–	1N 3E 43.5-55 cmbd; below Cemented Level
457	*Ochotona* sp.	L	p3	1.0	1.2	2N 2-3E 45-60 cmbd
470	*Ochotona* sp.	R	p3	1.1	1.3	2N 2-3E 45-60 cmbd
471	*Ochotona* sp.	L	p3	1.3	1.4	2N 2-3E 45-60 cmbd
1800	*Ochotona* sp.	R	p3	1.3	1.3	2N 2-3E 45-60 cmbd
1801	*Ochotona* sp.	R	p3	1.2	1.4	2N 2-3E 45-60 cmbd
1802	*Ochotona* sp.	R	dentary with p4-m3	–	–	2N 2-3E 45-60 cmbd
1803	*Ochotona* sp.	L	p3	1.3	1.2	1N 2E 50-55 cmbd
1804	*Ochotona* sp.	L	p3	1.3	1.3	1N 2E 55-60 cmbd
1805	*Ochotona* sp.	R	dentary with p4-m1 or m1-m2	–	–	1N 2E 55-60 cmbd
1806	*Ochotona* sp.	L	p3	1.3	1.6	1N 2E 55-60 cmbd
1807	*Ochotona* sp.	R	p3	1.3	1.5	1N 2E 55-60 cmbd
1808	*Ochotona* sp.	R	p3	1.2	1.4	1N 2E 55-60 cmbd
1809	*Ochotona* sp.	L	p3	1.3	1.4	1N 2E 55-60 cmbd
1810	*Ochotona* sp.	R	p3	1.3	1.5	1N 3E 55-60 cmbd
1811	*Ochotona* sp.	R	dentary	–	–	1N 3E 55-60 cmbd
1812	*Ochotona* sp.	R	dentary with m1-m2	–	–	1N 2E 60-65 cmbd
1813	*Ochotona* sp.	L	p3	1.3	1.6	1N 2E 60-65 cmbd
1814	*Ochotona* sp.	L	p3	1.2	1.2	1N 3E 60-65 cmbd
1815	*Ochotona* sp.	L	p3	1.2	1.2	1N 3E 60-65 cmbd

#	TAXON	SIDE	ELEMENT	*l*	*w*	PROVENIENCE
1816	*Ochotona* sp.	L	p3	1.2	1.1	2N 2-3E 60-65 cmbd
1817	*Ochotona* sp.	R	p3	1.3	1.5	2N 2-3E 60-65 cmbd
1818	*Ochotona* sp.	R	p3	1.0	1.1	2N 2-3E 60-65 cmbd
1819	*Ochotona* sp.	R	p3	1.3	1.4	2N 2-3E 60-65 cmbd
1820	*Ochotona* sp.	R	p3	1.3	1.2	1N 2E 65-70 cmbd
1821	*Ochotona* sp.	L	p3	1.3	1.5	1N 2E 65-70 cmbd
1310	*Ochotona* sp.	R	p3	1.2	1.2	1N 3E 65-70 cmbd
1311	*Ochotona* sp.	R	p3	1.3	1.4	1N 3E 65-70 cmbd
1822	*Ochotona* sp.	L	p3	1.3	1.3	2N 2-3E 65-70 cmbd
1823	*Ochotona* sp.	R	p3	1.1	1.1	2N 2-3E 65-70 cmbd
1824	*Ochotona* sp.	R	p3	1.4	1.4	2N 2-3E 65-70 cmbd
1825	*Ochotona* sp.	L	p3	1.5	1.3	2N 2-3E 65-70 cmbd
884	*Ochotona* sp.	L	p3	1.1	–	1N 2-3E 70-75 cmbd
1826	*Ochotona* sp.	R	p3	1.3	1.5	1N 2-3E 70-75 cmbd
1827	*Ochotona* sp.	R	p3	1.1	1.3	2N 2-3E 70-75 cmbd
1828	*Ochotona* sp.	R	dentary with p3-p4	1.1	1.3	1N 2-3E 75-80 cmbd
1829	*Ochotona* sp.	R	p3	1.3	1.3	1N 2-3E 75-80 cmbd
1830	*Ochotona* sp.	L	p3	1.2	1.3	1N 2-3E 75-80 cmbd
