

Research Article

A geometric morphometric approach to identifying recent and fossil woodrat molars with remarks on Late Pleistocene *Neotoma macrotis* from Rancho La Brea

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Abstract

Woodrats of the genus *Neotoma* are an important study system for ecological and paleoecological research. However, paleontological studies are often hindered by the difficulty of identifying woodrat remains to species. We address this limitation by using 2D landmark-based geometric morphometrics to classify 199 lower first molars (m1s) of five extant western North American *Neotoma* species (*N. albigula*, *N. cinerea*, *N. fuscipes*, *N. lepida*, and *N. macrotis*) collected throughout California. We then use discriminant analysis of principal components (DAPC) models to identify Late Pleistocene fossils of unknown species from the Rancho La Brea Tar Pits in Los Angeles, California. DAPC correctly identifies ~85–90% of extant individuals to species, with most misclassifications occurring between sister taxa *N. fuscipes* and *N. macrotis*. Most fossil m1s are classified as *N. macrotis* by DAPC, which may be the first confirmation of *N. macrotis* in the fossil record. We show that landmark-based geometric morphometric analyses are generally effective at differentiating m1s of extant *Neotoma* species in California and they are an auspicious method for unknown fossil identification. Further applications of this method across a broader range of geographic locations and species will better contextualize its utility.

Keywords: California; DAPC; landmarks; paleontology; Quaternary; rodents; species classification; tar pit; tooth identification

Introduction

Neotoma, commonly referred to as woodrat or packrat, is a North American cricetid rodent genus distributed from southern Mexico to northern Canada (Cordero and Epps, 2012; Soberón and Martínez-Gordillo, 2012; Coyner et al., 2015). Members of this genus are considered keystone species because their multi-chambered dens (middens) create nutrient-rich microhabitats that maintain local biodiversity (Matocq, 2009; Whitford and Steinberger, 2010). These middens are built with local plant and animal remains, and are consolidated with crystalized urine (Smith et al., 1995, 2009). Species of *Neotoma* are important paleoecological indicators because their middens, and the organic materials within, often fossilize in arid regions, thus preserving aspects of biotic communities over millennia (Cordero and Epps, 2012; Smith et al., 1995). In addition, because the intergenerational body size of some *Neotoma* species is highly responsive to long-term changes in ambient temperature, woodrats have been used as a ‘paleothermometer’ (Smith and Betancourt, 1998, 2003). *Neotoma* remains are therefore coveted for (paleo)ecological research and for studies

of adaptive responses to environmental change across space and time (Smith et al., 1995, 2009; Lyman and O’Brien, 2005; Brooke McEachern et al., 2006; Smith and Betancourt, 2006; Cordero and Epps, 2012; Becklin et al., 2024).

Paleoecological studies of *Neotoma* have largely focused on fossilized middens and fecal pellets (e.g., Smith et al., 1995, 2009; Smith and Betancourt, 2003; Mychajliw et al., 2020), in part due to the difficulty of identifying other remains such as teeth and bones to species using qualitative character observations and linear measurements (Harris, 1984; Betancourt et al., 1990; Zakrzewski, 1993; Repenning, 2004). However, midden preservation is skewed geologically towards younger localities and environmentally towards arid localities (Smith and Betancourt, 2006; Smith et al., 2009), which limits the temporal and geographic scope of research compared to skeletal elements (Betancourt et al., 1990; Zakrzewski, 1993). Species-level identification of *Neotoma* remains is important because different species exhibit different ecological niches, denning behaviors, habitat preferences, and climatic tolerances (Finley Jr., 1990; Lyman and O’Brien, 2005; Smith et al., 2009; Soberón and Martínez-Gordillo, 2012). Erroneous paleoecological interpretations can therefore occur if remains are misidentified.

Modern quantitative methods may help overcome the challenges of identifying *Neotoma* skeletal remains to species. Indeed, advancements in geometric morphometrics and complementary multivariate analyses over the last few decades have produced powerful toolkits for quantifying shape and shape change among

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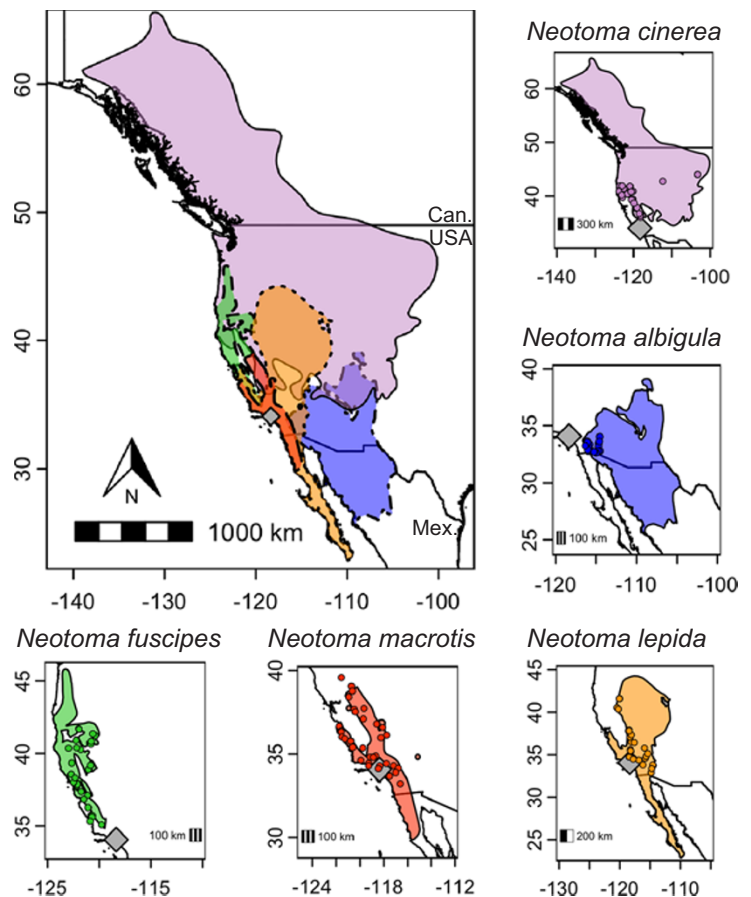


Figure 1. Distribution maps of the five extant *Neotoma* species examined here. The overview map shows the full extent of—and overlap among—each species range. Individual species maps indicate the points of sampling locations of individual specimens included in this study. Rancho La Brea, the locality where fossil *Neotoma* specimens were collected, is marked by a gray diamond on each map. Species range data obtained from (Patterson et al., 2007).

biological subjects in a variety of systems (e.g., Zelditch et al., 2004; Webster and Sheets, 2010; Adams et al., 2013; Baken et al., 2021; Mitteroecker and Schaefer, 2022). These techniques have made differentiating closely related, speciose, and morphologically similar species more feasible (e.g., Martínez and Di Cola, 2011; Jansky et al., 2016; Changbunjong et al., 2021; Wyatt et al., 2021; Alhajeri, 2025). Geometric morphometric analyses are less subjective than qualitative character observations and offer several advantages over traditional linear morphometrics, including the ability to partition object shape from size and capture spatial distributions of shape change (Zelditch et al., 2004). This method allows entire shape configurations to be visualized and analyzed collectively and is therefore appropriate for quantifying complex morphological conditions such as the spatial relationships between the lophs and folds of *Neotoma* teeth (Zakrzewski, 1993).

