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Cover: Right dentary of *Sylvilagus audubonii* (LACMP23-34374) from Rancho La Brea, Project 23, Deposit 13 in lateral view. Scale bar=5mm.

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A protocol for differentiating late Quaternary leporids in southern California with remarks on Project 23 lagomorphs at Rancho La Brea, Los Angeles, California, USA

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Leporid remains are common in Quaternary fossil assemblages and are useful paleoenvironmental indicators. Identifying leporid fossils to species is challenging, though previous work has shown that identifications are more feasible if fossils can be narrowed down to a subset of potential species occurring across limited spatial scales. We sampled 120 adult and nine juvenile dentaries of six extant western North American species (*Lepus americanus*, *L. californicus*, *L. townsendii*, *Sylvilagus audubonii*, *S. bachmani*, and *S. nuttallii*) to establish useful characters for genus and species-level identification of late Quaternary leporid fossils in California. Most individuals can be differentiated from individuals of other species using a combination of lower third premolar enamel folding patterns and dental measurements. However, it is difficult to discriminate dental elements among *L. californicus* and *L. townsendii* and elements of *S. nuttallii* from *S. audubonii*, *S. bachmani*, and *L. americanus*. Here we present criteria for differentiating western leporid dental remains, apply the criteria to identify specimens recovered from several late Quaternary fossil deposits at Rancho La Brea (RLB), California, collectively known as Project 23, and reconstruct changes in relative fossil leporid abundances there. Using our criteria, we identified two extant species, *S. audubonii* and *S. bachmani,* among the Project 23 fossils. In addition to relative abundance changes across several RLB deposits, *S. audubonii* and *S. bachmani* generally become larger through time, possibly in response to local environmental changes. Establishing region-specific identification criteria as done here may prove useful for discerning morphologically similar species at prehistoric sites elsewhere.

Keywords: fossil, *Lepus*, morphometrics, p3, Pleistocene, *Sylvilagus*

INTRODUCTION

Leporids (rabbits and hares) occupy diverse habitats, provide important ecosystem services, and are prevalent in Quaternary paleofaunas throughout North America (Kurtén and Anderson 1980, Smith et al. 2018). As such, their fossils are useful indicators of paleoenvironments and for tracking environmental changes through time (e.g., Hulbert 1984, Driver and Woiderski 2008, Wicks et al. 2015, Somerville et al. 2018). However, identifying isolated leporid fossils to species is challenging due to extensive morphological variation and range overlap among taxa (Hall and Kelson 1959, Dalquest 1979, White 1991). Useful characters for differentiating species in one region are not always useful for differentiating the same species in another region due to intraspecific variation across spatial gradients (Hall and Kelson 1959); this problem is compounded across temporal gradients due to changing climates and shifting geographic ranges. Isolated elements of common North American leporids, including *Lepus* Linnaeus (1758) spp. and *Sylvilagus* Gray (1867) spp., generally cannot be differentiated using morphology alone (Dalquest 1979, Kurtén and Anderson 1980, Jass 2009), with some exceptions. Individuals of some species can be differentiated based on the degree of enamel folding (crenulation) across the posterobuccal re-entrant of the lower third premolar (p3) (Dalquest

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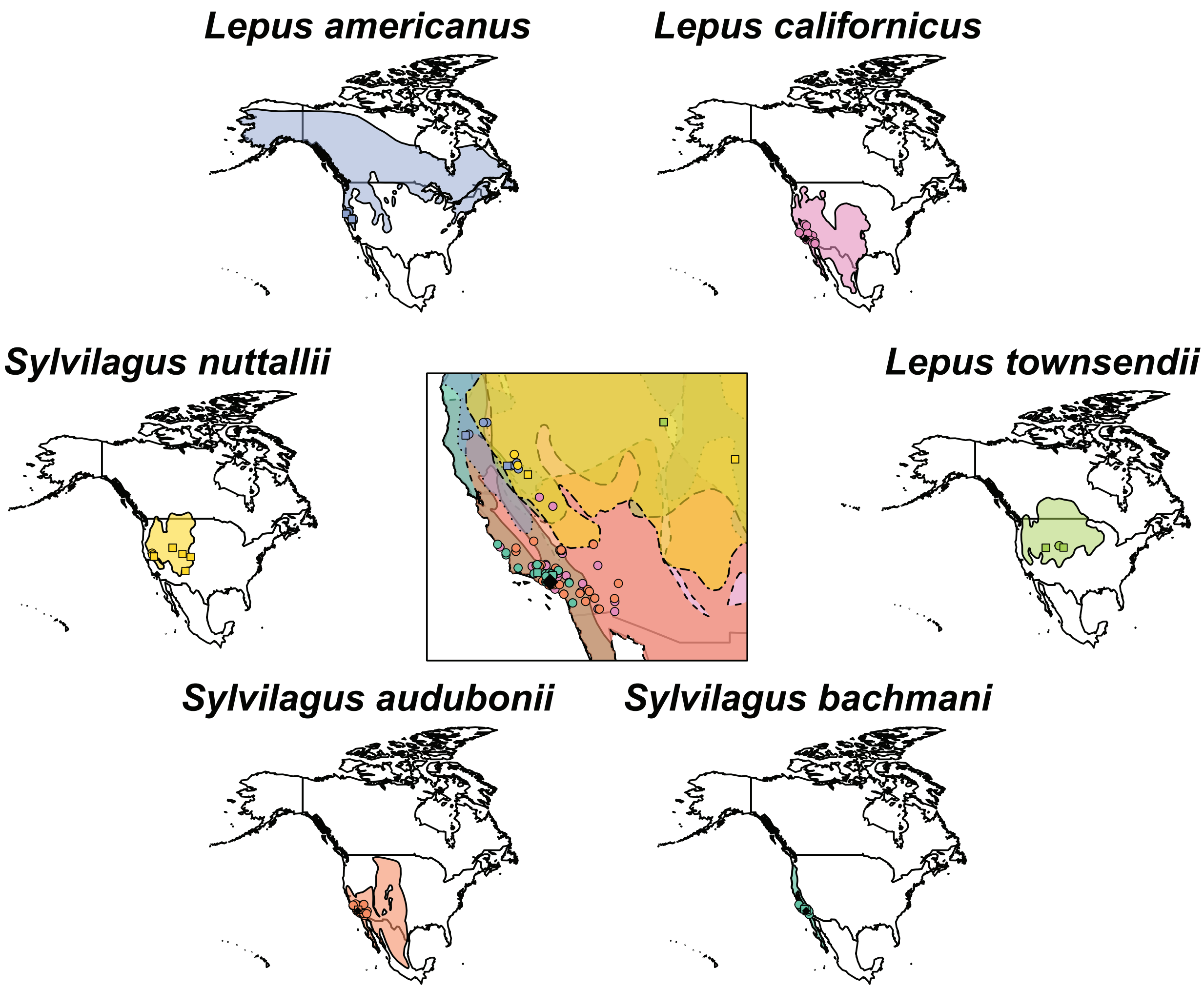

Figure 1. Maps illustrating the modern distributions of the six extant leporid species examined. Points indicate sampling locations of individual specimens. Rancho La Brea, the fossil locality where unknown leporid specimens were collected, is marked by a black diamond. Species range data were obtained from (Patterson et al. 2007).

et al. 1989) and the addition of craniomandibular size measurements can sometimes help differentiate species of *Lepus* and *Sylvilagus* (Pettus 1956). Most individuals, however, cannot be differentiated using this method exclusively (White 1991, Jass 2009), in the absence of additional contextual information.

Despite the difficulty of identifying isolated leporid elements to species, studies have been more successful at discriminating leporid taxa within limited spatial scales. For example, Hulbert (1984) found no size overlap in maxillary and mandibular measurements of recent *Lepus californicus*/*Sylvilagus aquaticus* and *S. audubonii*/*S. floridanus* collected throughout the state of Texas. Leporid fossils from central Texas were differentiated between those taxonomic pairs using size alone, though discriminant analyses were needed to differentiate *L. californicus* Gray (1837) from *S. aquaticus* and *S. audubonii* Baird (1857) from *S. floridanus* (Hulbert 1984). Dice (1925) examined extant leporids near San Francisco and San Diego, California, and observed that p3 enamel crenulation is usually "smooth" in *L. californicus* and *S. bachmani* Waterhouse (1838) and highly crenulated or "wavy" in *S. audubonii*. Those criteria and size were used to identify leporid fossils from Pits 1059, 2050, and 2051 at Rancho La Brea in Los Angeles, CA.

The taxonomic resolution at which isolated leporid fossils can be identified is thus dependent on the extent of size/shape variation within and among taxa that occur (or occurred) in the focal region of study. Since there is no one set of criteria for identifying North American leporid fossils, region-specific "keys" must be employed using characters relevant to those locations. One fundamental assumption that should be acknowledged when implementing region-specific protocols is that the geographic range and morphology of the fossil taxa of interest have not shifted temporally to the extent that

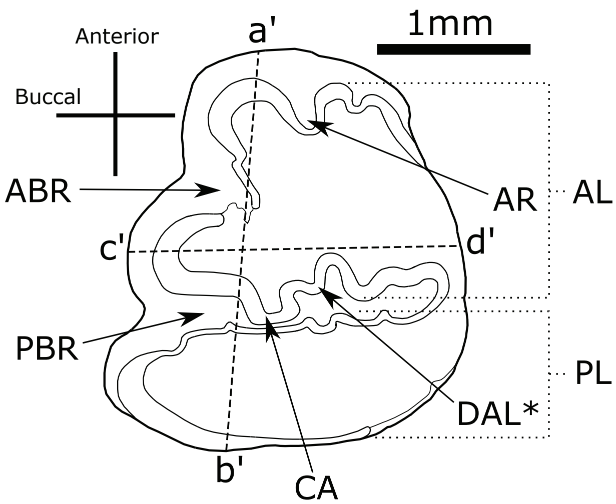

Figure 2. Lower left third premolar (p3) outline of LACM-53879 *Sylvilagus audubonii* (also pictured in Fig. 3B) illustrating tooth terminology and applied length (a'- b') and width (c'- d') measurements. **AL**=anterolophid, **PL**=posterolophid, **AR**=anterior re-entrant, **ABR**=anterobuccal re-entrant, **PBR**=posterobuccal re-entrant, **CA**=central angle, **DAL**=double anterior loop, *****=not present on all specimens.

comparative specimens within the study region are no longer representative of the fossil taxon. Indeed, some small mammals have undergone considerable range shifts during the late Quaternary (Graham 1986). It may therefore be necessary to include extralimital taxa and/or extralimital individuals of focal taxa to mitigate the chance of excluding representative specimens from the comparative identification pool. Deciding whether this assumption is appropriate or not will depend on several factors including the size of the study region, the temporal distance between comparative and fossil taxa, and the ecology of the focal taxa (e.g., their dispersal ability and rate of morphological change among generations). We focus on developing a set of criteria for identifying isolated leporid elements in California that, given this assumption and the known ecology of the focal taxa today, is likely reasonable to apply to identify late Pleistocene fossils from Rancho La Brea (RLB).