1831	*Ochotona* sp.	L	p3	1.2	1.2	2N 2-3E 75-80 cmbd
1832	*Ochotona* sp.	L	p3	1.2	1.2	2N 2-3E 75-80 cmbd
1833	*Ochotona* sp.	L	p3	1.2	1.1	2N 2-3E 75-80 cmbd
1834	*Ochotona* sp.	L	p3	1.0	1.1	2N 2-3E 75-80 cmbd
1835	*Ochotona* sp.	L	p3	1.1	1.0	2N 2-3E 75-80 cmbd
1836	*Ochotona* sp.	L	p3	1.1	1.2	2N 2-3E 75-80 cmbd
1837	*Ochotona* sp.	R	p3	–	–	1N 2-3E 80-85 cmbd
1839	*Ochotona* sp.	R	p3	1.3	1.3	2N 2-3E 80-85 cmbd
1840	*Ochotona* sp.	R	p3	1.3	1.3	2N 2-3E 80-85 cmbd
1841	*Ochotona* sp.	R	p3	–	–	2N 2-3E 80-85 cmbd
1842	*Ochotona* sp.	L	p3	1.3	1.6	1N 2-3E 85-90 cmbd
1843	*Ochotona* sp.	L	p3	1.3	1.3	1N 2-3E 85-90 cmbd
1844	*Ochotona* sp.	L	p3	1.2	1.2	1N 2-3E 85-90 cmbd
1845	*Ochotona* sp.	R	p3	1.1	1.2	2N 2-3E 85-90 cmbd
1846	*Ochotona* sp.	L	p3	1.3	1.3	2N 2-3E 85-90 cmbd
1847	*Ochotona* sp.	R	p3	1.1	1.2	2N 2-3E 85-90 cmbd
1848	*Ochotona* sp.	R	p3	–	–	2N 2-3E 85-90 cmbd
1849	*Ochotona* sp.	R	p3	1.2	1.3	2N 2-3E 85-90 cmbd and below
1850	*Ochotona* sp.	L	p3	1.0	1.0	2N 3E 85-110 cmbd; below flowstone
1851	*Ochotona* sp.	L	p3	1.2	1.3	2N 3E 85-110 cmbd; below flowstone
1852	*Ochotona* sp.	L	p3	1.3	1.4	2N 3E 85-110 cmbd; below flowstone
1853	*Ochotona* sp.	R	p3	1.2	1.3	2N 3E 85-110 cmbd; below flowstone
1854	*Ochotona* sp.	L	p3	1.2	1.3	1-2N 2-3E 87-102 cmbd; below pedestaled rocks
1855	*Ochotona* sp.	R	dentary with p3-p4	1.1	1.1	1-2N 2-3E 87-102 cmbd; below pedestaled rocks
1856	*Ochotona* sp.	R	p3	1.2	1.5	2N 2-3E 90-95 cmbd
1857	*Ochotona* sp.	L	p3	1.3	1.4	2N 2-3E 90-95 cmbd
1858	*Ochotona* sp.	L	p3	1.3	1.4	2N 2-3E 90-95 cmbd
1859	*Ochotona* sp.	L	p3	–	–	1N 2-3E 90 cmbd and below
1860	*Ochotona* sp.	R	p3	–	–	2N 2-3E 95-102 cmbd
1861	*Ochotona* sp.	R	p3	1.4	1.5	2N 3E 100-105 cmbd
1862	*Ochotona* sp.	L	p3	1.4	1.4	2N 3E 100-105 cmbd
1863	*Ochotona* sp.	R	p3	1.3	1.4	2N 3E 100-105 cmbd
1864	*Ochotona* sp.	R	p3	1.3	1.6	2N 3E 100-105 cmbd

#	TAXON	SIDE	ELEMENT	*l*	*w*	PROVENIENCE
1865	Ochotonidae	R	p3	–	–	1N 2E 65-70 cmbd
1866	*Sylvilagus* or *Lepus* sp.	R	p3	2.9	3.1	1N 3E 25-60 cmbd; Wall Scrapings