Here we apply a relatively simple landmark configuration to individual teeth that are more frequently preserved in fossil assemblages than complete elements (Harris, 1984; Repenning, 2004), thus broadening its utility across paleontological study systems. Specifically, we quantify shape variation in the lower first molar (m1) of five extant western North American species and use these data to identify fossil *Neotoma* m1s from Rancho La Brea (RLB), a near-coastal late Quaternary Lagerstätte in Hancock Park, Los Angeles, California (Fig. 1). Over millennia, oil-infiltrated sediments at RLB produced surficial asphalt seeps, which led to the entrapment and preservation of millions of fossil organisms representing over 600 taxa, including *Neotoma* (Dice, 1925; Stock and Harris, 1992; Holden et al., 2017; Mychajliw et al., 2020).

A recent study of *Neotoma* tooth morphology found that 2D shape outlines of upper first molars were largely unreliable for

classifying species (Tomé et al., 2020). Our analysis of discrete m1 landmarks could be complementary, however, because lower first cheek teeth often vary among closely related small mammal species and tend to be the most useful teeth for species-level identification (e.g., Thaler, 1980; Dalquest and Stangl Jr., 1983; Harris, 1984; Dalquest et al., 1989; Wallace, 2006). In addition, analysis of discrete landmarks may be advantageous over shape outlines because landmarks can capture shape disparity in homologous structures of the tooth while 2D outlines capture shape of the occlusal periphery, which can be substantially affected by ontogeny and wear (Repenning, 2004; Tomé et al., 2020). This study addresses the question “Can 2D landmark analysis of lower first molars differentiate extant *Neotoma* species and identify unknown fossils?”

Methods

Study system

We examined five western North American *Neotoma* species currently present in California: *N. albigula* (white-throated woodrat), *N. cinerea* (bushy-tailed woodrat), *N. fuscipes* (dusky-footed woodrat), *N. lepida* (desert woodrat), and *N. macrotis* (big-eared woodrat). The *N. lepida* species complex has undergone relatively recent taxonomic revisions (Patton et al., 2007; Bradley et al., 2022), and we did not attempt to morphologically differentiate among members of that complex in this study, instead we used *N. lepida* as a representative species. Collectively, these five representative species occupy broad geographic distributions and habitats ranging from boreal forest to desert (Smith et al., 2009). We sampled

right m1s from 39 individuals of *N. cinerea* and 40 individuals of all other species ($n = 199$) collected in California between 1904 and 2015 (Fig. 1, Supplementary Table 1) from the University of California Museum of Vertebrate Zoology (MVZ). To examine morphological variation by geographic distance within species, an additional 13 *N. cinerea* were sampled from eastern Idaho and western South Dakota at MVZ and the South Dakota School of Mines and Technology Museum of Geology (SDSM). Populations from western South Dakota occur near the easternmost extent of the species' range, >1,300 miles northeast of California *N. cinerea* (Fig. 1).

We also sampled 16 fossilized left and right m1s from four Project 23 (P23) Deposits (1, 7B, 13, and 14) at RLB (Fig. 1, Supplementary Table 1). Project 23 is the collective name for sixteen fossiliferous asphalt deposits discovered in 2006 during construction of a parking structure adjacent to RLB (Fuller et al., 2014; Holden et al., 2017). These deposits were salvaged in 23 large wooden crates that are now housed and excavated in Hancock Park. P23 deposits provide new opportunities to acquire and study fossils of organisms from lower trophic levels such as small mammals, invertebrates, and plants that were not prioritized when RLB's historic deposits were excavated in the early twentieth century (Stock and Harris, 1992; Holden et al., 2017; Fox et al., 2019; Mychajliw et al., 2020). P23 fossils are Late Pleistocene and radiocarbon dates obtained thus far range from >50,000 to approximately 26,000 ^{14}C yr BP in age (Fuller et al., 2014, 2020; Holden et al., 2017; Fox et al., 2023). *Neotoma* fossils are uncommon at RLB (Dice, 1925; Fox, 2020) and this m1 sample exhausts what was available from those deposits at the time of sampling.

Due to the geographic and temporal positions of the RLB faunas, it is unlikely that P23 *Neotoma* fossils are from a different species than the five extant species/species complexes examined here. Therefore, comparison of fossil molars with these extant California species is appropriate. By doing this, however, we assume that (1) geographic ranges of *Neotoma* have not shifted over the last 50,000 years to the extent that species currently residing hundreds of miles from Los Angeles (e.g., *N. mexicana*) were present there in the past and (2) that intraspecific tooth morphology has not changed more than interspecific tooth morphology in that time. The former assumption is made under the rationale that animals with the ability to adapt in place and undergo body size or other changes in response to climate change, including *Neotoma* (Smith et al., 1995), will likely do so rather than undergo drastic, long-distance range shifts (Lyons, 2003). However, if that assumption is incorrect and the RLB fossils represent a species not included in our reference dataset, morphological mismatches should be detectable between fossils and all extant species sampled.

Data acquisition and preparation

We photographed recent and fossil *Neotoma* teeth and dentaries using Dino-Lite Edge AM4815ZTL and Dino-Lite Edge Plus AM4917MZT digital microscopes. The orientation of the occlusal surface of each specimen and its distance from the camera lens was standardized to the extent possible to mitigate specimen presentation and imaging error (Arnqvist and Mårtensson, 1998; Fruciano, 2016; Fox et al., 2020). No sampling filters (e.g., by age, sex, or tooth wear stage) were implemented aside from omitting very young specimens with unerupted or partially erupted dentition. However, filtered data subsets were later created to evaluate wear stage effects on m1 morphology and species classification. Image sets of recent and fossil specimens were assembled in TpsUtil 32

(Rohlf, 2018a) and digitized in TpsDig 2.32 (Rohlf, 2018b) by author NSF. Right m1s were landmarked when present. If right m1s were not available, images of left m1s were flipped to imitate right dentition prior to landmark digitization.

Fourteen landmarks were digitized along the m1 occlusal surface of each specimen. There is no unanimously accepted dental terminology for *Neotoma* (see Zakrzewski, 1993; Repenning, 2004; Martin and Zakrzewski, 2019). Therefore, our landmark definitions follow the most recent terminology of Martin and Zakrzewski (2019) for m1 conids, lophids, and flexids/reentrant folds (see Table 1 and Fig. 2 for landmark definitions and placement, respectively). We mainly used type 1 and type 2 landmarks (Bookstein, 1997); however, some type 3 landmarks were included to capture the morphology of the woodrat tooth periphery (Fig. 2). One landmark (landmark 14) also varied in type among specimens depending on wear stage and/or species (Fig. 2). For this landmark, different definitions are indicated depending on which condition occurs (Table 1).

