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Research Article

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Integrative species delimitation reveals an Idaho-endemic ground squirrel, *Urocitellus idahoensis* (Merriam 1913)

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Abstract

The "small-eared" species group of *Urocitellus* ground squirrels (Sciuridae: Xerinae: Marmotini) is endemic to the Great Basin, United States, and surrounding cold desert ecosystems. Most specific and subspecific lineages in this group occupy narrow geographic ranges, and some are of significant conservation concern; despite this, current taxonomy remains largely based on karyotypic or subtle pelage and morphological characteristics. Here, we leverage 2 multilocus DNA sequence data sets and apply formal species delimitation tests alongside morphometric comparisons to demonstrate that the most widespread small-eared species (*U. mollis* Kennicott, 1863 sensu lato; Piute Ground Squirrel) is comprised of 2 nonsister and deeply divergent lineages. The 2 lineages are geographically separated by the east-west flowing Snake River in southern Idaho, with no sites of sympatry currently known. Based on robust support across the nuclear genome, we elevate populations previously attributed to *U. mollis* from north of the Snake River to species status under the name *Urocitellus idahoensis* (Merriam 1913) and propose the common name "Snake River Plains Ground Squirrel" for this taxon. We delimit 2 subspecies within *U. idahoensis*; *U. i. idahoensis* (Merriam 1913) in western Idaho and *U. i. artemesiae* (Merriam 1913) in eastern Idaho. *Urocitellus idahoensis* is endemic to Idaho and has a maximal range area of roughly 29,700 km^2 spanning 22 counties but occurs discontinuously across this area. Our work substantially expands knowledge of ground squirrel diversity in the northern Great Basin and Columbia Plateau and highlights the difficulty in delimiting aridland mammals whose morphological attributes are highly conserved.

Key words: Columbia Plateau, geometric morphometrics, Great Basin, Marmotini, mitonuclear discordance, Snake River, UCEs.

The genus *Urocitellus* Obolenskij, 1927 (Holarctic ground squirrels) comprises 12 recognized species of small- to medium-bodied, fossorial, and obligatorily heterothermic sciurids distributed across temperate North America and Asia (Helgen et al. 2009; Kays and Wilson 2010; Mammal Diversity Database 2023). Traditionally, the genus has been conceptualized as containing 2 species groups—the "big-eared" and "small-eared" groups—which appear reciprocally monophyletic (McLean et al. 2016, 2019, 2022) and differ from one another in aspects of body size, habitat preference, and ecology (Howell 1938; Davis 1939; Durrant and Hansen 1954; Rickart 1987). The big-eared group contains 7 larger-bodied and mesic-adapted species widely distributed across western North America (5 species), Beringia (1 species), and eastern Asia (1 species). Conversely, the small-eared group contains 5 species of smaller-bodied, pale-colored, and desert-dwelling squirrels endemic to the Great Basin and adjacent Columbia Plateau, United States (Howell 1938; Helgen et al. 2009; McLean et al. 2016, 2022).

Small-eared *Urocitellus* remain remarkably understudied from phylogenetic and population genetic perspectives despite the narrow geographic ranges and conservation concerns of most lineages. In his comprehensive treatment, Howell (1938) recognized 4 species of small-eared squirrels based on pelage, external morphological, and cranial characters: *U. brunneus* (Howell 1928); *U. idahoensis* (Merriam 1913); *U. townsendii* (Bachman 1839); and *U. washingtoni* (Howell 1938), including subspecific forms. Conversely, Nadler et al. (1982) and Rickart (1985, 1987) allied *idahoensis* with the widespread *U. t. mollis* and simultaneously demonstrated the distinctiveness of *U. t. canus*. Hoffmann et al. (1993) later synthesized available data to recognize 5 species: *U. brunneus* (Howell 1928); *U. canus* (Merriam 1898); *U. mollis* (Kennicott 1863); *U. townsendii* (Bachman 1839); and *U. washingtoni* (Howell 1938).

The treatments of subsequent workers have generally followed the 5-species scheme above (Thorington and Hoffmann 2005; Helgen et al. 2009; Thorington et al. 2012; Mammal Diversity

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Database 2023). Recently, Hoisington-Lopez et al. (2012) elevated subspecies within *U. brunneus*, thereby recognizing a sixth species (*U. endemicus*). These sister taxa are minimally diverged genetically (Hoisington-Lopez et al. 2012; McLean et al. 2016, 2022) but exhibit other differences (Yensen 1991; Hoisington-Lopez et al. 2012). For the purposes of this study, we combine individuals assignable to the *brunneus* and *endemicus* lineages under *U. brunneus* given our limited sampling of morphological and genetic characters for either lineage and thus inability to further test Hoisington-Lopez et al.'s (2012) taxonomic hypothesis. Similarly, the taxon *U. nancyae* (Nadler 1968), distributed between the Yakima and Columbia Rivers of Washington, was recently listed as a distinct species by the International Union for the Conservation of Nature Red List (Yensen 2019). *Urocitellus nancyae* is generally considered either a synonym or subspecies of *U. townsendii*, although chromosomal distinctions were documented (*U. townsendii* with 2N = 36, *U. nancyae* with 2N = 38; Nadler 1968). As with *U. brunneus*, we combine all individuals here under *U. townsendii* as traditionally defined, pending additional genetic sampling and integrative analysis. However, given the close relationship of populations within both *U. brunneus* and *U. townsendii*, we do not expect that these decisions impact our conclusions.

Roughly 40 years after the publication of karyotypes for most *Urocitellus* species, small-eared *Urocitellus* remain delimited taxonomically primarily by karyotype, geographic range, or a combination of the 2 (Helgen et al. 2009; Kays and Wilson 2010; Kays et al. 2022; Mammal Diversity Database 2023), so delimitations based on additional data are needed. The group does display significant karyotypic variation, with diploid numbers varying from 2N = 36 for *U. townsendii* to 2N = 46 for *U. canus* (Nadler 1966, 1968; Nadler et al. 1982; Rickart et al. 1985). Nadler et al. (1982:208) stated: "The Nearctic *townsendii* group proper [small-eared taxa] forms a cluster of its own on both biochemical and morphological evidence. However, chromosomal differentiation is considerable." Nevertheless, a reliance on karyotypic and allozyme electrophoretic approaches alone, especially given some incongruence between them, suggests a more integrative systematic revision of the whole group is warranted.