1867	*Sylvilagus* or *Lepus* sp.	R	p3	3.4	3.2	1N 3E 45-70 cmbd; Wall Collapse
1868	*Sylvilagus* or *Lepus* sp.	R	p3	3.3	3.2	2N 3E 30-35 cmbd
1869	*Sylvilagus* or *Lepus* sp.	L	p3	1.7	1.5	2N 3E 40-45 cmbd
1870	*Sylvilagus* or *Lepus* sp.	R	p3	2.4	2.4	2N 3E 40-45 cmbd
1871	*Sylvilagus* or *Lepus* sp.	L	p3	2.7	2.6	2N 3E 40-45 cmbd
1872	*Sylvilagus* or *Lepus* sp.	L	p3	2.5	1.8	1N 3E Cemented Level
1873	*Sylvilagus* or *Lepus* sp.	R	p3	3.2	3.2	2N 2E E Half Cemented Level
1874	*Sylvilagus* or *Lepus* sp.	R	dentary with p3-p4	2.4	2.2	1N 3E 43.5-55 cmbd; below Cemented Level
1875	*Sylvilagus* or *Lepus* sp.	L	p3	3.1	3.0	1N 3E 43.5-55 cmbd; below Cemented Level
1876	*Sylvilagus* or *Lepus* sp.	R	p3	3.1	2.9	1N 3E 43.5-55 cmbd; below Cemented Level
1877	*Sylvilagus* or *Lepus* sp.	R	p3	2.1	2.0	1N 3E 43.5-55 cmbd; below Cemented Level
1878	*Sylvilagus* or *Lepus* sp.	R	p3	2.3	2.2	1N 3E 43.5-55 cmbd; below Cemented Level
1879	*Sylvilagus* or *Lepus* sp.	R	p3	3.2	3.0	2N 2-3E 45-60 cmbd
1880	*Sylvilagus* or *Lepus* sp.	L	p3	2.5	2.2	2N 2-3E 45-60 cmbd
1881	*Sylvilagus* or *Lepus* sp.	L	p3	3.4	2.6	2N 2-3E 45-60 cmbd
1882	*Sylvilagus* or *Lepus* sp.	L	p3	3.9	3.5	2N 2-3E 45-60 cmbd
1883	*Sylvilagus* or *Lepus* sp.	R	p3	2.4	2.4	2N 2-3E 45-60 cmbd
463	*Sylvilagus* or *Lepus* sp.	L	p3	2.0	1.7	2N 2-3E 45-60 cmbd
452	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	2N 2-3E 45-60 cmbd
480	*Sylvilagus* or *Lepus* sp.	L	p3	2.2	1.2	2N 2-3E 45-60 cmbd
1884	*Sylvilagus* or *Lepus* sp.	L	p3	2.7	2.5	2N 2-3E 45-60 cmbd
1885	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	2N 2-3E 45-60 cmbd
1886	*Sylvilagus* or *Lepus* sp.	R	p3	3.3	3.0	2N 2-3E 45-60 cmbd
1887	*Sylvilagus* or *Lepus* sp.	L	p3	3.3	2.8	1N 2E 50-55 cmbd
1888	*Sylvilagus* or *Lepus* sp.	R	p3	3.2	3.0	1N 2E 55-60 cmbd
1889	*Sylvilagus* or *Lepus* sp.	R	p3	3.5	3.6	1N 3E 55-60 cmbd
1890	*Sylvilagus* or *Lepus* sp.	L	p3	2.1	2.0	1N 2E 60-65 cmbd
1891	*Sylvilagus* or *Lepus* sp.	L	p3	–	–	1N 3E 60-65 cmbd