MATERIALS AND METHODS

Extant taxa

Three leporid species are distributed in low-elevation areas of southern California today: *Lepus californicus* (black-tailed jackrabbit), *Sylvilagus audubonii* (desert cottontail), and *S. bachmani* (brush rabbit) (Fig. 1). To determine whether leporid fossils from this region can be differentiated among the species, we collected comparative morphometric data and observed p3 enamel crenulation patterns in 30 extant adult specimens each of *L. californicus*, *S. audubonii*, and *S. bachmani* from California at the Natural History Museum of Los Angeles County (LACM) and Museum of Vertebrate Zoology at Berkeley (MVZ) (Fig. 1; Appendix Table 1). In addition, we collected comparative data on ten adult individuals each of *L. americanus* Erxleben (1777) (snowshoe hare), *L. townsendii* Bachman (1839) (white-tailed jackrabbit) and *S. nuttallii* Bachman (1837) (mountain cottontail) from western North America at the Harvard Museum of Comparative Zoology (MCZ) and MVZ (Fig. 1; Appendix Table 1). The latter three species occur today only along the eastern periphery of northern and central California (Chapman 1975, Lim 1987) (Fig. 1); however, their presence should be considered at extralimital fossil localities since some mammalian ranges have shifted markedly throughout the late Quaternary (Graham 1986). We also observed the dental morphology of six *Brachylagus idahoensis* Merriam (1891) (pygmy rabbit) individuals (Appendix Table 1). *Brachylagus idahoensis* presently occurs along the eastern fringes of northern and central California; however, its tooth shape and size is distinctive from all other extant North American leporids (Green and Flinders 1980, Kurtén and Anderson 1980, Jass 2009) so

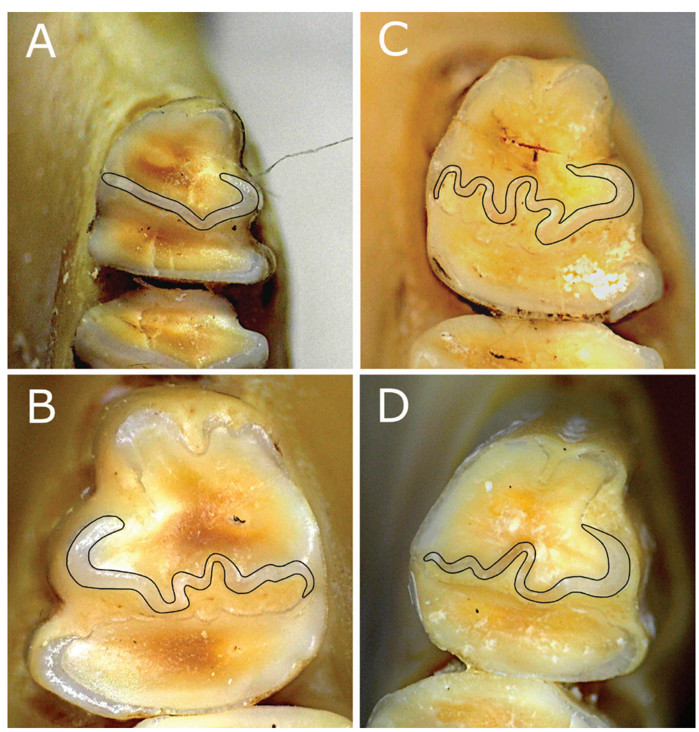

Figure 3. Occlusal views of extant leporid p3s illustrating the four enamel crenulation grouping patterns used in this study. Crenulation along the anterior and anterolateral wall of the posterobuccal re-entrant is outlined on each specimen. **A**. Right p3 of LACM-21374 *Sylvilagus bachmani* with “simple” crenulation. **B**. Left p3 of LACM-53879 *S. audubonii* with “moderate” crenulation. **C**. Right p3 of LACM-44966 *S. audubonii* with “complex” crenulation. **D**. Right p3 of LACM-29048 *Lepus californicus* with “alternate” crenulation. Images are magnified to illustrate crenulation patterns only and are not shown at a standardized scale.

it does not warrant further consideration for this study.

Modifying the categories of Dalquest et al. (1989), we sorted p3 crenulation patterns of each specimen into one of four grouping conditions: “simple,” “moderate,” “complex,” or “alternate” and obtained linear measurements of p3 length/p3 width (Fig. 2), diastema length, and toothrow length. Measurements were conducted using Fisherbrand Traceable ISO 17025 calibrated digital calipers as follows: p3 length=length from the apex of the anterior-most projection of the anterolophid (buccal to the anterior re-entrant) to the posterior edge of the posterolophid where enamel thickness begins to taper (Fig. 2); p3 width=buccolingual width from the apex of the buccal projection of the anterolophid (between the anterobuccal and posterobuccal re-entrants) to its lingual edge (Fig. 2); diastema length=length from the posterior edge of the incisor alveolus to the anterior edge of the p3 alveolus; toothrow length=length from the anterior edge of the p3 alveolus to the posterior edge of the m3 alveolus. We measured each feature three times and recorded the average of the three measurements. Measurements of juvenile specimens were not considered for taxonomic identifications, though p3 crenulation patterns were observed in juveniles to determine if ontogenetic differences in enamel patterning are present (Appendix Table 1).

All p3 crenulation types exhibit a thick enamel band at the buccal-most edge of the anterolophid, forming a semicircular curve or “hook,” which extends lingually across the anterior wall of the posterobuccal re-entrant. In specimens with “simple” crenulation, the band often extends posterolingually prior to the midline of the tooth, then reorients anterolingually towards the lingual edge, sometimes forming a checkmark-like pattern (Fig. 3A). Apart from this anteroposterior reorientation, termed the “central angle” by Dalquest et al. (1989), specimens with simple crenulation exhibit relatively smooth enamel with no prominent folding. Specimens with “moderate” crenulation exhibit two prominent anteriorly-oriented “loop” folds referred to here as the double anterior loop (DAL) lingual to the central angle (Fig. 2). The remainder of enamel lingual to the DAL is relatively smooth in specimens with moderate crenulation (Fig. 3B). Specimens with “complex” crenulation exhibit a DAL, as seen in the moderate condition, with additional folds extending from the DAL toward the lingual edge of the tooth (Fig. 3C). Finally, specimens with “alternate” crenulation exhibit prominent buccolingual folding across the anterior wall of the posterobuccal re-entrant but lack the DAL seen in specimens with moderate or complex crenulation (Fig. 3D).

Next, we employed random forest classification trees, an ensemble learning technique, to determine how accurately the six extant leporid species can be binned in their respective species-groups using our measurements and crenulation observations. Dental measurements of p3 length, p3 width, p3 length-to-width ratio (l/w), diastema length, toothrow length, and crenulation patterning were entered in the analysis. Only adult and suspected adult specimens of each species were included. Random forests were conducted on two datasets. The first dataset included only species that presently occur in low elevation areas of southern California (i.e., *Lepus californicus*, *Sylvilagus audubonii*, and *S. bachmani*) and the second dataset included all six species observed in our study. Both datasets were analyzed twice in the R programming package “randomForest” (Liaw and Wiener 2002), first using all six predictor variables and again with only p3 variables of length, width, l/w, and crenulation pattern. The latter modification was performed because isolated teeth are frequently recovered from vertebrate assemblages, limiting the availability of diastema and toothrow measurements. All dataset trials were run on 1000 trees with the number of variables for splitting at each tree node set to six or four depending on how many variables were entered in the analysis. All analyses were conducted using R [version 3.6.1, R Core Team (2019)].

Fossil taxa

Rancho La Brea today is a protected National Natural Landmark with a long (>100 year) history of fossil collection. The oil-impregnated sands near the surface have resulted in the accumulation and preservation of over 600 species of late Quaternary plants and animals, all housed at La Brea Tar Pits Museum. In 2006, during the building of a new underground parking structure at the Los Angeles County Museum of Art, sixteen new asphalt fossil deposits were discovered. They were removed in twenty-three wooden crates for subsequent excavation and are collectively referred to as Project 23 (Fuller et al 2014). Several deposits were too large for a single crate and thus were divided into multiple crates. Systematic excavation of each Project 23 deposit in 1m^2 x 25cm grids has resulted in thousands of well-preserved fossils. We screened approximately 4.5kg of matrix from various grids within Project 23 deposits 1, 7B, 13, and 14. This resulted in fifty-nine leporid p3s (including partial dentaries with p3s). Fossils were subsequently cataloged and housed in the Los Angeles County Museum Project 23 (LACMP23) collections.

Table 1. Linear dentary measurements and p3 crenulation patterns of recent adult *Lepus californicus*, *L. townsendii*, *Sylvilagus audubonii*, *S. bachmani*, and *S. nuttallii*. Asterisks indicate currently extralimital taxa from Los Angeles County and most of southern California. Specimen measurements in Appendix Table 1. **l**=length, **w**=width, **SD**=standard deviation.