This study reviews the systematics and phylogenetic placement of populations currently attributed to the Piute Ground Squirrel, *U. mollis* (Kennicott 1863). *Urocitellus mollis* is the most widely distributed small-eared *Urocitellus* with 3 subspecies recognized (Fig. 1; Howell 1938; Rickart 1987; Helgen et al. 2009). The most widespread subspecies, *U. m. mollis*, occurs throughout a large part of the Great Basin, United States—from the Snake River (Idaho) south to southern Nevada and from the eastern foothills of the Sierra Nevada in California and Nevada east to central Utah. Conversely, *U. m. idahoensis* (Merriam 1913) and *U. m. artemesiae* (Merriam 1913) occupy smaller, adjacent ranges in southwestern and southeastern Idaho, respectively, in steppe habitats of the Snake River Plain north of the Snake River (Fig. 1). All 3 subspecies share a common karyotype across the range of *U. mollis* (2N = 38, FN = 66; Nadler 1966, 1968; Rickart et al. 1985).

The taxonomic history of *U. mollis* offers a case-in-point for how reliance on single character types may mislead taxonomic inferences, especially in aridland mammals whose morphological attributes may be conserved, and highlights the urgency of integrating multiple data sources for delimitation (Padial et al. 2010). Using morphology, Merriam (1913) described *idahoensis* as a distinct species (*Citellus idahoensis*) based on larger body size and robustness of the cranium and dentition relative to *U. m. mollis* and *U. m. artemesiae*. He distinguished *U. m. artemesiae* (as *C. m. artemesiae*) from *U. m. mollis* based on its relatively small body size and a smaller and more-slender cranium along with dental distinctions (Merriam 1913). Merriam (1898, 1913) further described 1 species (*leurodon*) and 3 subspecies (*stephensi*, *pessimus, washoensis*) from within the range of modern *U. mollis*, but Howell (1938) subsumed all forms except *idahoensis* within *mollis,* also based on pelage and morphological characters. Using karyotypic data, Nadler (1966) and Rickart et al. (1985) documented a uniform karyotype across the geographic range of *U. mollis* and failed to recover evidence of hybridization between these forms and geographically adjacent but karyotypically distinctive species (i.e., *U. canus*; Merriam's Ground Squirrel). This body of information was used to redefine *U. mollis* (including *mollis*, *idahoensis*, and *artemesiae*) by Hoffmann et al. (1993).

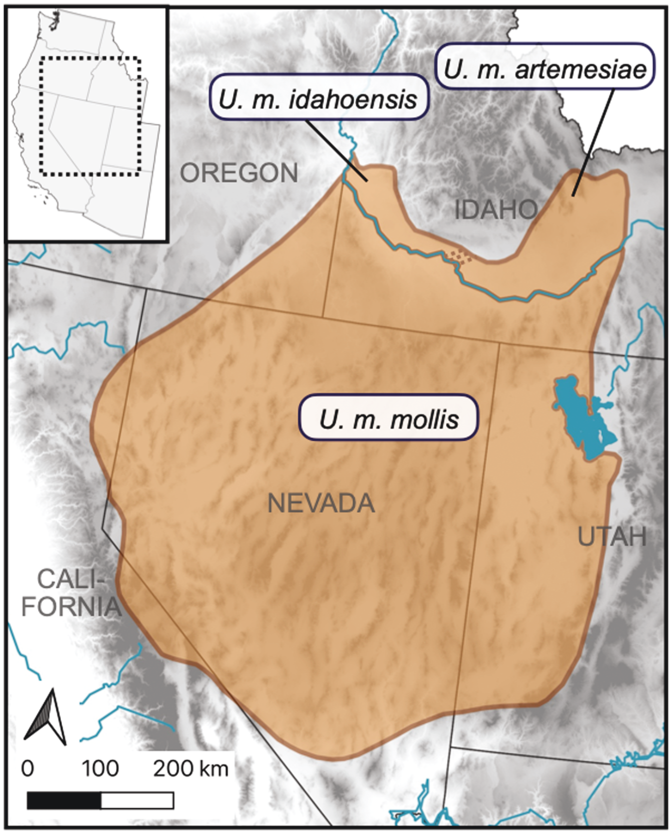

Fig. 1. Map of the western United States depicting geographic ranges of subspecies of *Urocitellus mollis*. The Snake River in Idaho delimits the northern range limit of *U. m. mollis* and the southern range limits of *U. m. idahoensis* and *U. m. artemesiae*, and stippling represents the presumed boundary of the latter 2 subspecies.

Here, we leverage comprehensive taxon sampling and multiple independent data sets to critically evaluate relationships of named forms within *U. mollis*, both with each other and relative to other small-eared taxa. We analyze (i) previously published genome-wide sequence data, reorganized here for targeted species delimitation tests; (ii) mitochondrial (mtDNA) genetic distances from a compilation of previously published cytochrome *b* gene (*CytB*) sequences; (iii) new two-dimensional geometric morphometric data from crania; (iv) new linear measurements from crania and dentitions; and (v) a large compilation of external body measurements from digitized museum specimens. This work refines our concepts of sciurid diversity and endemicity in Idaho and expands knowledge of mammalian diversification here and across the Great Basin and Columbia Plateau more broadly.

Materials and methods.

Nuclear DNA data sets.