Each recent specimen from California was digitized twice by author NSF with several weeks between sessions to quantify measurement error (ME), which can affect biological signals within geometric morphometric datasets (Arnqvist and Mårtensson, 1998; Fruciano, 2016; Fox et al., 2020; Collyer and Adams, 2024a). All landmark datasets were superimposed via Generalized Procrustes analysis (GPA) using the 'gpagen' function in the R package geomorph v.4.0.7 (Adams et al., 2024) before performing other analyses. Generalized Procrustes analysis translates all specimens to unit centroid size and optimally rotates them along a common coordinate system using a generalized least-squares algorithm to standardize specimen rotation, orientation, and scale (Rohlf and Slice, 1990; Adams et al., 2024).

Measurement error

Previous research has shown that artificial variation introduced from measurement error (ME) during the landmark digitization process can have a profound effect on statistical outcomes and biological interpretations (Fruciano, 2016; Robinson and Terhune, 2017; Fox et al., 2020). Therefore, measurement error was quantified among the two landmark digitization repetitions (hereafter referred to as data repetitions one and two) using the 'measurement.error' function in the R package RRPP v. 2.0 (Collyer and Adams, 2024b). This function evaluates repeatability of multivariate data measurements obtained from the same subjects using analysis of variance (ANOVA) with a modified residual randomization in a permutation procedure (RRPP) for restricted randomization (Collyer and Adams, 2024a, b). Measurement error ANOVA quantifies both random and systematic (non-randomly distributed) error in repeated measurements. Random error can artificially increase data variance and obscure biological signals while systematic error can skew biological signals and subsequently alter biological inferences (Arnqvist and Mårtensson, 1998; Fruciano, 2016; Collyer and Adams, 2024a).

Intraclass correlation coefficients (ICC) were also calculated to determine the ratio of among-subject to within-subject variance based on dispersion using the 'ICCstats' function in RRPP (Collyer and Adams, 2024b). 'ICCstats' generates three statistics: one for the population (ICC), one for measurement agreement among subjects (ICC_A), and one for consistency among repeated measurements (ICC_C) (Liljequist et al., 2019; Collyer and Adams, 2024a, b). Values closer to 1 indicate higher repeatability while values closer to 0 indicate lower repeatability among measurements. Models were

Table 1. Definitions of the 14-landmark configuration employed for specific differentiation of western North American *Neotoma* right m1s. Landmark types (i.e., 1, 2, 3; Bookstein, 1997) are listed as well. Tooth terminology is adapted from Martin and Zakrzewski (2019) and landmark placement is shown in Figure 2.

Landmark #	Type	Description
1	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the posterobuccal apex of the anterobuccal cingulum
2	2	Maxima of curvature along the leading edge of the protoflexid at the enamel–reentrant contact
3	2	Maxima of curvature along the trailing edge of the protoflexid at the enamel–reentrant contact
4	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the posterobuccal apex of the protoconid
5	3	Medialmost extent of the hypoflexid at the enamel–reentrant contact
6	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the buccal apex of the hypoconid
7	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the lingual apex of the posterolophid
8	3	Medialmost extent of the posteroflexid at the enamel–reentrant contact
9	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the lingual apex of the entoconid
10	2	Maxima of curvature along the trailing edge of the entoflexid at the enamel–reentrant contact
11	2	Maxima of curvature along the leading edge of the entoflexid at the enamel–reentrant contact
12	2	Maxima of curvature along the trailing edge of the metaconid at the enamel–dentine contact
13	1	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the lingual apex of the metaconid
14	1;2	Intersection of leading and trailing enamel edges at the enamel–dentine contact of the anterolingual apex of the anteroconid (Figure 2, top); maxima of curvature along the lingual edge of the anteroconid–metaconid complex at the enamel–dentine contact if the metaflexid reentrant is not well defined (Figure 2, bottom)

run with and without a ‘groups’ parameter; the groups parameter was included to account for morphological variation among the five extant *Neotoma* species examined (Collyer and Adams, 2024a, b). Fossil unknowns and *N. cinerea* collected outside California were not included in analyses of measurement error.

Species classification

Measurement error is ubiquitous and impossible to eliminate completely from geometric morphometric datasets (Fruciano, 2016). Yet previous research has shown that even small amounts of ME can have a substantial effect on biological signals and statistical outcomes, especially when morphological differences between target groups are subtle (Robinson and Terhune, 2017; Fox et al., 2020). We therefore examined discriminant analysis of principal components (DAPC) group classification statistics for both landmark data repetitions and used predicted group membership agreement among each as proxy for biological signal fidelity. DAPC first performs a principal components analysis (PCA) transformation to ensure predictor variables (i.e., landmark data) are uncorrelated (Jombart et al., 2010). Discriminant function analysis is then performed on the retained principal components to maximize variation among groups while minimizing variation within groups (Jombart et al., 2010; Jombart and Collins, 2022). With DAPC, the optimal number of principal components included in the discriminant analysis can be calculated to balance the trade-off between information capture and discrimination power (more principal components retained), and model overfitting (fewer principal components retained) (Jombart et al., 2010; Jombart and Collins, 2022).

DAPC was conducted on both GPA-transformed landmark data repetitions of recent m1s from California using the ‘dapc’ function in the R package adegenet v. 2.1.10 (Jombart et al., 2023). Twenty-eight x- and y-coordinate variables from the 14 landmarks (Table 1, Fig. 2) were entered as predictor variables to sort recent specimens into their known species groups. Cross-validation was implemented using the ‘xvalDapc’ function in adegenet to determine the optimal number of retained principal components based on the number of principal components that achieve the lowest root-mean-square error (RMSE) (Jombart and Collins, 2022). xvalDapc models were run dozens of times and the range of output values (numbers of principal components achieving lowest MSE) were recorded for each iteration. We then examined DAPC classification statistics (i.e., the percentage of recent specimens correctly assigned to their respective species groups) to determine which principal component number achieved the best compromise between discrimination power and overfitting. Hereafter, model one refers to the DAPC model constructed from landmark data repetition one and model two refers to the model constructed from data repetition two.

Landmark data from RLB fossil m1s and *Neotoma cinerea* from Idaho and South Dakota were entered in DAPC models as supplementary individuals. In other words, they were entered as observations to be sorted by models fitted with recent California specimen training data but were not included in model construction (Jombart and Collins, 2022). These “unknowns” were sorted into extant species groups using the ‘predict.dapc’ function in adegenet. Although species identities of *N. cinerea* outside California were known a priori, they were treated as unknowns to test the models’ ability to classify members of the