Measurements (mm)	p3 (l)	p3 (w)	p3 l/w	Diastema (l)	Toothrow (l)	Crenulation pattern (n)
***L. californicus* (n=30)**						
Max	3.96	3.39	1.37	25.48	19.19	Simple 17 (57%)
Min.	3.09	2.52	1.02	15.3	14.78	Alternate 10 (33%)
Mean	3.47	2.91	1.20	19.64	16.28	Moderate 2 (7%)
SD	0.22	0.23	0.08	1.90	0.98	Complex 1 (3%)
***L. townsendii* (n=10)**						
Max	3.65	3.32	1.21	20.31	18.16	Simple 9 (90%)
Min	3.25	2.79	1.05	17.72	16.06	Alternate 1 (10%)
Mean	3.45	3.04	1.14	19.38	17.09	Moderate 0 (0%)
SD	0.15	0.17	0.05	0.74	0.74	Complex 0 (0%)
***L. americanus* (n=10)**						
Max	2.90	2.60	1.16	15.15	13.89	Simple 8 (80%)
Min	2.40	2.32	1.00	13.49	12.19	Alternate 2 (20%)
Mean	2.61	2.41	1.08	14.41	13.11	Moderate 0 (0%)
SD	0.18	0.09	0.06	0.51	0.51	Complex 0 (0%)
***S. audubonii* (n=30)**						
Max	3.19	2.81	1.35	16.51	14.13	Simple 1 (3%)
Min	2.30	1.99	1.02	11.94	11.47	Alternate 0 (0%)
Mean	2.82	2.35	1.20	14.15	12.71	Moderate 10 (33%)
SD	0.21	0.18	0.10	1.07	0.63	Complex 19 (63%)
***S. bachmani* (n=30)**						
Max	2.80	2.26	1.44	14.20	13.29	Simple 26 (86%)
Min	2.09	1.68	1.14	10.34	10.11	Alternate 0 (0%)
Mean	2.44	1.93	1.27	12.17	11.58	Moderate 2 (7%)
SD	0.19	0.15	0.08	0.92	0.71	Complex 2 (7%)
***S. nuttallii* (n=10)**						
Max	2.98	2.47	1.31	14.66	13.35	Simple 6 (60%)
Min	2.2	1.68	1.10	11.29	10.21	Alternate 0 (0%)
Mean	2.50	2.09	1.20	12.97	11.94	Moderate 0 (0%)
SD	0.24	0.26	0.06	1.19	0.97	Complex 4 (40%)

We evaluated the fossil samples to determine likely taxonomic affinity according to the protocol we developed based on extant specimens, the chronological range of leporids in each deposit, and potential changes in body size through time. Radiocarbon dating of Project 23 materials was conducted at the University of California Irvine Keck Carbon Cycle AMS Laboratory using the ultrafiltration protocol of Fuller et al. (2015) to remove asphaltic contaminants. Dates were also obtained from Project 23 fossils not collected in this study to increase sample size. Potential body size changes were determined using a Welch two-sample t-test in R (version 3.6.1, R Core Team (2019)) to determine if significant size differences occur between our fossil samples and their assumed extant species representatives from southern California. Only non-juvenile, complete, fossil p3s from which length and width measurements could be obtained were included in size analyses (Appendix Table 2).

INTERSPECIFIC MORPHOLOGY

Most individuals of extant leporids in southern California exhibit only one or two of the four defined p3 crenulation conditions per species, although intraspecific variation does occur in these patterns. Approximately 90% of *Lepus californicus* have simple or alternate crenulation, 97% of *Sylvilagus audubonii* have moderate or complex crenulation, and 86% of *S. bachmani* have simple crenulation (Table 1). Crenulation-based identifications are least effective for discriminating *L. californicus* from *S. bachmani* since individuals of both taxa often exhibit simple crenulation—57% and 86% of sampled individuals of *L. californicus* and *S. bachmani* exhibit this condition respectively (Table 1). Since only sampled individuals of *Lepus* exhibit alternate crenulation, this morphotype likely indicates some form of *Lepus* in southern California specimens.

Sylvilagus bachmani exhibits the narrowest p3s of the five leporid species overall (mean p3 l/w=1.27) (Table 1; Fig. 4). Further, there is no overlap between *L. californicus* and *S. bachmani* in the ranges of different measurements, except for the p3 l/w (Table 1; Fig. 4A). Our samples of extant *L. californicus* are, on average, ~42% larger than extant *S. bachmani* and even the smallest *L. californicus* individual is >10% larger than the largest *S. bachmani* (Table 1; Fig. 4A). Of course, pre- and post-glacial populations of some small mammal species exhibit significant body size shifts (e.g., Smith et al. 1995, Blois et al. 2008) and mandibular features of fossil S. floridanus Allen (1890) from south-central Texas are significantly larger than those of recent populations (Pettus 1956). However,

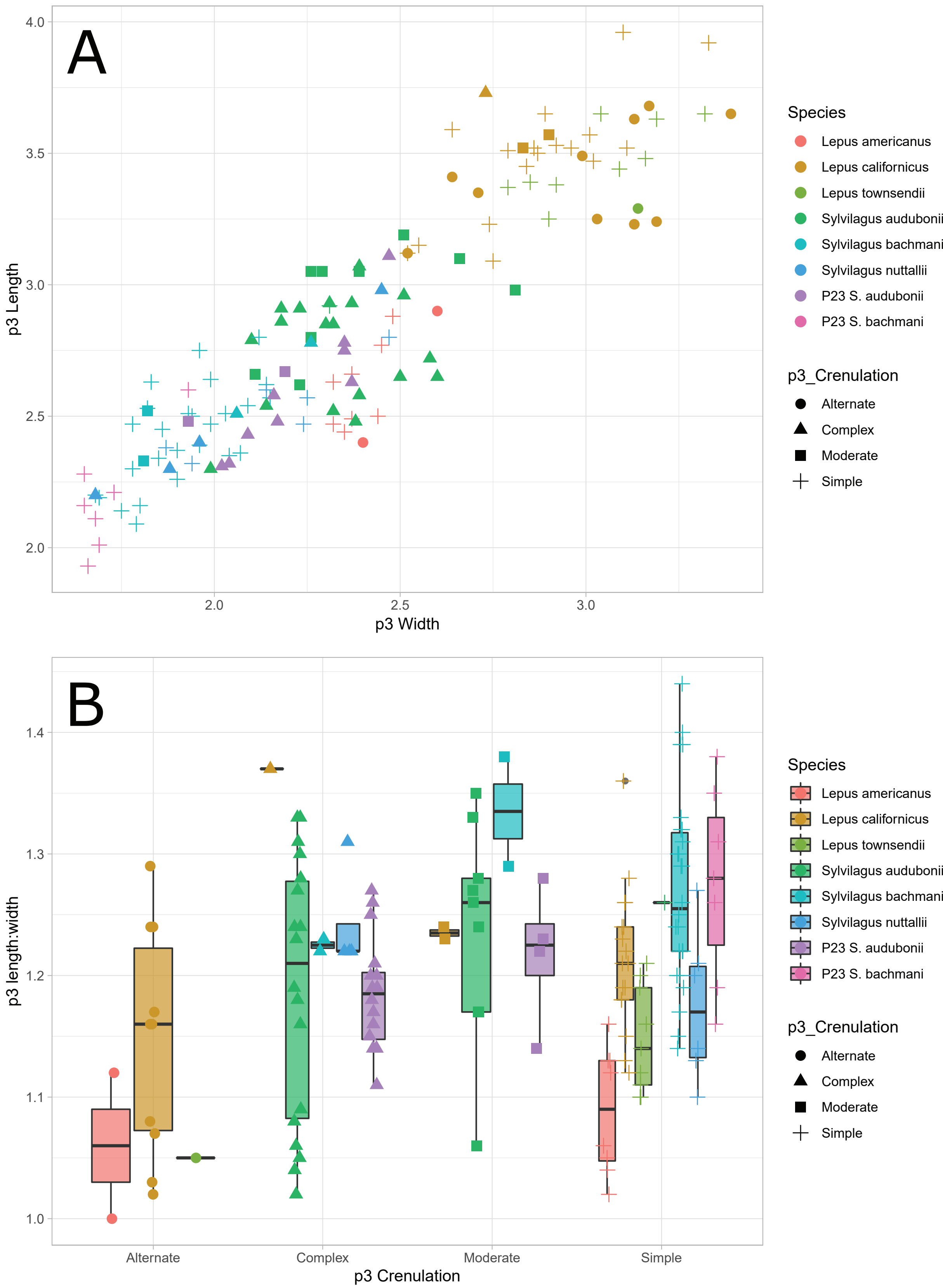

Figure 4. A. p3 length and width measurements of extant and Project 23 fossil leporids included in this study. All measurements are in millimeters. Juvenile and inferred juvenile individuals are not included. **B**. Boxplot of p3 l/w of the same recent and Project 23 fossil leporids grouped by crenulation pattern.

Table 2. Confusion matrices depicting radom forest classification results of four leporid dataset trials. Trials titled "Three species" show classification results for species currently distributed in low-elevation areas of southern California only (i.e., *Lepus californicus*, *S. audubonii*, and *S. bachmani*). Trials titled "Six species" show results for all species observed in this study. Trials titled "all variables" indicate that all six measured variables of p3 length, p3 width, p3 length-to-width-ratio, p3 crenulation pattern, diastema length, and toothrow length are included in the analysis. Trials titled "p3 variables only" indicate that only the first four p3 variables are included. The number of variables for splitting at each node was set to six for "all variables" and four for "p3 variables only." All trials were run on 1000 trees.