We used 2 independent, published nuclear DNA (nuDNA) data sets to test species delimitation hypotheses in *U. mollis* within the broader context of the small-eared group (summarized in Appendix I). All delimitations other than within *U. mollis* followed the existing taxonomy of the Mammal Diversity Database v1.11 (2023). The first data set was from McLean et al. (2016), who inferred the *Urocitellus* phylogeny based a data set of 5 nuclear genes (listed with approved symbol and unique identifiers from HUGO gene nomenclature): partial von Willebrand factor (*Vwf,* HGNC:12726), breast cancer 1 associated protein (*Brap*, HGNC:1099), fibrinogen beta chain (*Fgb*, HGNC:3662), glucosylceramidase beta 1 (*Gba1*, HGNC:4177), and growth hormone receptor (*Ghr*, HGNC:4263). Twelve species (and 33 of 36 subspecies) were represented in that study, including all subspecies within *U. mollis*. However, that study did not perform formal species delimitation and assumed an accurate taxonomy, including a monotypic *U. mollis*. We reanalyzed this 5-gene data set under an alternative taxonomic scheme that split northern and southern *U. mollis* (see *Species tree reconstruction* below) and formally compared the 2 delimitations (see *Tests of species delimitation hypotheses* below).

The second data set was from McLean et al. (2022), who analyzed >3,000 ultraconserved element loci (UCEs) from across the genomes of all 12 species of *Urocitellus*. Based on population clustering analyses of individuals, those authors instead assumed a bitypic *U. mollis* and modeled separate northern and southern lineages for species tree analyses. The study evaluated several alternative taxonomic schemes within small-eared species but not within *U. mollis*. Thus, we reanalyzed the same single nucleotide polymorphism (SNP) data derived from 2,733 original phased UCE loci, coding *U. mollis* as monotypic and formally comparing this delimitation with the previous one assuming 2 species-level lineages. We focus only on the phased SNP data of McLean et al. (2022) because these yielded a more precise resolution of species trees than unphased data (McLean et al. 2022).

All prior studies using field-collected specimens were conducted in accordance with recommendations of the American Society of Mammalogists Guidelines (Sikes et al. 2016) and through an approved institutional animal care and use protocol at the University of New Mexico.

Species tree reconstruction.

Since the analysis of McLean et al. (2016) assumed a monotypic *U. mollis*, our delimitation approach required species tree reestimation with all *U. mollis* individuals from north of the Snake River assigned to a new taxon set, reflecting their potentially unique species identity. For this analysis, we used hierarchical Bayesian inference in the *BEAST module in BEAST v2.6.3 (Bouckaert et al. 2014) and included all species of *Urocitellus* as well as 2 ground squirrel outgroup taxa. The analysis was specified as in McLean et al. (2016). The MCMC chains were run for 2 billion generations, sampling every 2,500 generations and discarding the first 50% as burn-in. Convergence was assessed by visualizing log files in Tracer v1.7.1 (Rambaut et al. 2018) and requiring ESS of >200 for parameters. Results were visualized as a maximum clade credibility phylogram, which we estimated using the *maxCladeCred* function in the phangorn package v2.6.3 (Schliep 2011). We also visualized sets of 5,000 random trees taken from each of these posterior distributions using the *densiTree* function in phangorn.

Tests of species delimitation hypotheses.

Working separately with the 5-gene and UCE data sets, we compared 2 delimitation hypotheses: one in which *U. mollis* encompasses populations north and south of the Snake River in Idaho (i.e., the current taxonomic concept), and a second in which northern and southern populations are distinct. We used path sampling implemented in the BEAST family of software packages, allowing us to approximate the marginal likelihoods of each hypothesis and compare competing delimitation models. Path sampling routines were performed separately for the 5-gene and UCE data sets.

Path sampling for the 5-gene data set was performed in *BEAST v2.6.3 using 48 steps and running each MCMC until convergence (at least 1 million generations each). The data set included representatives of all *Urocitellus* species, which was computationally intensive but facilitated more accurate parameter estimates. Convergence was assessed based on trace plots and requiring effective sample sizes (ESS) >200 for all parameters (in Tracer v1.7.2). Due to difficulty in estimating some parameters across steps, we simplified the site models for all 5 genes from GTR to HKY85, a departure from McLean et al. (2016) that was necessary to achieve MCMC convergence.

Path sampling for the UCE data set was performed using the BFD* approach (Leaché et al. 2014) as implemented within the SNAPP (Bryant et al. 2012) module in BEAST v2.6.3. The data set used for both analyses was an alignment of 299 biallelic SNPs representing all small-eared *Urocitellus* species; these were filtered from the larger data set of 2,733 phased UCEs to a level of 100% character matrix completeness to decrease computational burden. Runs were set up as in McLean et al. (2022), with path sampling performed for 48 steps and chains of 1 million generations per step.

From each path sampling analysis, we calculated Bayes Factors (2 × BF), where BF equaled the difference in marginal log-likelihood between the 2 delimitation hypotheses being compared. Bayes Factor values were evaluated as in Kass and Rafferty (1995), with 2lnBF greater than 10 taken as decisive support (following Leaché et al. 2014). All analyses were run on the Longleaf computing cluster at the University of North Carolina (https://its.unc.edu/).

Mitochondrial DNA comparisons.

To provide a mtDNA-based perspective on diversity in the group, we compiled available sequences of the *CytB* gene from small-eared *Urocitellus* published previously (Harrison et al. 2003; Hoisington-Lopez et al. 2012; McLean et al. 2016, 2022; $n = 41$ individuals, Appendix I). Mitonuclear discordance is documented in *Urocitellus* (McLean et al. 2016, 2022), and for this reason we do not rely on *CytB* for taxonomic recommendations. Nevertheless, *CytB* distances are commonly used in mammalian systematics to support species designations (Baker and Bradley 2006) and can provide a broader context to stimulate future research on the evolutionary causes of discordance. In the case of the Hoisington-Lopez et al. (2012) data set, we selected 3 individuals each from the *brunneus* and *endemicus* lineages, which we again combined as *U. brunneus* given their close genetic relationship and monophyly in all analyses to date. All *CytB* sequences were obtained from GenBank, aligned in MAFFT v7.487 (Katoh and Standley 2013), and analyzed using scripts from the "ape" package (Paradis and Schliep 2019) in R. We computed average pairwise distances among 6 nuDNA lineages (considering *U. mollis* samples from north of the Snake River as distinct). We also computed pairwise genetic distances among individuals and provided average genetic distances within each lineage, thus providing perspective on levels of intraspecific variation. Genetic distances were calculated using a Felsenstein 1984 (Felsenstein 1989) model of sequence evolution, and GenBank accession numbers are provided in Appendix I.