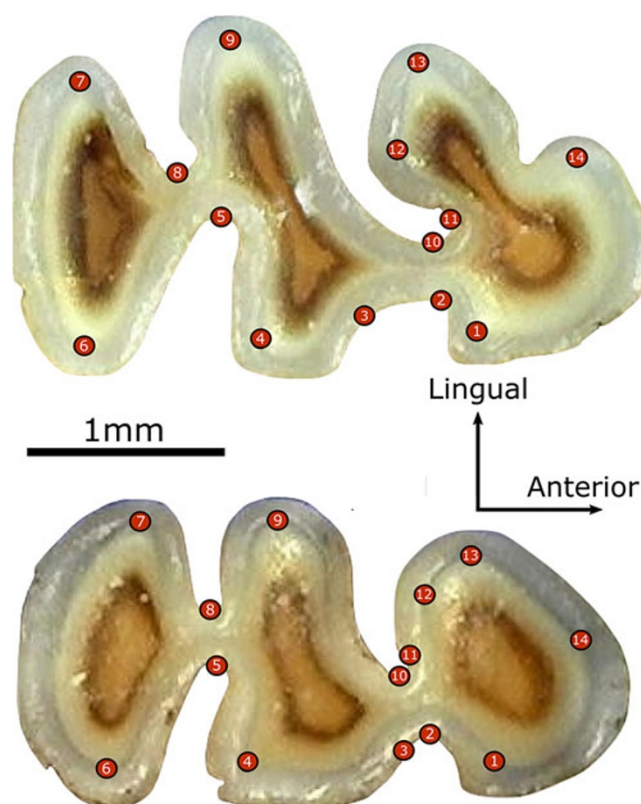


Figure 2. Landmark configuration employed on the right m1 of MVZ 3925 *Neotoma macrotis* (top) with a well-defined metaflexid reentrant (notch between landmarks 13 and 14) and right m1 of MVZ 199799 *N. lepida* (bottom) that lacks a discernible metaflexid in occlusal view. See Table 1 for landmark definitions.

same species from different geographic locations and environments. Predicted species assignments and posterior probabilities of group membership were recorded for unknowns in both data-repetition-training models. Only fossil unknowns assigned to the same species with posterior probabilities of group membership ≥ 0.80 in both models were considered to have high predictive fidelity.

Shape visualization and comparison

To visualize shape differences between extant *Neotoma* species from California and RLB fossils, wireframe outlines were created for the mean landmark configuration of each species using the 'define.links' function in geomorph (Adams et al., 2024). Wireframes of each extant species were then overlain with the mean landmark configuration of the RLB fossil population. Shape differences between extant species and fossils were quantified via vector displacement plots using the 'plotRefToTarget' function in geomorph. Mean fossil shape data were entered as the 'reference specimen' and mean shape data of each extant species were entered as the 'target specimen' comparison. Thus, plotted vectors signify the direction and magnitude of landmark displacement in each extant species relative to the corresponding landmarks of the fossil population. Vector plots were also used to compare the mean landmark configuration of extant *N. cinerea* from California with specimens east of California to visualize m1 shape differences across space and environments. Magnifications of shape differences among all groups were set to the default value of 1.

Tooth wear

The occlusal shape of *Neotoma* molars can vary substantially due to wear and ontogeny among conspecific individuals (Harris, 1984; Repenning, 2004; Tomé et al., 2020). To evaluate the sensitivity of our species classification results to wear, we vetted our original datasets of extant *Neotoma* species from California (data repetitions one and two) by removing specimens near both extremes of the wear spectrum. That is, we removed specimens with nearly unworn molars (wear stage 1, early stage 2) and very heavily worn molars (stage 5) based on the wear categories of Harris (1984) and Tomé et al. (2020). Twenty-eight of the 199 recent specimens initially sampled from California (~14%) were removed in this treatment (Supplementary Table 1). We performed DAPC on these data subsets and compared wear-vetted group classification results with classification results from the original dataset repetitions. We then visualized mean shape differences (across all extant California species) between our wear-vetted and unvetted datasets using vector displacement plots. Vector plots and DAPC were conducted using the methods described in the 'Shape visualization and comparison' and 'Species classification' sections above, respectively. All analyses were done in R v 4.4; (R Core Team, 2024).

Results

Measurement error ANOVA of the two extant *Neotoma* species data repetitions yield small random and systematic ME values relative to specimen variance in models with and without group parameters (Table 2). Systematic ME is also small relative to random ME, but statistically significant in all cases (Table 2). Repeatability values are high across the three ICC statistics in both models, but more so in the group-excluded model (~0.94 and ~0.92 for group-excluded and -included models, respectively, Table 2). In both models, ICC_C values are discernibly greater than ICC and ICC_A values (Table 2).

Of the 24 principal components generated via DAPC, the optimal number of retained principal components suggested by cross-validation is 6–22. Correct classification of extant species improves with each additional principal component retained up to 16 and plateaus thereafter. Therefore, 16 of the 24 principal components were retained in the final training models. Those models correctly classify 90.5% and 84.9% of specimens across all five extant species groups in models one and two, respectively (Table 3). Correct classification rates were 75–97.5% within species groups; *Neotoma cinerea* achieves the highest correct classification rate overall, and *N. macrotis* achieves the lowest correct classification rate in both models (Table 3). DAPC scatterplots show good morphospace separation of *N. cinerea* from all other extant species groups (Fig. 3). Substantial group overlap occurs between *N. fuscipes* and *N. macrotis* and, to a lesser extent, between *N. albigula* and *N. lepida* (Fig. 3).

Most fossil unknowns from RLB are identified as *N. macrotis* (12 of 16 specimens in both DAPC models, Table 4). All other specimens are identified as *N. fuscipes*. Both models agree on the species affinity of 14 of the 16 unknown specimens, and four of the 16 specimens meet our criteria for high predictive fidelity (all identified as *N. macrotis*, Table 4). All fossil unknowns plot within or near the observed morphospace of *N. fuscipes* and *N. macrotis* (Fig. 3). Shape differences in vector-displacement plots are obvious between the fossil population mean and extant *Neotoma albigula*, *N. cinerea*, and *N. lepida* means, particularly at landmarks 5, 10, and 11 (Figs. 2 and 4). Shape differences between the fossil population

Table 2. ANOVA and intraclass correlation coefficient (ICC) summary statistics for measurement error (ME) analysis of both extant *Neotoma* landmark dataset repetitions. Systematic ME, random ME, and ICC statistics were quantified using the ‘measurement.error’ and ‘ICCstats’ functions, respectively, in the R package ‘RRPP’ (Collyer and Adams, 2024b). “Without groups” = no group parameter for the five extant *Neotoma* species. “With groups” = group parameter for the five extant *Neotoma* species included.

Without groups	Df	SS	MS	R ²	η^2	SNR	Z	P
Specimens	198	4.7362	0.0239	0.9682		33.273	28.5473	0.001
Systematic ME	1	0.0134	0.0133	0.0027	0.0858	0.094	7.6943	0.001
Random ME	198	0.1423	0.0007	0.0291	0.9142			
Total	397	4.8919						
ICC Statistics ICC = 0.9367 ICC _A = 0.9368 ICC _C = 0.9417								
With groups	Df	SS	MS	R ²	η^2	SNR	Z	P
Specimens	198	3.4726	0.0175	0.7099		26.3021	25.7037	0.001
Systematic ME	1	0.0134	0.0134	0.0027	0.0858	0.1012	7.7878	0.001
Systematic ME: Groups	4	0.0103	0.0026	0.0021	0.0663	0.0781	3.7988	0.001
Random ME	194	0.1320	0.0007	0.0270	0.8479			
Total	397	4.8919						
ICC Statistics ICC = 0.9151 ICC _A = 0.9155 ICC _C = 0.9222								

Table 3. Discriminant analysis of principle components classification statistics of models built with extant *Neotoma* species data from the first (top) and second (bottom) landmarking repetition. All 28 landmark variables are included in the analysis. The first 16 of 24 principal components were retained for each repetition, as suggested via the ‘xvaldapc’ cross-validation function in the R package ‘adegent’ (Jombart et al., 2023). Columns indicate predicted species affinities; rows indicate actual species affinities; % Correct = the percentage of specimens correctly assigned to their species group; Na = *Neotoma albigula*; Nc = *Neotoma cinerea*; Nf = *Neotoma fuscipes*; Nl = *Neotoma lepida*; Nm = *Neotoma macrotis*.