Three species, all variables: Out-of-Bag estimate of error = 5.88%

	L. californicus	*S. audubonii*	*S. bachmani*	Taxon-specific error
L. californicus	29	0	0	0.0%
S. audubonii	0	24	3	10.11%
S. bachmani	0	2	27	6.90%

Three species, p3 variables only: Out-of-Bag estimate of error = 9.41%

	L. californicus	*S. audubonii*	*S. bachmani*	Taxon-specific error
L. californicus	28	1	0	3.45%
S. audubonii	2	22	3	18.52%
S. bachmani	0	2	27	6.90%

Six species, all variables: Out-of-Bag estimate of error = 14.91%

	L. americanus	*L. californicus*	*L. townsendii*	*S. audubonii*	*S. bachmani*	*S. nuttallii*	Taxon-specific error
L. americanus	9	0	0	0	0	1	10.0%
L. californicus	0	27	2	0	0	0	6.90%
L. townsendii	0	4	6	0	0	0	40.0%
S. audubonii	1	0	0	25	0	1	7.41%
S. bachmani	0	0	0	2	27	0	6.90%
S. nuttallii	2	0	0	2	2	3	66.67%

Six species, p3 variables only: Out-of-Bag estimate of error = 24.56%

	L. americanus	*L. californicus*	*L. townsendii*	*S. audubonii*	*S. bachmani*	*S. nuttallii*	Taxon-specific error
L. americanus	8	0	0	0	0	2	20.0%
L. californicus	1	23	5	0	0	0	20.69%
L. townsendii	0	6	4	0	0	0	60.0%
S. audubonii	1	2	0	22	1	1	18.52%
S. bachmani	0	0	0	2	26	1	10.35%
S. nuttallii	2	0	0	1	3	3	66.67%

temporal populations of *S. floridanus* do not exceed a 10% change in size measurements overall (Pettus 1956). We acknowledge that size overlap among recent or fossil *S. bachmani* and *L. californicus* may have occurred in the past due to unknown selective pressures. Therefore, we use relative tooth width and crenulation patterning (if alternate) to differentiate these species in addition to size and find that, based on our sample, misclassification does not occur between these two taxa if all three conditions are examined (Table 2). Overall, our observed dental characters are quite effective at differentiating leporids when only the three low-elevation southern California taxa are considered. Out-of-bag error is 5.88% and 9.41% for random forest classifications of *L. californicus*, *S. audubonii*, and *S. bachmani* using all dental variables and only p3 variables respectively (Table 2).

Differentiating southern California leporid species is more difficult when extralimital taxa (i.e., *L. americanus, L. townsendii*, and *S. nuttallii*) are considered. Random forest classification out-of-bag error is 14.91% and 24.56% for all variables and p3 variables respectively; though, in some cases, individual species misclassifications are substantially greater (Table 2). Crenulation patterns of *L. americanus and L. townsendii* are comparable to those of *L. californicus*, though *L. townsendii* exhibits overall wider p3s, longer toothrows, and shorter diastemas than *L. californicus* (Table 1; Fig. 4B). Nevertheless, misclassification between *L. californicus* and *L. townsendii* is high due to the general similarity of their dental characters (Table 2). *Lepus americanus* has the greatest relative p3 width of all observed leporids overall (mean l/w=1.08) and is obviously smaller than the other two *Lepus* species—there is no overlap in p3 length, diastema length, or toothrow length and no random forest misclassification between *L. americanus* and *L. californicus*/*L. townsendii* (Tables 1, 2; Fig. 4A). However, measurements of *L. americanus* do overlap in size with all three *Sylvilagus* species examined, occasionally resulting in their misclassification (Tables 1, 2; Fig. 4A). The simple or alternate p3 crenulation pattern of *L. americanus* can distinguish it from *S. audubonii*, and it can be differentiated from *S. bachmani* based on relative dentition width (mean p3 l/w=1.08 and 1.27 for *L. americanus* and *S. bachmani* respectively) (Tables 1, 2; Fig. 4B). Though, some specimens of *S. nuttallii* and *L. americanus* overlap in size and morphology (Table 2; Fig. 4).

Concerningly, size measurements and p3 crenulation patterns of *S. nuttallii* fall within the observed range of *S. audubonii*, *S. bachmani,* and *L. americanus* (Tables 1, 2; Fig. 4). *Sylvilagus nuttallii* p3s are proportionally wider than *S. bachmani* overall, though not as wide as *L. americanus*, and comparable in width to *S. audubonii* (Table 1; Fig. 4B). Of the six focal species, *S. nuttallii* is by far the most difficult to differentiate from others. Approximately 67% of *S. nuttallii* individuals are misclassified in random forests as *L. americanus*, *S. audubonii*, or *S. bachmani* (Table 2). Measured characters of *S. nuttallii* are marginally smaller than those of *S. audubonii*, overall, and the former taxon exhibits simple p3 crenulation more often than the latter (Table 1; Fig. 4). However, those differences are unlikely to be useful for specific identification unless fossil sample sizes are large.

ONTOGENETIC MORPHOLOGY

Juvenile samples were limited (n=9); nevertheless, ontogenetic differences in crenulation patterns of *Sylvilagus audubonii* were observed. Juvenile *S. audubonii* individuals tend to exhibit simple crenulation more frequently than adult individuals, a phenomenon also noted by Dice (1925). Further, juvenile *S. audubonii* with loose p3s that permit tooth-base examination, and other relativity small individuals of *S. audubonii* that may be juvenile or subadult, tend to exhibit more complex crenulation at the tooth base versus the occlusal surface (Fig. 5A, B; Appendix Table 1). No p3s in our observation (extant or fossil) exhibit more complex crenulation at the tooth surface than at the base. Therefore, we hypothesize that adult p3 posterobuccal re-entrant enamel patterning forms at the tooth base and gradually erupts towards the surface with ontogeny. Leporid teeth are hypselodont and relatively fast-growing (Ungar 2010). We could not find more specific information on the ontogenetic timing of leporid enamel growth-patterning in the literature, though it would be useful for paleontological identifications. Therefore, if this inference is true, crenulation at the p3 base is a more reliable species indicator than crenulation at the surface and crenulation discrepancies between the tooth surface and base may indicate juvenile and/or young adult individuals. Until such research is conducted, we tentatively refer to isolated leporid p3s with obviously dissimilar base-surface crenulation complexity (e.g., "complex" versus "simple") as juvenile. Isolated p3s with slight changes in base-surface crenulation complexity (e.g., "complex" versus "moderate") tend to be larger than those with more extreme crenulation changes and

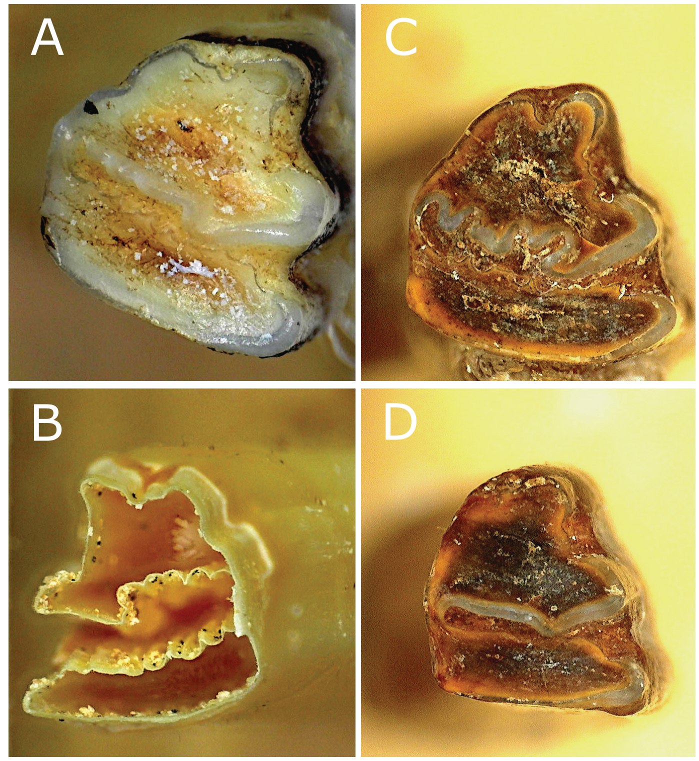

Figure 5. A, B. Right p3 of recent LACM-20731 *Sylvilagus audubonii* exhibiting simple crenulation at the surface of the tooth (**A**), and complex crenulation at the base of the tooth (**B**). **C**. Fossilized right p3 of LACMP23-30238 *S. audubonii* from Deposit 1 with complex crenulation at the occlusal surface. **D**. Fossilized right p3 of LACMP23-18270 *S. bachmani* from Deposit 1 at RLB with simple crenulation at the occlusal surface.

may indicate young adults or subadults; however, this is speculative. We tentatively refer to specimens with slight changes in crenulation complexity as "subadult?."

IDENTIFICATION CRITERIA

Due to suspected ontogenetic variation, enamel crenulation patterns should be observed at the tooth base when possible, and length/width measurements of juvenile specimens (i.e., specimens with markedly dissimilar p3 base-surface widths or crenulation complexity) should not be considered for species identification. Even when excluding juveniles, dentary measurements alone cannot differentiate the three southern California leporid species due to size overlap among adult *L. californicus*/*S. audubonii* and *S. audubonii*/*S. bachmani*. However, a combination of size-based measurements, p3 l/w, and p3 crenulation patterns can differentiate these taxa within a relatively small range of error (Table 2; Fig. 4). When the extralimital species *L. americanus, L. townsendii,* and *S. nuttallii* are included, species-level identification becomes more difficult due to increased morphometric and crenulation pattern overlap (Table 2; Fig. 4). *Lepus americanus* can be differentiated from *L. californicus* and *L. townsendii* via dentary and tooth dimensions, but not via crenulation patterning, and individual elements of *L. californicus* are difficult to differentiate from *L. townsendii* aside from a proportionally wider p3 exhibited by the latter species overall (Tables 1, 2; Fig. 4). Individuals of *Sylvilagus nuttallii* often cannot be differentiated from *S. bachmani* and *L. americanus* based on our observed dental characters (Table 2). Consequently, one may need to consider site-specific geographic probabilities to determine whether *S. nuttallii* is likely present at a locality. If so, specific identification of isolated leporid elements may not be feasible.