Cranial shape data sets.

To evaluate whether cranial variation in small-eared *Urocitellus* is concordant with nuDNA-based species delimitations, we collected and analyzed 2 cranial morphological data sets (Appendix II). The first was a set of 2D geometric morphometric (GMM) data representing all species and subspecies of small-eared *Urocitellus*. We also analyzed GMM data for only the *U. mollis* group (*artemesiae, idahoensis, and mollis*). The second craniometric data set was comprised of 14 traditional linear measurements taken for lineages in the *U. mollis* group.

Geometric morphometric data were collected by one of us (BSM) from 151 adult specimens of small-eared *Urocitellus*, including a minimum of 19 adult specimens of each species (mean 25, range 19 to 36; Supplementary Data SD1 and SD2). Representatives of the *brunneus* and *endemicus* lineages were pooled as *U. brunneus* due to low sample sizes, as stated above. Our age criterion was complete eruption and development of upper premolars 3 and 4 (P3 and P4, respectively). Both sexes were included in the analysis. Data were collected using the following procedure. Crania were first photographed in ventral aspect using a mounted Nikon D90 DSLR camera fitted with a Nikon AF-S 60mm macro autofocus lens and a standardized position. We then used Helicon Remote software (http://www.heliconsoft.com/) to obtain 15 to 25 high-resolution images throughout the depth of field for each cranium and stacked the images using Helicon Focus software, ensuring proper focus and accurate landmark placement throughout the depth of field. Twenty-four 2D landmarks (Supplementary Data SD1) were digitized on each stacked image using the software tpsDig v2.10 (Rohlf 2006). Landmarks were digitized on the left ventral side of the cranium for most specimens ($n = 83$) or digitized on the right side of other specimens ($n = 68$) where crania were damaged or incomplete. Thus, we implicitly assume the asymmetric component of bilateral shape variation to be small relative to interspecific variation. We performed a Procrustes superimposition using the complete landmark data in the R package "geomorph" v4.0.5 (Baken et al. 2021; Adams et al. 2022) using the function *gpagen*.

Traditional cranial measurement data were collected by one of us (EAR) over a period of 2 days (Supplementary Data SD3). The data set comprised 14 standard measurements (Table 4), and each was recorded to the nearest 0.1 mm using digital calipers. Measurements used here are defined in Helgen et al. (2009). We measured 55 adult specimens from the *U. mollis* group, including a minimum of 13 adult specimens for each subspecies (range 13 to 31). Both sexes were included in the analysis. Summary data for all specimens are presented in Table 4, and a subset of 40 specimens with intact or only slightly damaged skulls were used for further statistical analysis.

Analysis of cranial shape.

Our first objective in analyzing cranial shape was to isolate and test the effects of lineage identity and body size (i.e., evolutionary allometry) within and among 6 nuDNA groups. To answer this question, we used GMM data and a series of Procrustes ANOVAs implemented in the "geomorph" function *procD.lm*. We constructed a fully specified ANOVA considering the predictors of nuDNA group identity ($n = 6$; northern *U. mollis* assigned to a separate lineage), cranial size (logarithm of configuration centroid sizes), and their interaction (which modeled group-specific allometries). We compared this full model to reduced models that lacked either (i) the interaction term; or (ii) the interaction term and the cranial size term (thus ignoring allometry entirely). Comparisons were performed using analysis of variance.

Our second objective was to quantify the classification accuracy of crania to the same 6 nuDNA groups (northern *U. mollis* again assigned to a separate lineage), which is more relevant to our delimitation tests and combines signals from both size and shape. First, we performed canonical variates analysis (CVA) using the CVA function in the R package "Morpho" v2.9 (Schlager 2017), paired with jackknife cross-validation to compute probabilities of group assignment in morphospace. The input for CVA was a principal components analysis (PCA) transformation of the original Procrustes landmark configuration, which we performed using the "geomorph" function *gm.prcomp* to avoid including redundant shape information in the CVA. Second, we estimated pairwise group differences in mean shape statistically using the *pairwise* function in the "RRPP" package v1.3.1 (Collyer and Adams 2021) in R, which is a test of differences between least-squares group means. The input was the simplest Procrustes ANOVA from above, with species identity as the sole predictor variable.

Our third objective was to probe cranial variation just within *U. mollis* as it is currently defined (including subspecies *artemesiae*, *idahoensis*, and *mollis*). This critical delimitation routine was performed using both (i) GMM data and (ii) traditional linear measurements. Analysis of GMM data for *U. mollis* was exactly as above for the entire small-eared group, with configurations subset to include *U. mollis* and realigned using Procrustes superimposition. Analysis of linear measurement data was done using a PCA of the correlation matrix of log10-transformed measurements, using the *prcomp* function in R with the scale parameter set to TRUE. We visualized the spread and extent of nuDNA groups in cranial shape space using plotting routines in the "ggplot2" package (Wickham 2016) in R.

External morphological data and analysis.

To evaluate concordance of external morphological variation with nuDNA-based delimitations, we analyzed 3 external measurements from small-eared *Urocitellus* that are traditionally recorded for museum specimens: total body length (TL), tail vertebrae length (TV), and hindfoot length (HF). We also computed a fourth measurement: head and body length (HBL). To assemble measurement data, we used a hybrid approach that leveraged biodiversity informatic tools and in-person visits to museum collections holding specimens spanning the geographic range of the small-eared clade (Supplementary Data SD4).

External measurements assembled informatically were accessed in the FuTRES trait data store (https://futres.org/), a resource for reporting individual-level trait measurements that currently contain data for modern, archaeological, and fossil mammal specimens (Balk et al. 2022). Data accessed via FuTRES were originally harvested from specimen records contained in VertNet (https://vertnet.org/) using extensions of the traiter toolkit (Guralnick et al. 2016) and republished in the FuTRES v1.0 data shapshot (https://doi.org/10.5281/zenodo.6569644, Guralnick et al. 2022). External measurement data for additional specimens were assembled by 2 of us (BSM, EAR) during in-person visits to the National Museum of Natural History (United States), the University of Kansas Natural History Museum, and the Natural History Museum of Utah.