Replicate 1 Model	Na	Nc	Nf	Nl	Nm	% Correct
Na	36	1	1	1	1	90.0
Nc	1	38	0	0	0	97.4
Nf	1	1	34	0	4	85.0
Nl	1	0	0	39	0	97.5
Nm	2	0	5	0	33	82.5
Total predicted group membership accuracy = 90.5%						
Replicate 2 Model	Na	Nc	Nf	Nl	Nm	% Correct
Na	32	1	1	4	2	80.0
Nc	0	38	0	1	0	97.4
Nf	1	0	32	0	7	80.0
Nl	3	0	0	37	0	92.5
Nm	1	0	8	1	30	75.0
Total predicted group membership accuracy = 84.9%						

and extant *N. fuscipes* and *N. macrotis* are subtle and no strong vector displacements were observed (Fig. 4). Most recent specimens of *N. cinerea* from Idaho and South Dakota are correctly identified as *N. cinerea* (11 of 13 in both DAPC models), and both models agree on the species affinity of all specimens (Table 4). Most of these eastern specimens cluster within or near the morphospace of California *N. cinerea* (Fig. 3). However, discernible differences in mean m1 shape configurations occur between California *N. cinerea* and eastern specimens at landmarks 2, 3, 6, and 12 (Fig. 2, Supplementary Fig. 1).

DAPC species classification models improve marginally for wear-vetted datasets versus unvetted datasets overall (91.2% from 90.5% and 87.1% from 84.9%) across all extant species for models one and two, respectively (Table 3, Supplementary Table 2).

Species-specific classification results improve slightly for all species except *Neotoma lepida* in both models. Vector displacement plots of mean m1 shape show no discernible difference between wear-vetted and unvetted datasets for either model (Supplementary Fig. 2).

Discussion

We examined whether we could differentiate extant *Neotoma* species and identify unknown fossils from Late Pleistocene Rancho La Brea localities in Los Angeles, California. Overall, we found that 2D landmark analysis of lower first molars is an appropriate approach for these goals, and we were able to identify a subset of fossils at RLB as *N. macrotis* with reasonable certainty.

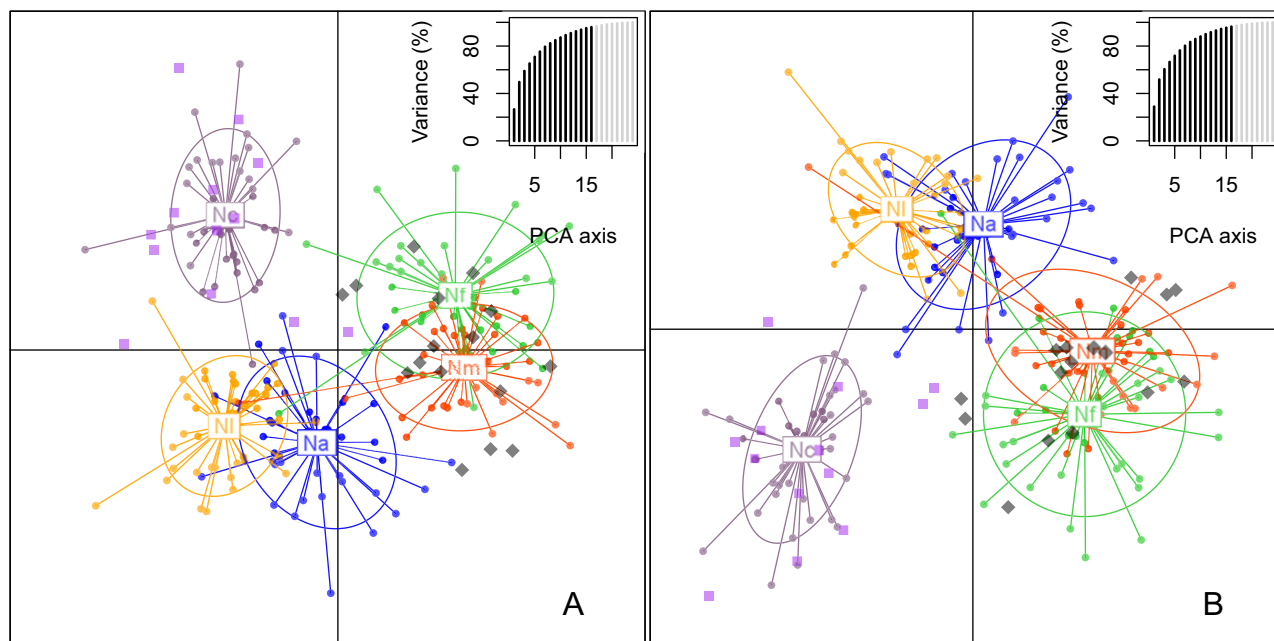


Figure 3. Discriminant analysis of principal components (DAPC) scatterplot using the first 16 of 24 principal components generated from (A) model one (the first landmarking repetition of *Neotoma* m1s) and (B) model two (the second repetition). Data from extant *N. albigula* (Na), *N. cinerea* (Nc), *N. fuscipes* (Nf), *N. lepida* (Ni), and *N. macrotis* (Nm) from California were used to train the models; the 16 Project 23 fossil unknowns (dark gray diamonds) and 13 extant *N. cinerea* east of California (purple squares) were entered as supplementary individuals. Inset shows the cumulative variance explained by each principal component. Black bars and gray bars represent principal components included and excluded, respectively, based on DAPC cross-validation analysis in the R package adegenet (Jombart et al., 2023).

Classification results

DAPC of 28 m1 landmark-coordinate variables was conducted to determine if (1) the five extant *Neotoma* species can be differentiated by tooth morphology and (2) these data can be used to identify fossils of unknown species affinity. DAPC was performed on both landmark repetitions to evaluate data replicability and biological signal variability due to ME. Our DAPC training models are relatively accurate overall, correctly predicting species affinities of 84.9–90.5% of the 199 recent California specimens examined (Table 3). Thus, in general, m1s of extant *Neotoma* species can be differentiated using this geometric morphometric approach. Our results also are robust to tooth wear variability given the marginal improvement in DAPC classification statistics (Table 3, Supplementary Table 2) and indiscernible mean shape differences (Supplementary Fig. 2) between wear-vetted and unvetted datasets.

Analyses of ME among the two dataset repetitions indicate that landmark ME is relatively low, explaining only ~3% of the total data variance (R^2 values, Table 2). Systematic measurement error, which is generally of greater concern for altering biological signals and interpretations than random ME (Arnqvist and Mårtensson, 1998; Collyer and Adams, 2024a), is also low relative to random ME (η^2 values, Table 2) and specimen variation (signal-to-noise ratio (SNR) values, Table 2). However, systematic ME contributions are statistically significant in both the group-included and group-excluded models (Table 2). High ICC values (> 0.9 , Table 2) indicate good repeatability and thus relatively low ME among datasets (Liljequist et al., 2019; Collyer and Adams, 2024b). Yet discrepancies between ICC_C and ICC/ICC_A statistics (Table 2) further imply these datasets are affected by systematic ME (Collyer and Adams, 2024a).