From these findings, we employ the following general criteria for identification of leporid fossils in southern California, recognizing there may still be some uncertainty in the final identifications and that protocol applicability may differ depending on site and study-specific conditions:

- p3s >3.1mm in length and >2.5 mm in width that exhibit simple (Fig. 3A) or alternate (Fig. 3D) crenulation – or, alternatively, dentaries with diastema and toothrow lengths >18.2mm and >15.5mm respectively – can be attributed to *Lepus*. Diastema and toothrow size thresholds assume that some individuals of the next largest taxon, *S. audubonii*, may be up to 10% larger than the largest extant individual(s) sampled in our study (Table 1).
- p3s <3.1mm in length that exhibit simple crenulation can be attributed to *Lepus americanus*/*Sylvilagus bachmani*/*S. nuttallii*. *Lepus americanus* and *Sylvilagus bachmani* can be further differentiated statistically and/or using relative tooth width if multiple individuals are present—i.e., with multiple individuals, whether the relative tooth widths of those individuals cluster within the range of variation of *S. bachmani* versus *L. americanus* may become more apparent (Table 2; Fig. 4). *Lepus americanus* has the widest dentition of the six observed species and *S. bachmani* has the narrowest, and there is little p3 l/w overlap and no statistical misclassification among individuals of these two species (Tables 1, 2; Fig. 4B). Individuals of *S. nuttallii* can exhibit size and morphological characters within the observed range of *L. americanus* and *S. bachmani* and are therefore difficult to identify.
- p3s with moderate (Fig. 2B) or complex (Fig. 2C) crenulation and mean l/w ~1.20 can be attributed to *S. audubonii*/*S. nuttallii*. *Sylvilagus nuttallii* exhibit simple crenulation more frequently than *S. audubonii* (Table 1; Fig. 4B). However, differentiating *S. audubonii* and *S. nuttallii* is difficult without large sample sizes, especially if *S. bachmani* and/or *L. americanus* is present, since different individuals of *S. nuttallii* can be misidentified as any one of those three species (Table 2).

SYSTEMATIC PALEONTOLOGY

Though some uncertainty remains when using the criteria outlined above to determine the taxonomic affinity of individual fossil specimens and the number of identified specimens per taxon (NISP) (Tables 1, 2), large sample sizes should allow taxon occurrences to be inferred assuming that spatiotemporal shifts in species distributions and morphology are minimal among the extant and fossil specimens examined. In other words, if several recent or fossil specimens of unknown taxonomic affinity cluster within the morphological range of a known, extant, taxon-group (e.g., Fig. 4), one can be reasonably certain that the extant taxon is present in the unknown sample pool even if there are morphological outliers that impact abundance calculations. Our findings show that some leporid species are more morphologically distinct than others. Individuals of *Sylvilagus* *nuttallii*, for example, share physical characteristics with *S. audubonii*, *S. bachmani*, and/or *L. americanus* and thus are often misclassified (Table 2; Fig. 4). Consequently, estimating *S. nuttallii* NISP is often impractical since its range largely overlaps with one or more of those other species (Fig. 1). However, it may be possible to detect *S. nuttallii* presence at localities in California if fossil sample sizes are large. With large sample sizes, one may infer *S. nuttallii* presence via a process of elimination if several leporid p3s are 1) relatively small (i.e., are < 3.1mm and therefore not likely *L. californicus* or *L. townsendii*), 2) exhibit l/w between 1.15 and 1.25 (i.e., are likely not *L. americanus* or *S. bachmani*), and 3) exhibit simple crenulation (i.e., are likely not *S. audubonii*). This criterion is not suitable for identification of individual specimens or detecting *S. nuttallii* if it is rare within a fauna and/or if there are few individuals sampled; though, it should facilitate detection of *S. nuttallii* if it is common and well-sampled at a locality. Using these criteria, we identified the 59 fossil leporid specimens sampled from Project 23 at RLB as the following:

LAGOMORPHA Brandt, 1855
LEPORIDAE Fischer 1817
SYLVILAGUS Gray 1867
SYLVILAGUS AUDUBONII Baird 1857

Referred specimens—LACMP23-39811, left dentary fragment with p3, p4, m2; LACMP23-32047, right dentary fragment with p3-m1; LACMP23-39819, right dentary fragment with p3-m1; LACMP23-39820, right dentary fragment with partial p3-m2. The following specimens represent complete left p3s: LACMP23-28084, LACMP23-28555, LACMP23-28661, LACMP23-31781, LACMP23-35608, LACMP23-35763, LACMP23-35847, LACMP23-35885, LACMP23-35937, LACMP23-40167, LACMP23-40209, LACMP23-40284, LACMP23-40285, LACMP23-40286, LACMP23-40287. The following specimens represent complete right p3s: LACMP23-28341, LACMP23-28519, LACMP23-28556, LACMP23-28858, LACMP23-33962, LACMP23-34117, LACMP23-35614, LACMP23-35696, LACMP23-35836, LACMP23-35839, LACMP23-35840, LACMP23-35881, LACMP23-35883, LACMP23-39874, LACMP23-40166, LACMP23-40210, LACMP23-40211. The following specimens represent partial left p3s and left p3 fragments: LACMP23-28266, LACMP23-31782, LACMP23-34259, LACMP23-34260, LACMP23-35771, LACMP23-40039, LACMP23-40288. The following specimens represent partial right p3s and right p3 fragments: LACMP23-28105, LACMP23-35618, LACMP23-35619, LACMP23-35645, LACMP23-39929, LACMP23-40110, LACMP23-40168, LACMP23-40212, LACMP23-40291.

Remarks—Fifty-two specimens from Project 23 are assigned to *S. audubonii* based on moderate or complex p3 crenulation (Table 2; Figs. 4, 5C). We cannot eliminate the possibility that some specimens belong to *S. nuttallii*; however, we consider this unlikely since most p3s with l/w <1.25 (i.e., those not likely belonging to *S. bachmani*) exhibit moderate or complex crenulation at the tooth surface and/or base (Fig. 4; Appendix Table 2). If *S. nuttalli* was present and common in the local region encompassing Project 23, we would expect proportionally more non-narrow p3s to exhibit simple crenulation. Further, *S. nuttallii* is currently restricted to intermountain regions >100 miles from Los Angeles (Hall and Kelson 1959, Chapman 1975). All specimens with more complex crenulation at the tooth base relative to the occlusal surface are considered juvenile individuals of *S. audubonii*. Excluding suspected juveniles, p3s from Project 23 are, overall, ~9% smaller than extant *S. audubonii* (mean=2.55mm, 2.14mm, and 1.19 for p3 length, width, and l/w respectively; Fig. 4, Appendix Table 2). Size changes between extant (n=30) and fossil (n=25) *S. audubonii* are statistically significant ($t=4.6205$, $df=48.06$, $p<0.001$ for p3 length; $t=4.5672$, $df=51.154$, $p<0.001$ for p3 width).

SYLVILAGUS BACHMANI Waterhouse 1839

Referred specimens—LACMP23-32045, left dentary fragment with p3. The following specimens represent complete left p3s: LACMP23-29229, LACMP23-33861. The following specimens represent complete right p3s: LACMP23-28082, LACMP23-34262, LACMP23-35844, LACMP23-36615.

Remarks—Seven specimens from Project 23 are assigned to *S. bachmani* based on simple p3 crenulation at the occlusal surface and base of the tooth, p3 lengths <3.1 mm, and a mean p3 l/w >1.25 (Table 2, Figs. 4, 5D). Since adult individuals of this species usually exhibit simple crenulation (Table 1; Fig. 4), it is difficult to identify juveniles from surface-base changes in crenulation complexity. However, specimens can be identified as juvenile if the width at the occlusal surface is less than the width at the tooth base (White 1991). Excluding potential juvenile p3s of *S. bachmani* from Project 23, the sample is ~11% smaller than recent *S. bachmani* (mean=2.19mm, 1.71mm, and 1.28 for p3 length, width, and l/w respectively; Fig. 4; Appendix Table 2). Size changes between extant (n=30) and fossil (n=7) *S. bachmani* are statistically significant ($t=2.8861$, $df=8.2077$, $p=0.0198$ for p3 length; $t=4.6124$, $df=12.923$, $p<0.001$ for p3 width).

PALEOECOLOGICAL IMPLICATIONS

Here we present a region-specific protocol for identifying leporid dental remains to genus and species in California and demonstrate its utility and limitations for identifying Project 23 leporid fossils at RLB. Determining the spatial and taxonomic boundaries of comparative specimen pools to use when developing such a protocol, and whether the assumptions and limitations therein are appropriate, is a study-specific decision based, in part, on the spatial and temporal breadth of the unknown specimens in question and their ecology and evolution. Assumptions of relative morphological and geographic range stasis are inherent to many such protocols. In this study, for example, we assume: 1) that intraspecific dental crenulation patterning and morphology of the extant and fossil leporids from Project 23 has not changed substantially in southern California over the last 50,000 years, and 2) that leporid ranges have not shifted during that time to the extent that extralimital species not included in our study, such as *Sylvilagus floridanus*, whose westernmost distribution is currently hundreds of kilometers east of Los Angeles, resided there during the late Pleistocene. The limitations of those assumptions are dependent, in part, on the spatial and morphological breadth of the comparative specimens examined and the spatial and temporal distance between comparative specimens and the unknown specimens of interest. Increasing the spatial and taxonomic/morphological coverage of comparative specimen pools will improve identification fidelity of unknowns (i.e., one can be more certain that all potential taxonomic representatives of unknown specimens are included). However, a trade-off may also occur between the spatial and morphological breadth of comparative sample coverage and specimen identification accuracy, as shown in our classification results of local specimen pools versus local and extralimital specimen pools (Table 2; Fig 4).