We curated the combined external measurement data by removing all specimens with missing values for each of the 3 traits of interest. We investigated obvious outliers by visiting their digital occurrence records on the Global Biodiversity Information Facility or Arctos and correcting obvious trait extraction errors manually. For the remaining data, we used scripts from the "OutlierDetection" package in R (Tinwari and Kashikar 2019) as in Balk et al. (2022) to identify additional putative outliers. Specifically, we used the univariate outlier detection method based on Euclidean distances, with a cutoff of 95% for all traits. The derived HBL metric was also subjected to outlier detection. Following this routine, the final database included 1,051 records, with a mean of 131 (range 37 to 283) observations per species in the combined TL, TV, and HBL data set (subspecies of *U. mollis* considered separately) and a mean of 39 (range 37 to 307) observations per species for the HF data set. Sample sizes are reported separately here given the substantially lower amount of HF measurements available, especially from older specimens. Distributions of traits were plotted using routines in the "ggridges" (Wilke 2024) and "ggplot2" packages in R.

Because age verification was not possible for all specimens in the external measurement database, we reanalyzed a subset of *U. mollis* specimens for the same external measurements and 2 additional ratios (TV/HBL, HF/HBL). These specimens were originally collected and measured by a total of 3 individuals at 2 institutions, and they have associated age class information, making them useful for comparing central tendencies and ranges of the *U. mollis* lineages in question.

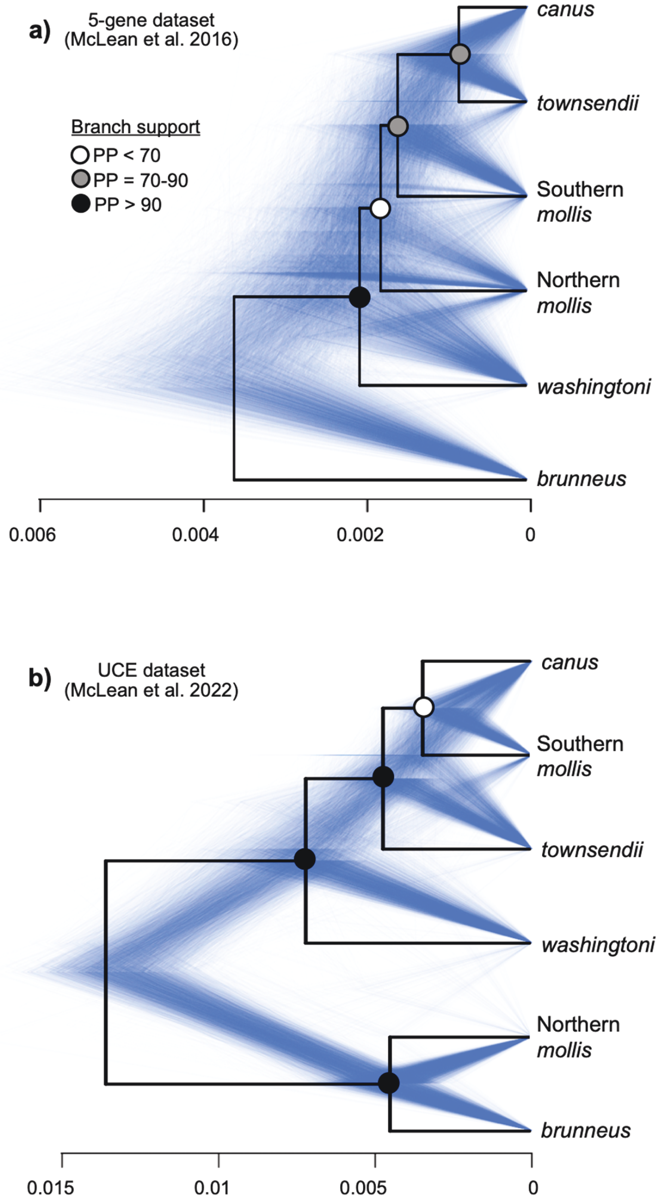

Fig. 2. Maximum clade credibility (MCC) phylograms of small-eared *Urocitellus* inferred from Bayesian analysis of a) 5 nuclear genes in *BEAST and b) 2,733 ultraconserved element loci in SNAPP. For each plot, the MCC phylogram (single bold bifurcating tree) is plotted over 5,000 trees drawn from the posterior distribution of each analysis (underlying shaded trees). Outgroups (differing for each study) were trimmed for clarity. Shading on nodes reflects ranges of Bayesian posterior probability values as described in the legend. Representatives of the *brunneus* and *endemicus* lineages were pooled here as "*U. brunneus*" given their close genetic relationship.

Results

Species trees and nuDNA-based delimitation.

Species trees based on different nuDNA data sets varied in their support for the placement of northern and southern *U. mollis* (Fig. 2). Relationships among small-eared species were resolved by the 5-gene data set with a range of posterior probabilities. We recovered *U. brunneus* (containing the *brunneus* and *endemicus* lineages) as sister to all other small-eared species with high support (PP = 0.96). We recovered a clade containing *canus*, *townsendii*, and southern *mollis* with moderate support (PP = 0.79; Fig. 2a). However, uncertainty existed in the placement of northern *U. mollis*, which we recovered as sister to the former 3-taxon clade with low support (PP = 0.41). Relationships were better-resolved in the UCE-based species trees (Fig. 2b; McLean et al. 2022), which supported a *brunneus* + northern *mollis* clade (PP = 0.98) and placed it sister to a clade containing all other small-eared species (including southern *mollis*; PP = 0.98; Fig. 2b). While placement of southern *mollis* also varied among different UCE data sets and inference methods in McLean et al. (2022), none supported monophyly of *U. mollis* as currently defined.