The extent to which ME affects biological signals varies among specimens, taxa, and studies. Species classification patterns are very

similar among the two DAPC models in our study. For example, predicted group memberships are most accurate for *N. cinerea* and *N. lepida*, and least accurate for *N. macrotis* in both models (Table 3). However, DAPC-predicted group memberships are not identical for individual specimens in both models, and neither are DAPC scatterplot patterns (Fig. 3). This suggests that ME does affect biological signal to some extent. Of greater concern is how ME affects predicted group memberships of fossil unknowns because unlike our recent specimens, it is impossible to independently verify fossil species identity (ancient DNA retrieval has thus far been unsuccessful at RLB; Gold et al., 2014). Predicted group memberships were consistent among training models in 14 of the 16 fossil individuals (~88%) and the models were able to correctly identify most individuals of extant *N. cinerea* (~85%) from distant geographic locations (Table 4). Therefore, while it is impossible to determine the accuracy of our models for identifying fossil unknowns, this approach appears robust due to the relatively high accuracy of DAPC training models in sorting known extant California species, the overall consistency in their predictions of fossil species identities among landmarking repetitions, and the models' ability to correctly identify most specimens across space, which is often used as an ecological substitute for time (Pickett, 1989; Blois et al., 2013).

Most errors and inconsistencies in recent and fossil-group membership predictions occur between *Neotoma fuscipes* and *N. macrotis* (Tables 3 and 4). This is not surprising as *N. macrotis* was considered a subspecies of *N. fuscipes* until phenotypic and molecular analyses found species-level differences among them (Matocq, 2002a, b). Indeed, DAPC and vector displacement plots show more morphological similarity between *N. fuscipes* and *N. macrotis* than any other two species examined here (Figs. 3 and 4). DAPC classifies most (12 of 16) fossil unknowns from RLB as *N. macrotis* and the remaining specimens are classified as *N. fuscipes* (Table 4, Fig. 3). Marked shape differences occur between RLB m1s and the m1s

Table 4. Classification results of 16 fossil *Neotoma* m1s from Project 23 Deposits 1, 7B, 13, and 14 at Rancho La Brea and extant *N. cinerea* east of California. Predicted species-group membership (PGM) of each specimen is listed for each DAPC training model (1 and 2) followed by their 0–1 posterior probabilities (PP) of group membership. Values closer to one indicate higher probabilities of belonging to a particular species than values closer to 0. Underlined text indicates fossil specimens assigned to the same extant species in both models with posterior probabilities ≥ 0.80 in each. Taxa in bold indicate eastern specimens of *N. cinerea* misclassified as other species. ID = Idaho; SD = South Dakota; LACMP = Los Angeles County Museum of Paleontology; MVZ = University of California Museum of Vertebrate Zoology; SDSM = South Dakota School of Mines and Technology Museum of Geology.

Locality	Age	Catalog #	Model 1 PGM	PP	Model 2 PGM	PP
P23 Deposit 1	Late Pleistocene	LACMP23–28509	<i>N. macrotis</i>	0.63	<i>N. macrotis</i>	0.66
P23 Deposit 14	Late Pleistocene	LACMP23–31175	<i>N. fuscipes</i>	0.33	<i>N. macrotis</i>	0.45
P23 Deposit 14	Late Pleistocene	LACMP23–31976	<i>N. macrotis</i>	0.73	<i>N. fuscipes</i>	0.55
P23 Deposit 14	Late Pleistocene	LACMP23–33922	<i>N. macrotis</i>	0.81	<i>N. macrotis</i>	0.72
P23 Deposit 14	Late Pleistocene	LACMP23–34168	<u><i>N. macrotis</i></u>	0.96	<u><i>N. macrotis</i></u>	0.98
P23 Deposit 7B	Late Pleistocene	LACMP23–35665	<u><i>N. macrotis</i></u>	0.82	<u><i>N. macrotis</i></u>	0.85
P23 Deposit 7B	Late Pleistocene	LACMP23–35668	<i>N. fuscipes</i>	0.73	<i>N. fuscipes</i>	0.53
P23 Deposit 7B	Late Pleistocene	LACMP23–35780	<i>N. macrotis</i>	0.67	<i>N. macrotis</i>	0.56
P23 Deposit 7B	Late Pleistocene	LACMP23–35782	<i>N. fuscipes</i>	0.75	<i>N. fuscipes</i>	0.89
P23 Deposit 7B	Late Pleistocene	LACMP23–35806	<i>N. macrotis</i>	0.74	<i>N. macrotis</i>	0.66
P23 Deposit 7B	Late Pleistocene	LACMP23–35934	<i>N. macrotis</i>	0.85	<i>N. macrotis</i>	0.64
P23 Deposit 7B	Late Pleistocene	LACMP23–36312	<i>N. fuscipes</i>	0.81	<i>N. fuscipes</i>	0.68
P23 Deposit 13	Late Pleistocene	LACMP23–40158	<u><i>N. macrotis</i></u>	0.98	<u><i>N. macrotis</i></u>	0.96
P23 Deposit 13	Late Pleistocene	LACMP23–40402	<u><i>N. macrotis</i></u>	0.98	<u><i>N. macrotis</i></u>	0.87
P23 Deposit 14	Late Pleistocene	LACMP23–40662	<i>N. macrotis</i>	0.63	<i>N. macrotis</i>	0.53
P23 Deposit 14	Late Pleistocene	LACMP23–40663	<i>N. macrotis</i>	0.66	<i>N. macrotis</i>	0.52
Bannock Co., ID	Recent	MVZ 51944	<i>N. cinerea</i>	0.92	<i>N. cinerea</i>	0.99
Pennington Co., SD	Recent	SDSM 117647	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 117648	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171654	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171655	<i>N. fuscipes</i>	0.79	<i>N. fuscipes</i>	0.48
Pennington Co., SD	Recent	SDSM 171656	<i>N. lepida</i>	0.99	<i>N. lepida</i>	0.77
Pennington Co., SD	Recent	SDSM 171657	<i>N. cinerea</i>	0.99	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171658	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171659	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171660	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171661	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00
Pennington Co., SD	Recent	SDSM 171662	<i>N. cinerea</i>	0.46	<i>N. cinerea</i>	0.58
Pennington Co., SD	Recent	SDSM 171663	<i>N. cinerea</i>	1.00	<i>N. cinerea</i>	1.00

of extant *N. albigula*, *N. cinerea*, and *N. lepida*, particularly among landmarks 5, 10, and 11, which capture the shape of the hypoflexid and entoflexid reentrant folds (Table 1, Figs. 2 and 4). However, RLB fossils are virtually indistinguishable from extant *N. fuscipes* and *N. macrotis* (Fig. 4).