Facilitating species-level identifications is imperative for increasing the resolution at which (paleo)ecological questions can be addressed (e.g., how organisms interact with each another and their environment and how taxon-specific habitats or entire ecosystems change over time). Assuming that the assumptions outlined for this protocol are true, we identified two unique leporid species from Project 23 (*S. audubonii* and *S. bachmani*) and observed differences in their relative abundance among Project 23 deposits (Table 3). Radiocarbon dating of Project 23 fossils shows that *S. bachmani* is less abundant in overall younger deposits than older ones (Table 3; Appendix Table 3). Further, *Lepus californicus* is thus far absent from excavated Project 23 deposits that pre-date the Last Glacial Maximum but present in deposits that yield glacial and post-glacial dates within the RLB Hancock Collection (Stock and Harris 1992, O'Keefe et al. 2009). This faunal change may have significant paleoenvironmental implications for Los Angeles since *S. bachmani*, as its common name implies, requires dense brushy habitats while *L. californicus* avoids dense vegetation. The contemporary range of *S. bachmani* is restricted to the Pacific coast of North America from Washington to Baja California and inhabits coastal chaparral and forest biomes with dense brush cover (Chapman 1974). Conversely, extant *L. californicus* occupy coastal chaparral, desert, savannah, and grassland biomes (Best 1996). *Lepus californicus* prefer open, arid habitats—including those with shortgrass, sagebrush, and juniper vegetation—and avoid tall grasses and forests where visibility is reduced (Best 1996). *Sylvilagus audubonii* also occupy coastal chaparral, desert, savannah, and grassland biomes and prefer arid areas with relatively sparse vegetation (Chapman and Willner 1978). In general, individuals of *Sylvilagus* require more vegetation cover than *Lepus* to escape predation since the former taxon usually hides from predators and the latter tends to run (Chapman et al. 1982, Driver and Woiderski 2008). Considering the ecologies of extant members of these species, RLB may have become more sparsely vegetated and possibly more arid towards the Last Glacial Maximum.

Table 3. Number of sampled p3s from Project 23 (n=59) assigned to each California leporid species per deposit. Mean deposit-specific radiocarbon ages are calculated from specimen dates in Appendix Table 3. The percentage of p3s assigned to each species relative to the total number of identifiable p3s recovered from each deposit is listed in parentheses. See Appendix Table 2 for measurements, crenulation patterns, and inferred life stages of individual fossil specimens.

p3 NISPs per Deposit	*L. californicus*	*S. audubonii*	*S. bachmani*
Deposit 1, ~37 ka BP	- (0%)	9 (82%)	2 (18%)
Deposit 13, ~37 ka BP	- (0%)	20 (100%)	- (0%)
Deposit 7B, ~45 ka BP	- (0%)	16 (94%)	1 (6%)
Deposit 14, >45 ka BP	- (0%)	7 (64%)	4 (36%)

In contrast to the smaller sizes observed among recent individuals of *S. floridanus* relative to fossil specimens from Friesenhahn Cave, TX (Pettus 1956), recent *S. audubonii* and *S. bachmani* from southern California are generally larger than fossil specimens from RLB (Fig. 4A). Differences in the directionality of size change among S. *audubonii*/*S. bachmani* and *S. floridanus* could be influenced by several factors including differences in the behavioral ecologies of the focal taxa and/or spatiotemporal differences in the late Quaternary environments and associated selective pressures of south-central Texas and southern California. More extensive research on microvertebrate faunas and floras is needed to reconstruct the late Quaternary environments of Los Angeles and other parts of California through time. However, exploratory inferences such as these and comprehensive paleoecological studies alike benefit from species-level data. We advocate building regional keys for identifying speciose, morphologically variable, or otherwise difficult fossil taxa to improve site-specific paleoecological inferences, so long as the inherent assumptions of doing so are considered appropriate for study-specific systems and objectives.

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APPENDICES

Appendix Table 1. Dental measurements and p3 crenulation observations of all recent leporids sampled in this study. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of juvenile or inferred juvenile specimens are not considered for species identification protocols.

Museum number	Species	Life stage	p3 length	p3 width	p3 l/w ratio	Diastema length	Toothrow length	p3 Crenulation
LACM-3713	*Lepus californicus*	Adult	3.51	2.79	1.26	18.39	16.25	Simple
LACM-3822	*Lepus californicus*	Adult	3.96	3.10	1.28	20.37	17.57	Simple
LACM-6410	*Lepus californicus*	Adult	3.12	2.52	1.24	15.30	15.06	Alternate
LACM-21235	*Lepus californicus*	Adult	3.09	2.75	1.12	17.73	15.73	Simple
LACM-28172	*Lepus californicus*	Adult	3.50	2.87	1.22	19.17	15.31	Simple
LACM-28184	*Lepus californicus*	Adult	3.52	2.83	1.24	19.58	15.46	Moderate
LACM-28233	*Lepus californicus*	Adult	3.73	2.73	1.37	17.90	14.78	Complex
LACM-29047	*Lepus californicus*	Adult	3.52	2.96	1.19	19.27	15.09	Simple
LACM-29048	*Lepus californicus*	Adult	3.49	2.99	1.17	18.58	16.00	Alternate
LACM-29049	*Lepus californicus*	Adult	3.57	2.90	1.23	19.41	15.13	Moderate
LACM-30729	*Lepus californicus*	Adult	3.41	2.64	1.29	21.41	16.07	Alternate
LACM-30802	*Lepus californicus*	Adult	3.47	3.02	1.15	20.29	16.63	Simple
LACM-49513	*Lepus californicus*	Adult	3.12	2.52	1.24	15.30	15.31	Simple
LACM-49514	*Lepus californicus*	Adult	3.53	2.92	1.21	19.78	16.17	Simple
LACM-49515	*Lepus californicus*	Juvenile?	2.52	2.03	1.24	NA	12.63	Simple
LACM-49519	*Lepus californicus*	Adult	3.57	3.01	1.19	20.41	16.67	Simple
LACM-67485	*Lepus californicus*	Adult	3.45	2.84	1.21	18.16	15.54	Simple
LACM-84807	*Lepus californicus*	Adult	3.52	2.86	1.23	20.99	16.25	Simple
LACM-87443	*Lepus californicus*	Adult	3.35	2.71	1.24	19.13	15.70	Alternate
LACM-88149	*Lepus californicus*	Adult	3.15	2.55	1.24	NA	16.17	Simple
LACM-90240	*Lepus californicus*	Adult	3.65	2.89	1.26	20.72	16.75	Simple
LACM-95608	*Lepus californicus*	Adult	3.59	2.64	1.36	20.00	16.59	Simple
LACM-R6	*Lepus californicus*	Adult	3.23	3.13	1.03	25.48	19.19	Alternate
MVZ-1900	*Lepus californicus*	Adult	3.23	2.74	1.18	18.64	16.31	Simple
MVZ-7166	*Lepus californicus*	Adult	3.24	3.19	1.02	20.48	16.48	Alternate
MVZ-10683	*Lepus californicus*	Adult	3.63	3.13	1.16	20.77	16.99	Alternate
MVZ-10684	*Lepus californicus*	Adult	3.92	3.33	1.18	19.73	17.33	Simple
MVZ-24147	*Lepus californicus*	Adult	3.52	3.11	1.13	19.68	17.21	Simple
MVZ-27627	*Lepus californicus*	Adult	3.68	3.17	1.16	20.82	16.59	Alternate
MVZ-29158	*Lepus californicus*	Adult	3.65	3.39	1.08	20.54	18.25	Alternate
MVZ-29160	*Lepus californicus*	Adult	3.25	3.03	1.07	21.65	15.95	Alternate
MCZBOM-183	*Lepus townsendii*	Adult	3.25	2.90	1.12	18.83	16.06	Simple

Appendix Table 1 (cont.). Dental measurements and p3 crenulation observations of all recent leporids sampled in this study. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of juvenile or inferred juvenile specimens are not considered for species identification protocols.

Museum number	Species	Life stage	p3 length	p3 width	p3 l/w ratio	Diastema length	Toothrow length	p3 Crenulation
MCZBOM-184	*Lepus townsendii*	Adult	3.39	2.85	1.19	19.02	16.83	Simple
MCZBOM-185	*Lepus townsendii*	Adult	3.29	3.14	1.05	19.65	16.48	Alternate
MCZBOM-186	*Lepus townsendii*	Adult	3.37	2.79	1.21	20.31	16.18	Simple
MCZBOM-221	*Lepus townsendii*	Adult	3.38	2.92	1.16	19.92	16.69	Simple
MCZBOM-222	*Lepus townsendii*	Adult	3.63	3.19	1.14	19.17	18.16	Simple
MCZBOM-223	*Lepus townsendii*	Adult	3.65	3.32	1.10	19.60	17.93	Simple
MCZBOM-224	*Lepus townsendii*	Adult	3.48	3.16	1.10	19.84	17.71	Simple
MCZBOM-225	*Lepus townsendii*	Adult	3.65	3.04	1.20	19.77	17.46	Simple
MCZBOM-964	*Lepus townsendii*	Adult	3.44	3.09	1.11	17.72	17.36	Simple
MVZ-13759	*Lepus americanus*	Adult	2.88	2.48	1.16	14.64	13.61	Simple
MVZ-20901	*Lepus americanus*	Adult	2.63	2.32	1.13	14.83	13.89	Simple
MVZ-23649	*Lepus americanus*	Adult	2.49	2.37	1.05	15.15	13.26	Simple
MVZ-23896	*Lepus americanus*	Adult	2.40	2.40	1.00	14.35	13.00	Alternate
MVZ-31899	*Lepus americanus*	Adult	2.90	2.60	1.12	14.64	13.57	Alternate
MVZ-32186	*Lepus americanus*	Adult	2.77	2.45	1.13	13.62	13.01	Simple
MVZ-33081	*Lepus americanus*	Adult	2.47	2.32	1.06	14.42	12.19	Simple
MVZ-36577	*Lepus americanus*	Adult	2.44	2.35	1.04	14.59	12.76	Simple
MVZ-119485	*Lepus americanus*	Adult	2.50	2.44	1.02	13.49	12.64	Simple
MVZ-165872	*Lepus americanus*	Adult	2.66	2.37	1.12	14.40	13.18	Simple
LACM-158	*Sylvilagus audubonii*	Adult	3.10	2.66	1.17	15.30	13.90	Moderate
LACM-254	*Sylvilagus audubonii*	Juvenile?	1.90	1.57	1.21	8.67	9.06	Simple
LACM-446	*Sylvilagus audubonii*	Adult	2.66	2.11	1.26	13.29	11.81	Moderate
LACM-653	*Sylvilagus audubonii*	Adult	2.79	2.10	1.33	13.23	12.02	Complex
LACM-916	*Sylvilagus audubonii*	Adult	2.96	2.51	1.18	12.88	12.93	Complex
LACM-3811	*Sylvilagus audubonii*	Adult	2.98	2.81	1.06	14.44	13.40	Moderate
LACM-4154	*Sylvilagus audubonii*	Juvenile	NA	NA	NA	NA	NA	Simple
LACM-5479	*Sylvilagus audubonii*	Subadult?	2.91	2.51	1.16	14.92	13.43	Moderate; Complex
LACM-7986	*Sylvilagus audubonii*	Adult	2.80	2.26	1.24	14.04	12.30	Moderate
LACM-90208	*Sylvilagus audubonii*	Adult	2.85	2.32	1.23	14.21	13.04	Complex
LACM-20731	*Sylvilagus audubonii*	Subadult?	2.84	2.42	1.17	15.12	13.54	Simple; Complex
LACM-21803	*Sylvilagus audubonii*	Adult	2.85	2.30	1.24	15.21	12.55	Complex
LACM-29050	*Sylvilagus audubonii*	Adult	2.93	2.31	1.27	14.19	12.64	Complex
LACM-32961	*Sylvilagus audubonii*	Adult	3.07	2.39	1.28	14.36	12.62	Complex
LACM-44966	*Sylvilagus audubonii*	Adult	2.86	2.18	1.31	14.48	12.45	Complex
LACM-44967	*Sylvilagus audubonii*	Adult	3.05	2.39	1.28	16.51	13.67	Moderate
LACM-49525	*Sylvilagus audubonii*	Adult	3.19	2.51	1.27	15.23	14.13	Moderate
LACM-49526	*Sylvilagus audubonii*	Adult	2.54	2.14	1.19	14.30	12.08	Complex
LACM-53876	*Sylvilagus audubonii*	Adult	2.92	2.31	1.26	13.04	12.96	Simple