Tests of species delimitation hypotheses supported the distinctiveness of *U. mollis* occurring north and south of the Snake River (Table 1). There was decisive support (i.e., 2lnBF exceeding 10) for distinct northern and southern *U. mollis* lineages based on the 5-gene data set (2lnBF = 78.40), despite the lack of topological resolution in species tree analysis of those data (Fig. 2a). Even more decisive support was found for this same hypothesis (relative to a hypothesis of *U. mollis* monophyly) based on the UCE data set (2lnBF = 397.12). While the placement of northern and southern *U. mollis* varied between the independent nuDNA data sets, both supported a taxonomic scheme where northern and southern *U. mollis* were assigned to distinct lineages.

Aspects of mtDNA variation.

Pairwise genetic distances among all individual *CytB* gene sequences analyzed here ranged from 0% to 9.09%. Average pairwise distances among the 6 nuDNA lineages (i.e., with northern and southern *mollis* as distinct) ranged from 2.27% (*canus*–southern *mollis* comparison) to 8.68% (*brunneus* [*brunneus* + *endemicus*]–*townsendii* comparison; Table 2). The average *CytB* distance between northern and southern *mollis* was 4.09%. This was lower

Table 1. Bayes factor-based tests of species delimitation hypotheses for *U. mollis* based on nuclear DNA sequence data.

Model	Marginal L	2lnBF
Five gene data set		
6 spp (northern *mollis* distinct)	−7,875.92	—
5 spp (northern + southern *mollis*)	−7,836.72	78.40
Ultraconserved element data set		
6 spp (northern *mollis* distinct)	−4,135.14	—
5 spp (northern + southern *mollis*)	−3,936.58	397.12

Two hypotheses were compared: a 5-species model reflecting current taxonomy and a 6-species model recognizing distinctiveness of *U. mollis* north of the Snake River in Idaho. Tests were performed separately on a data set of 5 nuclear genes (McLean et al. 2016) and 299 phased SNPs from ultraconserved element loci (McLean et al. 2022). Both data sets included multiple representatives of each species-level lineage. For each analysis are reported the delimitation hypothesis, model rank (within sequence data sets), marginal log-likelihood from path sampling analysis, and 2 × log Bayes Factor.

than all other between-species comparisons except for the *canus*–southern *mollis* comparison above (Table 2), and it corresponds with mtDNA-based phylogenies, which differ from nuDNA in suggesting a closer (though not reciprocally monophyletic) relationship of northern and southern *U. mollis* (Harrison et al. 2003; Herron et al. 2004; McLean et al. 2016, 2022). Interestingly, the greatest average within-lineage CytB distance was found in northern *U. mollis* (2.61%), which included the *idahoensis* and *artemesiae* subspecies (Table 2).

Aspects of cranial and external variation.

Ventral cranial shape in small-eared *Urocitellus* was best predicted by a combination of nuDNA lineage identity ($F = 8.04$, $P = 0.001$) and among-group allometry ($F = 10.61$, $P = 0.001$; Table 3). This top-ranked Procrustes ANOVA outranked a simpler model containing lineage as a sole factor ($P = 0.044$), as well as a more complex model that included lineage-specific allometries ($P = 0.068$). As suggested from the top model, group means were distinguishable, and all pairwise lineage comparisons ($n = 15$) supported group differences, except in 1 case (northern and southern *U. mollis* comparison; $P = 0.08$).

While lineages were statistically distinguishable based on ventral cranium shape, there was nevertheless a substantial overlap in ordination space (Fig. 3). We found *U. brunneus* (including *brunneus* and *endemicus* lineages) to be most strongly differentiated on canonical axis 1, which represented 53.2% of the total among-group variation. All *U. brunneus* specimens were accurately classified as that species. The remaining 5 nuDNA groups were incompletely differentiated along this and subsequent canonical axes, with classification accuracies ranging from 55% (southern *U. mollis*) to 86% (*U. canus*). As in the ANOVA above, northern and southern *U. mollis* exhibited the least pairwise differentiation in cranial shape and the lowest percentages of correct jackknife classifications (70% and 55%, respectively; Fig. 3). The highest pairwise misclassifications that we observed were southern *U. mollis* incorrectly assigned to northern *U. mollis* (4 of 20 specimens incorrect), and northern *U. mollis* incorrectly assigned to either southern *U. mollis* or *U. townsendii* (each 3 of 27 specimens incorrect).

Conversely, in analyses considering only the *U. mollis* group, subspecies were more easily discriminated using GMM and traditional linear measurements. The latter were more useful in discriminating subspecies, so we limit discussion to these. In a PCA based on 14 log10-transformed measurements from 40 adult specimens (including 9 *U. m. artemesiae*, 8 *U. m. idahoensis*, and 23 *U. m. mollis*), the first 4 components accounted for 75.7% of the total variance (Fig. 4). All variables had positive loadings on the first component, and most (12 of 14) were of moderate to high magnitude (0.533 to 0.915) indicating that the first component reflected size variation. Component 2 accounted for an addition 12.1% of the total variance, with the highest magnitude negative loadings for the length of the bulla and maxillary toothrow and positive loading for the length of the bony palate, thus separating individuals with long palates and small bullae and large teeth from those with the opposite features. This axis separated *U. m. mollis* from *U. m. idahoensis* + *artemesiae*. Component 3 (10% of the variance) separated individuals with broad postorbital regions, narrow breadth across auditory bullae, and smaller teeth from those with the converse. Component 4 (8.6%) separated individuals on the basis of anterior palatal breadth but otherwise was uninterpretable.

External body proportions did not clearly separate lineages of small-eared *Urocitellus*. Substantial overlap was observed in standard measures of TL, HBL, TV, and HF. Outside of *U. mollis*, the *U. brunneus* lineage presented the greatest and most distinctive values for these measurements (Fig. 5), a finding similar to the cranial shape data (Fig. 3). Interestingly, the magnitude of variation observed across 3 lineages of *U. mollis* was comparable to that seen across the entire small-eared group (Fig. 5). The *U. m. idahoensis* lineage had the greatest mean HBL, TV, and HF, while the *U. m. artemesiae* lineage had the smallest averages for all measurements. *Urocitellus m. mollis* was typically intermediate for these same measurements.