Because most fossils are classified as *N. macrotis* in both landmark data repetitions, and several have high predictive fidelity (Table 4, Fig. 3), the presence of *N. macrotis* among the P23 faunas of RLB is strongly supported. It is more difficult to discern whether *N. fuscipes* is also present among these faunas, or if it is an erroneous model prediction given the comparatively low identification rates of this species and elevated misclassification rates among extant *N. fuscipes* and *N. macrotis* in both models (Tables 3 and 4). Previous work has shown that unknowns assigned to

groups in low frequency should be interpreted cautiously, especially when models are not completely accurate at sorting training subjects of known group affinity (Fox et al., 2020). Until stronger support for *N. fuscipes* is provided (e.g., via larger fossil sample sizes), we attribute only one woodrat species, *N. macrotis*, to the P23 faunas of RLB.

Systematic paleontology

Rodentia (Bowdich, 1821)

Cricetidae (Fischer, 1817)

Neotoma (Say and Ord, 1825)

Neotoma macrotis (Thomas, 1893)

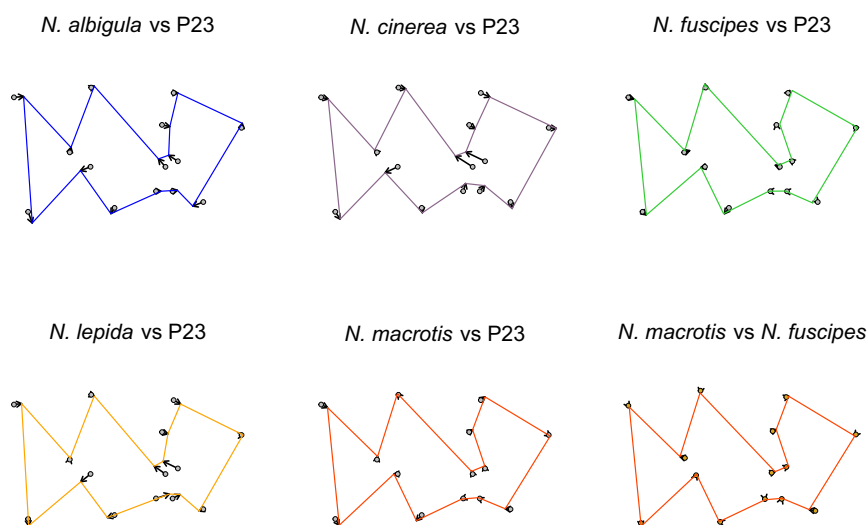


Figure 4. Vector displacement plots of mean m1 landmark shape configurations for the five extant *Neotoma* species ($n = 39\text{--}40$ each) examined overlain with the mean landmark shape configuration of fossil *Neotoma* ($n = 16$) from Project 23 deposits at Rancho La Brea (P23). Configurations were generated using the first landmarking repetition. Also shown is the overlay of extant *N. macrotis* and *N. fuscipes* shape configurations (lower right). Arrows indicate the magnitude and direction of vector displacement between the reference and target groups. Plots were created using the 'define.links' and 'plotRefToTarget' functions in the R package geomorph (Adams et al., 2024).

Referred specimens. m1s: Los Angeles County Museum of Paleontology (LACMP) LACMP23-34168, LACMP23-35665, LACMP23-40158, LACMP23-40402.

Remarks. Four *Neotoma* m1s from P23 Deposit 7B (LACMP23-35665), P23 Deposit 13 (LACMP23-40158, LACMP23-40402), and P23 Deposit 14 (LACMP23-34168) are assigned to *N. macrotis* based on predicted group membership assignment and posterior probabilities of group membership ≥ 0.80 in both DAPC models (Table 4).

Neotoma cf. *N. macrotis* (Thomas, 1893)

Referred specimens. m1s: LACMP23-28509, LACMP23-31175, LACMP23-31976, LACMP23-33922, LACMP23-35668, LACMP23-35780, LACMP23-35782, LACMP23-35806, LACMP23-35934, LACMP23-36312, LACMP23-40662. Left dentary with m1-m2: LACMP23-40663.

Remarks. Twelve *Neotoma* specimens from P23 Deposit 1 (LACMP23-28509), P23 Deposit 7B (LACMP23-35668, LACMP23-35780, LACMP23-35782, LACMP23-35806, LACMP23-35934, LACMP23-36312), and P23 Deposit 14 (LACMP23-31175, LACMP23-31976, LACMP23-33922, LACMP23-40662, LACMP23-40663) are assigned to *Neotoma* cf. *N. macrotis*. This includes specimens with predicted group membership of *N. fuscipes* in one or both DAPC models and/or posterior probabilities of *Neotoma macrotis* group membership ≤ 0.80 in one or both models.

Biogeographic implications

To our knowledge, this is the first report of *N. macrotis* from a prehistoric locality, likely due to the taxon's recent distinction as a unique species and due to the challenges of identifying isolated elements of *Neotoma* to species in general. An early study of RLB small mammals was unable to identify fossil *Neotoma* dentaries from Localities 2050 and 2051 to species (Dice, 1925). It was noted, however, that *N. lepida* and *N. macrotis* (then *Neotoma fuscipes macrotis*) were likely candidates based on size. Similarly, a recent study of small-mammal coprolites likely belonging to *Neotoma* from P23 Deposit 1 noted the fecal pellets were within the size range of extant *N. lepida* and *N. macrotis* (Mychajliw et al., 2020). This is now the third study to independently support the occurrence of *N. macrotis* among RLB paleofaunas and

the first to provide size-independent morphological evidence for it. Conversely, occurrence of *N. lepida* is not supported based on the small fossil m1 sample size acquired here. While it is possible that *N. lepida* and other unexamined members of the *N. lepida* species complex (e.g., *N. bryanti*) are present in the RLB paleofaunas, it is unlikely that any members are represented in this sample given the morphological similarity among the *N. lepida* complex (Patton et al., 2007; Bradley et al., 2022) and the strong differentiation between *N. lepida* and *N. fuscipes*/*N. macrotis* specimens (Table 3, Figs. 3 and 4). Additional m1 samples from other deposits spanning different geologic ages are needed to discern whether other *Neotoma* species were present in the Los Angeles region during the Late Pleistocene and Holocene.

Rancho La Brea is located within the contemporary range of *N. macrotis* (Fig. 1), so its presence among these paleofaunas is not surprising. Rancho La Brea is also less than 100 miles from the southernmost *N. fuscipes*–*N. macrotis* contact zone (Fig. 1) (Matocq, 2002a), and the range of *N. fuscipes* may have shifted slightly southward towards RLB as past climate change shifted regions of habitat suitability for the species during Pleistocene glacial periods. Recent projections of the geographic distribution of *N. fuscipes* place it in southern California at the last glacial maximum (LGM), 21,000 yr BP (Boria et al., 2021), presenting another line of evidence that it was potentially in the Los Angeles region in earlier glacial times captured by P23. However, morphological differentiation among extant *N. fuscipes* and *N. macrotis* is the result of complex, ongoing ecological and evolutionary processes. Clear divergence in craniodental traits at species contact zones is consistent with competition-driven character displacement, but an asymmetric pattern of morphological change between the two species occurs as distance from the contact zone increases (Matocq and Murphy, 2007). Even within *N. fuscipes*, there is marked genotypic (Matocq, 2002a, b; Boria et al., 2021) and phenotypic (Hooper, 1938; Matocq, 2002a) variation among geographic populations in California. Those observations are evident in this study as more variation is expressed in the m1 morphological ellipse of *N. fuscipes* than in any other California *Neotoma* species examined, some of which overlap with *N. macrotis* (Fig. 3). Interpreting whether *N. fuscipes* and *N. macrotis*, or *N. macrotis* alone, is present at RLB is further complicated because these two species today have multiple contact zones, including at least one area of sympatry where they hybridize (Matocq, 2002a; Coyner et al., 2015). It may therefore be

impossible to identify some specimens within the *N. fuscipes*–*N. macrotis* complex to species based on tooth shape alone, especially if they occur near the contemporary range intersections of both species where hybridization can occur. In such cases, genomic analyses may be required for specific identification.