Appendix Table 1 (cont.). Dental measurements and p3 crenulation observations of all recent leporids sampled in this study. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of juvenile or inferred juvenile specimens are not considered for species identification protocols.

Museum number	Species	Life stage	p3 lengt	p3 width	p3 l/w ratio	Diastema length	Toothrow length	p3 Crenulation
LACM-53879	*Sylvilagus audubonii*	Adult	3.05	2.29	1.33	12.98	12.57	Moderate
LACM-73039	*Sylvilagus audubonii*	Adult	2.91	2.18	1.33	13.39	12.63	Complex
LACM-85733	*Sylvilagus audubonii*	Adult	2.91	2.23	1.30	NA	12.52	Complex
LACM-90015	*Sylvilagus audubonii*	Adult	3.05	2.26	1.35	NA	13.12	Moderate
LACM-90207	*Sylvilagus audubonii*	Adult	2.93	2.37	1.24	15.38	12.91	Complex
LACM-97340	*Sylvilagus audubonii*	Juvenile	NA	NA	NA	NA	NA	Simple; Complex
MVZ-5318	*Sylvilagus audubonii*	Juvenile	NA	NA	NA	NA	NA	Simple
MVZ-6385	*Sylvilagus audubonii*	Adult	2.30	1.99	1.16	12.07	11.47	Complex
MVZ-7025	*Sylvilagus audubonii*	Adult	2.58	2.39	1.08	15.21	12.39	Complex
MVZ-7168	*Sylvilagus audubonii*	Adult	2.62	2.23	1.17	13.29	11.87	Moderate
MVZ-7170	*Sylvilagus audubonii*	Adult	2.52	2.32	1.09	11.94	12.18	Complex
MVZ-7171	*Sylvilagus audubonii*	Juvenile?	NA	NA	NA	NA	NA	Simple
MVZ-10673	*Sylvilagus audubonii*	Adult	2.72	2.58	1.05	14.11	12.45	Complex
MVZ-28714	*Sylvilagus audubonii*	Juvenile	NA	NA	NA	NA	NA	Simple
MVZ-107653	*Sylvilagus audubonii*	Adult	2.65	2.60	1.02	13.66	12.68	Complex
MVZ-107654	*Sylvilagus audubonii*	Adult	2.65	2.50	1.06	15.07	12.98	Complex
MVZ-107655	*Sylvilagus audubonii*	Adult	2.48	2.38	1.04	14.37	12.17	Complex
LACM-192	*Sylvilagus bachmani*	Adult	2.75	1.96	1.40	12.55	12.95	Simple
LACM-193	*Sylvilagus bachmani*	Adult	2.51	2.03	1.24	NA	11.15	Simple
LACM-252	*Sylvilagus bachmani*	Adult	2.63	1.83	1.44	12.75	12.09	Simple
LACM-364	*Sylvilagus bachmani*	Adult	2.47	1.78	1.39	11.82	11.21	Simple
LACM-6403	*Sylvilagus bachmani*	Adult	2.53	1.82	1.39	11.46	11.20	Simple
LACM-6406	*Sylvilagus bachmani*	Adult	2.19	1.69	1.30	12.03	11.41	Simple
LACM-6407	*Sylvilagus bachmani*	Adult	2.20	1.68	1.31	10.83	10.11	Simple
LACM-6408	*Sylvilagus bachmani*	Adult	2.80	2.12	1.32	12.19	11.89	Simple
LACM-7314	*Sylvilagus bachmani*	Adult	2.54	2.09	1.22	11.61	11.68	Simple
LACM-21374	*Sylvilagus bachmani*	Adult	2.37	1.90	1.25	10.86	11.31	Simple
LACM-21375	*Sylvilagus bachmani*	Adult	2.45	1.86	1.32	11.97	11.03	Simple
LACM-21376	*Sylvilagus bachmani*	Adult	2.14	1.75	1.22	10.34	10.35	Simple
LACM-21377	*Sylvilagus bachmani*	Adult	2.33	1.81	1.29	10.67	10.86	Moderate
LACM-30032	*Sylvilagus bachmani*	Adult	2.78	2.26	1.23	14.20	13.29	Complex
LACM-30780	*Sylvilagus bachmani*	Adult	2.50	1.94	1.29	12.80	11.57	Simple
LACM-49529	*Sylvilagus bachmani*	Adult	2.52	1.82	1.38	11.97	11.67	Moderate
LACM-49531	*Sylvilagus bachmani*	Adult	2.62	2.14	1.22	13.02	12.05	Simple
LACM-91507	*Sylvilagus bachmani*	Adult	2.51	1.93	1.30	12.78	11.64	Simple
MVZ-2699	*Sylvilagus bachmani*	Adult	2.30	1.78	1.29	11.40	10.95	Simple
MVZ-2700	*Sylvilagus bachmani*	Adult	2.16	1.80	1.20	12.92	11.41	Simple
MVZ-3888	*Sylvilagus bachmani*	Adult	2.35	2.04	1.15	13.76	12.5	Simple
MVZ-3889	*Sylvilagus bachmani*	Adult	2.47	1.99	1.24	13.59	11.26	Simple

Appendix Table 1 (cont.). Dental measurements and p3 crenulation observations of all recent leporids sampled in this study. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of juvenile or inferred juvenile specimens are not considered for species identification protocols.

Museum number	Species	Life stage	p3 length	p3 width	p3 l/w ratio	Diastema length	Toothrow length	p3 Crenulation
MVZ-3891	*Sylvilagus bachmani*	Adult	2.09	1.79	1.17	11.71	10.82	Simple
MVZ-5315	*Sylvilagus bachmani*	Adult	2.39	1.96	1.22	11.90	12.27	Simple
MVZ-6364	*Sylvilagus bachmani*	Adult	2.36	2.07	1.14	12.85	11.76	Simple
MVZ-24459	*Sylvilagus bachmani*	Adult	2.26	1.90	1.19	11.80	10.91	Simple
MVZ-29187	*Sylvilagus bachmani*	Adult	2.34	1.85	1.26	11.61	11.43	Simple
MVZ-29188	*Sylvilagus bachmani*	Adult	2.64	1.99	1.33	12.32	12.39	Simple
MVZ-29189	*Sylvilagus bachmani*	Adult	2.57	2.15	1.20	12.29	11.89	Simple
MVZ-182871	*Sylvilagus bachmani*	Adult	2.51	2.06	1.22	12.84	12.38	Complex
MCZBOM-187	*Sylvilagus nuttallii*	Juvenile?	2.16	1.75	1.23	11.45	10.82	Simple
MCZBOM-188	*Sylvilagus nuttallii*	Adult	2.38	1.87	1.27	12.55	11.86	Simple
MCZBOM-189	*Sylvilagus nuttallii*	Adult	2.80	2.47	1.13	14.66	13.35	Simple
MCZ-7678	*Sylvilagus nuttallii*	Adult	2.47	2.24	1.10	14.43	12.51	Simple
MCZ-7747	*Sylvilagus nuttallii*	Adult	2.57	2.25	1.14	12.58	12.09	Simple
MCZBANGS-9347	*Sylvilagus nuttallii*	Adult	2.40	1.96	1.22	12.24	11.33	Complex
MCZBANGS-9348	*Sylvilagus nuttallii*	Juvenile?	2.13	1.67	1.28	10.71	10.59	Complex
MCZBANGS-9349	*Sylvilagus nuttallii*	Adult	2.30	1.88	1.22	12.15	11.63	Complex
MCZBANGS-9350	*Sylvilagus nuttallii*	Adult	2.20	1.68	1.31	11.29	10.21	Complex
MCZ-10517	*Sylvilagus nuttallii*	Adult	2.98	2.45	1.22	14.40	13.32	Complex
MVZ-11315	*Sylvilagus nuttallii*	Adult	2.32	1.94	1.20	11.90	11.11	Simple
MVZ-66012	*Sylvilagus nuttallii*	Adult	2.60	2.14	1.21	13.50	11.98	Simple
MVZ-36347	*Brachylagus idahoensis*	Adult	1.64	1.52	1.08	10.50	8.93	Simple
MVZ-36348	*Brachylagus idahoensis*	Adult	1.69	1.63	1.04	10.55	9.40	Simple
MVZ-36349	*Brachylagus idahoensis*	Adult	1.70	1.60	1.06	10.59	9.05	Simple
MVZ-36350	*Brachylagus idahoensis*	Adult	1.63	1.47	1.11	10.41	9.24	Simple
MVZ-36351	*Brachylagus idahoensis*	Adult	1.81	1.53	1.18	11.38	9.28	Simple
MVZ-36352	*Brachylagus idahoensis*	Adult	1.73	1.57	1.10	10.30	9.09	Simple

Appendix Table 2. Dental measurements and p3 crenulation observations of all fossil leporids sampled from Project 23 deposits at Rancho La Brea. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of inferred juveniles are not considered for estimating mean fossil species sizes. * indicates specimens included in t-test statistics for size comparison with extant specimens.