Table 2. Average pairwise cytochrome *b* distances among 6 nuclear DNA genetic lineages of small-eared *Urocitellus* ($N = 41$ total sequences).

	brunneus	***canus***	***mollis* North**	***mollis* South**	***townsendii***	***washingtoni***
brunneus	0.34 (10)					
canus	5.38	1.18 (8)				
mollis North	6.33	4.23	2.61 (7)			
mollis South	6	2.27	4.09	1.55 (3)		
townsendii	8.68	7.55	8.19	7.75	1.07 (7)	
washingtoni	7.99	6.88	8.17	7.1	7.45	0.19 (6)

Representatives of the *brunneus* and *endemicus* lineages were pooled here as "*U. brunneus*" given their close genetic relationship. Distances were calculated assuming a Felsenstein 1984 model of sequence evolution (Felsenstein 1989). Average within-lineage genetic distances (with sample sizes in parentheses) are shown on the diagonal.

Discussion

Delimiting temperate mammal diversity.

New species of mammals have been described at a steady and elevated rate over the past 2 decades, with a majority of cryptic diversity emerging from tropical regions (Reeder et al. 2007; Burgin et al. 2018). A global reanalysis (Parsons et al. 2022) likewise predicted that the highest densities of future new species delimitations may be concentrated in low-latitude and tropical regions, although

Table 3. Summary of the top-ranked Procrustes Analysis of Variance relating ventral cranial shape to nuclear DNA lineage identity and cranial size in small-eared *Urocitellus*.

Variable	*df*	SS	F	Z	P
Log(centroid size)	1	0.010230	10.6087	5.4979	0.001
NuDNA lineage	5	0.038769	8.0409	8.8556	0.001
Residuals	144	0.138859			
Total	150	0.187858			

This model outranked a simpler model containing lineage identity alone, as well as a more complex model including an additional lineage × size term (species-specific allometries). See the main text for further details about ANOVA construction.

Table 4. Cranial and dental measurements (X ± 1 SD and ranges in millimeters) of adult *Urocitellus mollis* sensu lato subspecies.

Measurement	*U. m. artemesiae*	*U. m. idahoensis*	*U. m. mollis*
Condylobasal length (CBL)	34.3 ± 1.0 32.7–36.2 (10)	36.9 ± 0.9 36.2–39.0 (8)	36.0 ± 1.3 33.4–38.6 (31)
Zygomatic breadth (ZB)	23.9 ± 0.6 22.8–24.7 (11)	25.2 ± 0.8 24.1–26.7 (8)	24.7 ± 0.9 23.1–26.6 (31)
Breadth of braincase (BBC)	17.0 ± 0.4 16.2–17.9 (13)	17.8 ± 0.5 17.3–18.4 (8)	17.2 ± 0.4 16.5–18.0 (30)
Height of braincase (HBC)	12.4 ± 0.2 12.2–12.9 (12)	13.2 ± 0.3 12.7–13.5 (8)	13.1 ± 0.5 12.2–13.9 (29)
Interorbital breadth (IOB)	7.7 ± 0.4 7.0–8.4 (13)	8.0 ± 0.3 7.6–8.6 (9)	8.1 ± 0.5 7.2–9.4 (28)
Postorbital breadth (POB)	9.9 ± 0.5 8.7–10.6 (14)	10.3 ± 0.4 9.7–10.7 (9)	9.6 ± 0.5 8.6–10.4 (30)
Length of auditory bulla (LAB)	7.6 ± 0.3 7.1–8.1 (13)	8.7 ± 0.2 8.4–8.9 (8)	8.5 ± 0.3 8.0–9.1 (31)
Width across auditory bullae (WAAB)	20.2 ± 0.6 19.3–21.4 (12)	21.7 ± 0.7 20.8–23.2 (8)	21.0 ± 0.7 19.7–22.3 (28)
Length of bony palate (LBP)	13.7 ± 0.2 13.4–13.9 (14)	14.7 ± 0.5 14.0–15.9 (9)	14.7 ± 0.5 13.7–15.8 (30)
Postpalatal length (PPL)	13.6 ± 0.4 12.9–14.5 (12)	14.4 ± 0.2 13.8–14.6 (8)	13.8 ± 0.5 13.0–15.1 (30)
Palatal breadth at M1	5.2 ± 0.3 4.8–5.7 (15)	5.8 ± 0.3 5.4–6.2 (9)	5.2 ± 0.4 4.2–5.9 (30)
Palatal breadth at M3	4.6 ± 0.3 4.1–5.1 (15)	5.0 ± 0.2 4.7–5.3 (9)	5.0 ± 0.4 4.0–5.7 (3)
Length of maxillary toothrow (P3–M3)	7.9 ± 0.4 7.3–8.5 (15)	8.5 ± 0.2 8.3–8.9 (9)	8.5 ± 0.2 8.0–9.0 (30)
Width of M2 (WM2)	2.5 ± 0.1 2.3–2.7 (15)	2.7 ± 0.1 2.5–2.9 (9)	2.6 ± 0.1 2.4–3.0 (30)

Sample sizes in parentheses.

variables of body mass, range area, and extent of prior research and sampling were also predictive of undescribed diversity.

Despite its relatively high latitude, northwestern North America has emerged as a nexus of cryptic diversity in some temperate mammals (Hafner and Upham 2011; Riddle et al. 2014; Malaney et al. 2017; Colella et al. 2021), including the family Sciuridae (Phuong et al. 2014; Arbogast et al. 2017; Herrera et al. 2022; Mills et al. 2023), and spanning both coastal and interior faunas. This overlooked diversity is perhaps unsurprising given the dynamic tectonic, paleooceanic, and paleoclimatic history of the region and its impacts on mammal diversity through deeper time (Badgley 2010; Badgley et al. 2014). Unfortunately, accurate delimitation in these faunas is often labor-intensive because many lineages are morphologically conserved (including ground squirrels; McLean et al. 2018), subsumed within widespread taxa (requiring range-wide sampling), or most convincingly diagnosed with genome-scale data (i.e., cryptic species). Thus, integrative taxonomic analyses are essential even in well-studied taxa throughout North America to better define biodiversity and trends across the continent.