Methodological developments

We have shown that landmark-based shape configurations can help overcome the challenges of identifying isolated *Neotoma* molars in both modern and prehistoric systems. Previously, most species-level identifications of *Neotoma* teeth, bones, and fecal pellets were inferred based on contemporary species distributions and size. Such methods are only appropriate if one can assume no range shifts occurred in the past and if focal species are near the size minima and maxima of the genus where little interspecific overlap occurs (e.g., *N. albigula* and *N. cinerea*; Lyman and O'Brien, 2005; *N. lepida* and *N. cinerea*; Smith et al., 2009).

Shape-based identification of *Neotoma* remains have been attempted with mixed outcomes. For example, Zakrzewski (1993) and Repenning (2004) described morphological characters of extant and fossil *Neotoma* dentition and inferred biogeographic (Repenning, 2004), biostratigraphic (Zakrzewski, 1993; Repenning, 2004), phylogenetic, and evolutionary (Zakrzewski, 1993) patterns based on those characters. It was acknowledged, however, that specific relationships among fossil taxa could not be inferred, in part, because complex features such as spatial relationships between different tooth reentrant folds and lophs are difficult to quantify via direct observation (Zakrzewski, 1993). Harris (1984) attempted to statistically differentiate m1s of eight extant *Neotoma* species to facilitate fossil identification using a combination of linear measurements and qualitative characters. It was shown that most specimens could be correctly sorted into their respective species groups, but only when split into species pairs prior to discriminant analysis (Harris, 1984). Additional data corrections were implemented to account for tooth-wear differences (Harris, 1984) and, while somewhat successful, those treatments could be difficult to replicate for other studies.

More recently, Tomé et al. (2020) used elliptical Fourier analysis of 2D shape outlines to classify upper first molars (M1s) of six *Neotoma* species. Only 57% of specimens were correctly classified in that study, and four of the species groups were sorted at less than 20% accuracy (Tomé et al., 2020). Discrepancies between our classification results and those of Tomé et al. (2020) are likely due to study design differences. For example, while both studies used a geometric morphometric technique, our study examined 14 discreet landmarks placed on anatomically homologous loci of the m1, while Tomé et al. (2020) examined M1 shape using a semiautomated 'high-density' method generating more than 100 points per outline. It could be that m1s exhibit more interspecific variation than M1s, or 'traditional' landmarks could be more effective at capturing interspecific shape variation than shape outlines in this system.

The degree to which mathematically applied, high-density, geometric morphometric configurations can obscure biological signals remains unclear, but recent work suggests these methods should be interpreted cautiously (Cardini, 2020; Shui et al., 2023). Occlusal outlines of *Neotoma* molars could also be more sensitive to wear-based shape variation than our discrete landmark configuration. Tomé et al. (2020) found that removing specimens with more wear (stage 4) and less wear (stage 2) than average (stage 3) provided little improvement to species classification results.

However, the most extreme wear stages (1 and 5) were excluded from that study (Tomé et al., 2020). Our statistical and visual comparisons of wear-vetted and unvetted datasets showed little change when specimens near both wear extremes (stages 1, early 2, and 5) were removed (Table 3 versus Supplementary Table 2, Supplementary Fig. 2). Specimens exhibiting those wear stages encompassed a relatively small proportion of our original dataset (~14%, Supplementary Table 1), and it would be beneficial to evaluate datasets with higher proportions of specimens near both extremes of the wear spectrum in the future. Nevertheless, our results suggest that data noise generated by m1 wear did not substantially alter interspecific morphological signals captured by our landmark configuration.

Other sources of variation in classification results could include differences in sampling approaches among studies. Tomé et al. (2020) examined six *Neotoma* species with species-group sizes between 20 and 90 while our study examined five species with group sizes between 39 and 40. Both the number of groups and group sample sizes entered in discriminant function and canonical variate analyses can have a large effect on model outcomes (Kovarovic et al., 2011). Tomé et al. (2020) also sampled specimens across a larger geographic range than we did and noted that M1 shape of some *Neotoma* species could be more affected by local diet and environment than phylogeny. For extant species with broad distributions such as *N. cinerea* (Fig. 1), we would thus expect more intraspecific variation to be captured if we sampled across more of their range due to local environmental adaptations. Indeed, our limited sample of *N. cinerea* from Idaho and South Dakota showed morphological differences from our California sample (Supplementary Fig. 1). Shape configuration differences were most prominent at landmarks 2, 3, 6, and 12, which correspond to features of the protoflexid, hypoconid, and metaconid (Table 1, Fig. 2, Supplementary Fig. 1). Despite those differences, our DAPC models were able to correctly identify most individuals to species regardless of their geographic origin (Tables 3 and 4). It is potentially significant that the two individuals misclassified outside California (SDSM 171655 and SDSM 171656) are from the eastern edge of the species' range and exhibit wear stages 5 and 1, respectively. This suggests that, while our landmark protocol bodes well for extant and fossil *Neotoma* identification, interactions between phylogeny, wear/ontogeny, diet, geography, and environment may affect tooth morphology in complex ways. Therefore, additional applications of this method across a broader range of taxa, individuals, and locations are needed to better contextualize its advantages and limitations for species classification.

Summary and conclusions

We found that 2D geometric morphometric analysis of *Neotoma* m1s is generally effective at differentiating five extant western North American species. Most individuals were correctly classified within their respective species groups via DAPC; although higher rates of morphological overlap and misclassification occur between the two most recently diverged species, *N. fuscipes* and *N. macrotis* (Table 3, Figs. 3 and 4). By applying this method to classify fossil *Neotoma* m1s, we identified *N. macrotis* in the P23 deposits of RLB during the Late Pleistocene. Our study shows that landmark-based shape configurations can provide a size and contemporary range-independent option for identifying *Neotoma* remains to species. Because fossil teeth tend to preserve over a wider range of environments and time periods than fossil middens, this method could

extend the spatiotemporal range of *Neotoma* species occurrences and further our understanding of their biogeography and paleoecology. Our relatively simple identification procedure should be applicable to other study systems and locations in North America.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/qua.2025.9>.

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Data availability. Specimen images and landmark coordinate data are available at Zenodo: <https://doi.org/10.5281/zenodo.15127876>. Analytical input data, code, and output data/figures are available on GitHub: <https://github.com/boispaleolab/Neotoma.m1.GM>.

Competing interests. The authors declare no competing interests.

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