LACMP23 Number	Deposit	Element	Assigned Species	Assigned Life Stage	p3 length	p3 width	l/w ratio	p3 Crenulation
28082*	1	rt p3	*Sylvilagus bachmani*	Adult	2.21	1.73	1.28	Simple
28084*	1	lt p3	*Sylvilagus audubonii*	Adult	2.48	1.93	1.28	Moderate
28105	1	partial rt p3	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex?
28266	1	partial lt p3	*Sylvilagus audubonii*	Juvenile	NA	1.75	NA	Simple; Complex
28341	1	rt p3	*Sylvilagus audubonii*	Juvenile	1.97	1.67	1.18	Simple; Complex
28519	1	rt p3	*Sylvilagus audubonii*	Juvenile	2.16	1.73	1.25	Moderate
28555*	1	lt p3	*Sylvilagus audubonii*	Adult	2.32	2.04	1.14	Complex
28556	1	rt p3	*Sylvilagus audubonii*	Juvenile	1.74	1.36	1.28	Simple; Moderate
28661*	1	lt p3	*Sylvilagus audubonii*	Subadult?	2.42	1.94	1.25	Moderate; Complex
28858	1	rt p3	*Sylvilagus audubonii*	Juvenile	2.26	1.77	1.28	Simple; Moderate
29229*	1	lt p3	*Sylvilagus bachmani*	Adult	2.16	1.65	1.31	Simple
31781	14	lt p3	*Sylvilagus audubonii*	Juvenile	1.86	1.70	1.09	Simple; Complex
31782	14	partial lt p3	*Sylvilagus audubonii*	Juvenile	NA	1.93	NA	Simple; Moderate
32045*	14	lt dentary frag. with p3	*Sylvilagus bachmani*	Adult	2.60	1.93	1.35	Simple
32047*	14	rt dentary frag. with p3-m1	*Sylvilagus audubonii*	Adult	2.67	2.19	1.22	Moderate
33861*	14	lt p3	*Sylvilagus bachmani*	Adult	2.28	1.65	1.38	Simple
33962	14	rt p3	*Sylvilagus audubonii*	Juvenile	2.01	1.62	1.24	Simple; Moderate
34117*	14	rt p3	*Sylvilagus audubonii*	Subadult?	2.27	2.01	1.13	Moderate; Complex
34259	14	partial lt p3	*Sylvilagus audubonii*	Juvenile	2.07	1.64	1.26	Complex
34260	14	partial lt p3	*Sylvilagus audubonii*	Juvenile	NA	1.55	NA	Simple; Complex
34262*	14	rt p3	*Sylvilagus bachmani*	Adult	2.11	1.68	1.26	Simple
35608*	7B	lt p3	*Sylvilagus audubonii*	Subadult?	2.64	2.23	1.18	Moderate; Complex
35614*	7B	rt p3	*Sylvilagus audubonii*	Adult	2.66	NA	NA	Complex
35618	7B	rt p3 frag.	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
35619*	7B	partial rt p3	*Sylvilagus audubonii*	Adult	2.58	2.16	1.19	Complex
35645	7B	rt p3 frag.	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
35696*	7B	rt p3	*Sylvilagus audubonii*	Adult	2.63	2.37	1.11	Complex
35763*	7B	lt p3	*Sylvilagus audubonii*	Adult	2.31	2.02	1.14	Complex
35771	7B	lt p3 frag.	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
35836*	7B	rt p3	*Sylvilagus audubonii*	Adult	3.11	2.47	1.26	Complex
35839*	7B	rt p3	*Sylvilagus audubonii*	Adult	2.78	2.35	1.18	Complex
35840*	7B	rt p3	*Sylvilagus audubonii*	Adult	2.43	2.09	1.16	Complex
35844*	7B	rt p3	*Sylvilagus bachmani*	Adult	1.93	1.66	1.16	Simple
35847*	7B	lt p3	*Sylvilagus audubonii*	Adult	2.48	2.17	1.14	Complex
35881	7B	rt p3	*Sylvilagus audubonii*	Juvenile	2.12	1.82	1.16	Simple; Complex
35883*	7B	rt p3	*Sylvilagus audubonii*	Adult	2.75	2.35	1.17	Complex

Appendix Table 2 (cont.). Dental measurements and p3 crenulation observations of all fossil leporids sampled from Project 23 deposits at Rancho La Brea. Specimens with two crenulation patterns (X; X) exhibit discrepancies between the tooth surface and base respectively. All measurements are in millimeters and measurements of inferred juveniles are not considered for estimating mean fossil species sizes. * indicates specimens included in t-test statistics for size comparison with extant specimens.

LACMP23 Number	Deposit	Element	Assigned Species	Assigned Life Stage	p3 length	p3 width	l/w ratio	p3 Crenulation
35885	7B	lt p3	*Sylvilagus audubonii*	Juvenile	1.98	1.72	1.15	Simple; Complex
35937	7B	lt p3	*Sylvilagus audubonii*	Juvenile	1.80	1.50	1.20	Simple; Complex
36615*	14	rt p3	*Sylvilagus bachmani*	Adult	2.01	1.69	1.19	Simple
39811*	13	lt dentary frag. with p3, p4, m2	*Sylvilagus audubonii*	Adult	2.59	2.04	1.27	Complex
39819*	13	rt dentary frag. with p3-m1	*Sylvilagus audubonii*	Adult	3.01	2.40	1.25	Complex
39820	13	rt dentary frag. w/ partial p3-m2	*Sylvilagus audubonii*	Adult	2.56	NA	NA	Complex
39874*	13	rt p3	*Sylvilagus audubonii*	Subadult?	2.22	1.89	1.18	Moderate; Complex
39929	13	rt p3 frag.	*Sylvilagus audubonii*	Unknown	NA	NA	NA	Complex?
40039	13	partial lt p3	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
40110	13	partial rt p3	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
40166*	13	rt p3	*Sylvilagus audubonii*	Adult	2.61	2.19	1.19	Complex
40167	13	lt p3	*Sylvilagus audubonii*	Juvenile/ Subadult	2.12	1.72	1.23	Moderate; Complex
40168	13	rt p3 frag.	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
40209*	13	lt p3	*Sylvilagus audubonii*	Adult	2.63	2.19	1.20	Complex
40210*	13	rt p3	*Sylvilagus audubonii*	Adult	2.49	2.05	1.21	Complex
40211*	13	rt p3	*Sylvilagus audubonii*	Adult	2.44	2.13	1.15	Complex
40212	13	worn rt p3 frag	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex?
40284	13	worn lt p3	*Sylvilagus audubonii*	Adult	3.03	NA	NA	Complex
40285*	13	worn lt p3	*Sylvilagus audubonii*	Adult	2.34	2.06	1.14	Moderate
40286*	13	lt p3	*Sylvilagus audubonii*	Adult	2.65	2.15	1.23	Moderate
40287*	13	lt p3	*Sylvilagus audubonii*	Adult	2.26	1.89	1.20	Complex
40288	13	lt p3 frag.	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex
40291	13	rt p3 frag	*Sylvilagus audubonii*	Adult	NA	NA	NA	Complex?

Appendix Table 3. Carbon-14 data from leporid specimens sampled from Project 23 Deposits 1, 7B, 13, and 14. All specimens were analyzed at the University of California Irvine Keck Carbon Cycle AMS Laboratory (UCIAMS).

UCIAMS Number	LACMP23 Number	Deposit	Element	C/N (atomic)	^{14}C age (years BP)	^{14}C age error
191095	5233	1	rt dentary frag. w/ p3-m1	3.33	35750	610
191096	18270	1	rt dentary frag. w/ p3-m2	3.48	35440	580
191097	22009	1	rt dentary frag. w/ p3-m3	3.60	35150	580
191098	25476	1	rt anterior dentary w/ p3-m2	3.38	36050	630
191099	28903	1	rt dentary frag. w/ p3-p4	3.34	33830	480
191100	30238	1	rt anterior dentary w/ p3-m2	3.59	35780	600
191101	31269	1	rt anterior dentary w/ p3-m2	3.26	46200	2200
191102	31423	1	rt anterior dentary	3.46	35420	580
198294	28902	1	lt partial dentary w/ p3-m2	3.45	39700	810
216783	35774	7B	rt maxilla frag..	3.34	42600	1400
216784	36332	7B	lt distal humerus	3.24	41500	1200
216785	36336	7B	rt anterior dentary w/ p4-m1	3.32	50200	3500
217079	36331	7B	lt anterior dentary frag.	3.31	46200	2400
223495	35541	13	lt posterior dentary w/p4-m2	3.31	39220	460
223497	36693	13	lt dentary frag. w/p4-m2	3.46	39240	670
223499	36896	13	lt dentary frag. w/ m1-m2	3.33	33590	340
223502	36989	13	lt anterior dentary w/p4	3.48	44000	1200
223503	37612	13	lt dentary w/ p4-m2	3.40	46200	1600
223505	39811	13	lt anterior dentary frag. w/ p3, p4, m2	3.39	33260	320
223506	39812	13	lt posterior dentary frag. w/ m1-m2	3.35	36260	470
223507	39818	13	lt posterior dentary frag.	3.49	31230	270
223508	39822	13	lt dentary frag. w/ p4-m2	3.36	31980	280
191103	31033	14	rt anterior dentary w/ p3-m2	3.47	>47800	NA
191104	31036	14	rt anterior dentary w/ p3-m1	5.56	>49900	NA
191105	31056	14	rt anterior dentary w/ p3-m2	4.04	>49900	NA
191242	31031	14	rt anterior dentary w/ p3-m2	3.51	>50800	NA
223516	40637	14	rt humerus	3.30	26780	160