1892	*Sylvilagus* or *Lepus* sp.	R	dentary with p3-m2	2.5	2.5	1N 3E 60-65 cmbd
1893	*Sylvilagus* or *Lepus* sp.	R	p3	3.0	2.7	2N 2-3E 60-65 cmbd
1894	*Sylvilagus* or *Lepus* sp.	L	p3	–	–	1N 2E 65-70 cmbd
1895	*Sylvilagus* or *Lepus* sp.	R	p3	3.6	3.4	1N 2E 65-70 cmbd
1896	*Sylvilagus* or *Lepus* sp.	R	p3	2.5	2.2	1N 3E 65-70 cmbd
1897	*Sylvilagus* or *Lepus* sp.	R	p3	2.8	2.4	1N 3E 65-70 cmbd
1898	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	1N 2-3E 70-75 cmbd
1899	*Sylvilagus* or *Lepus* sp.	L	p3	3.3	2.8	1N 2-3E 70-75 cmbd
1900	*Sylvilagus* or *Lepus* sp.	R	p3	3.3	2.9	2N 2-3E 70-75 cmbd
1901	*Sylvilagus* or *Lepus* sp.	R	p3	2.9	2.5	2N 2-3E 70-75 cmbd
1902	*Sylvilagus* or *Lepus* sp.	R	p3	2.9	2.8	2N 2-3E 70-75 cmbd
1903	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	2N 2-3E 70-75 cmbd
1904	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	2N 2-3E 70-75 cmbd
1905	*Sylvilagus* or *Lepus* sp.	R	p3	–	3.5	2N 2-3E 70-75 cmbd
1906	*Sylvilagus* or *Lepus* sp.	L	p3	2.3	2.0	2N 2-3E 70-75 cmbd
1907	*Sylvilagus* or *Lepus* sp.	L	p3	3.0	2.6	2N 2-3E 75-80 cmbd
1908	*Sylvilagus* or *Lepus* sp.	L	p3	3.0	2.8	2N 2-3E 75-80 cmbd
1909	*Sylvilagus* or *Lepus* sp.	R	p3	2.9	2.9	2N 2-3E 75-80 cmbd
1910	*Sylvilagus* or *Lepus* sp.	R	dentary with p3-m2	3.6	3.4	2N 2-3E 75-80 cmbd
1911	*Sylvilagus* or *Lepus* sp.	L	p3	3.7	–	1N 2-3E 80-85 cmbd
1912	*Sylvilagus* or *Lepus* sp.	R	p3	2.7	2.6	2N 2-3E 80-85 cmbd

#	TAXON	SIDE	ELEMENT	*l*	*w*	PROVENIENCE
1913	*Sylvilagus* or *Lepus* sp.	L	p3	–	–	2N 2-3E 80-85 cmbd
1914	*Sylvilagus* or *Lepus* sp.	L	p3	–	–	2N 2-3E 80-85 cmbd
1915	*Sylvilagus* or *Lepus* sp.	L	p3	3.0	2.5	2N 2-3E 80-85 cmbd
1916	*Sylvilagus* or *Lepus* sp.	R	p3	3.4	3.7	2N 2-3E 80-85 cmbd
1917	*Sylvilagus* or *Lepus* sp.	R	p3	–	–	2N 2-3E 80-85 cmbd
1918	*Sylvilagus* or *Lepus* sp.	L	P3	–	–	2N 2-3E 90-95 cmbd
1919	*Sylvilagus* or *Lepus* sp.	L	dentary with p3-m2	–	–	2N 2-3E 90-95 cmbd
1119	*Sylvilagus* or *Lepus* sp.	L	p3	2.9	2.7	2N 3E 85-110 cmbd; below flowstone
1920	*Sylvilagus* or *Lepus* sp.	L	p3	–	–	2N 3E 100-105 cmbd