The highest species diversity in small-eared *Urocitellus* exists in the northern Great Basin (especially southern Idaho) and Columbia Plateau in Oregon and Washington, a region where recent studies have uncovered some other distinctive mammal lineages. Herrera et al. (2022) reported 2 cryptic, species-level lineages of chipmunk (*Neotamias*) based on whole genome data: the Crater chipmunk (*N. cratericus*), which is restricted to Craters of the Moon lava flows and nearby mountain ranges of central Idaho north of the Snake River; and the Coulee chipmunk (*N. grisescens*), which has a narrow range in the Channeled Scablands of central Washington. Riddle et al. (2014) restricted the pocket mouse *Perognathus parvus* sensu lato to the Columbia Plateau in Washington and Oregon, elevating the Great Basin population of that taxon (*P. mollipilosus*) to species status. Strikingly, these sister species exhibit up to 18.8% mtDNA divergence from one another based on the cytochrome oxidase subunit 3 (*coIII*) gene. These studies further highlight the importance of the Columbian Plateau and Great Basin in the deep biogeographic history of some small mammals in the region.

Although molecular systematics of *Urocitellus* ground squirrels was actively researched half a century ago (e.g., Nadler 1966, 1968;

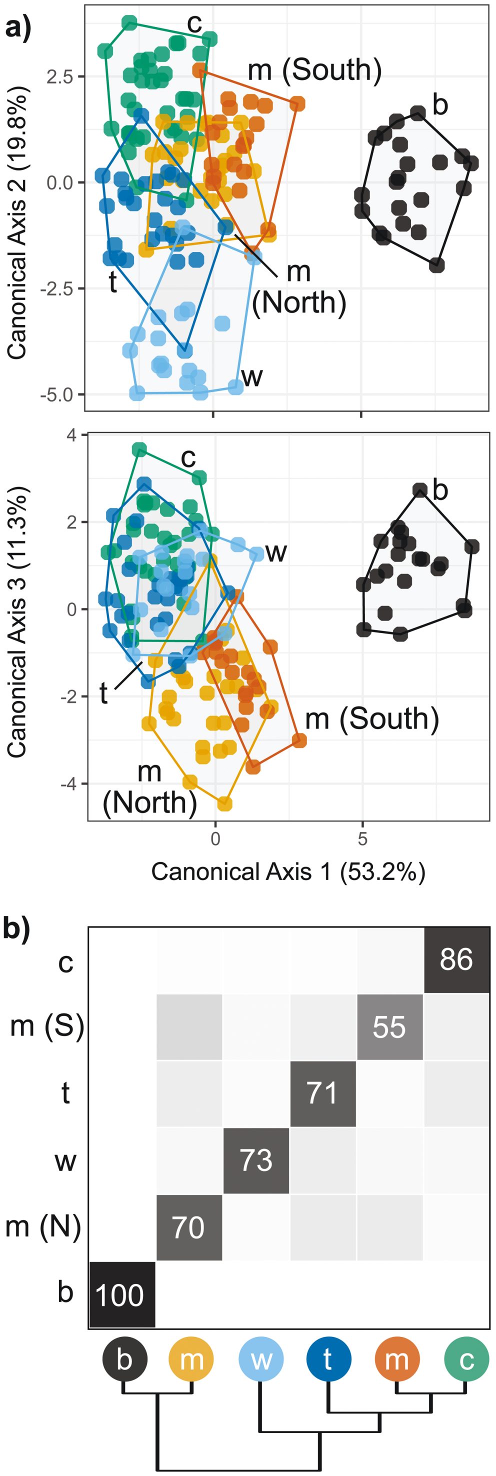

Fig. 3. Cranial shape variation in 6 nuclear DNA lineages of small-eared *Urocitellus* based on 24 two-dimensional landmarks. a) Plots of group-wide variation from canonical axes 1 and 2 (top), and 1 and 3 (bottom). b) Heatmap of classification accuracies among all pairwise combinations of the 6 genetic lineages. Percent accurate classifications for each species are specified with numbers on the diagonal. b = *brunneus*, c = *canus*, w = *washingtoni*, t = *townsendii*, m (North) = northern *mollis*, m (South) = southern *mollis*. The cladogram at the bottom is the tree in Fig. 2b. Representatives of the *brunneus* and *endemicus* lineages were pooled here due to low sample sizes.

Nadler et al. 1982, 1984), integrative tests of existing taxonomic delimitations have been lacking apart from the work of Hoisington-Lopez et al. (2012) on *U. brunneus*. We focused here on delimitation in a single, widely distributed small-eared species (*U. mollis*; Piute Ground Squirrel) distributed across much of the Great Basin as ecologically defined (Grayson 2011). Nuclear DNA data supported distinct evolutionary histories in *U. mollis* populations occurring north and south of the Snake River in Idaho. We failed to recover these geographic lineages of *U. mollis* sensu lato as reciprocally monophyletic in any analysis, and Bayes Factor-based species delimitation tests decisively rejected their monophyly (Table 1) regardless of exact topological resolution.

The clear and convincing nuDNA evidence for unrecognized species-level diversity within *U. mollis* contrasts with more subtle differentiation in cranial morphology, external morphology, pelage, and even mtDNA sequences. Whereas GMM-based analyses of the ventral cranium did not strongly discriminate northern and southern *U. mollis* (Figs 3 and 4b), traditional linear measurements encompassing the entire cranium did this when taxonomic sampling was limited to just the focal taxa. Linear measurements also separated subspecies *idahoensis* and *artemesiae* within the northern *mollis* lineage (Fig. 4a). Thus, evidence from morphology of the entire cranium supports nuDNA-based delimitation hypotheses presented here.

Considering external morphology, we observed a high degree of conservatism in the group. Even though some statistical differences

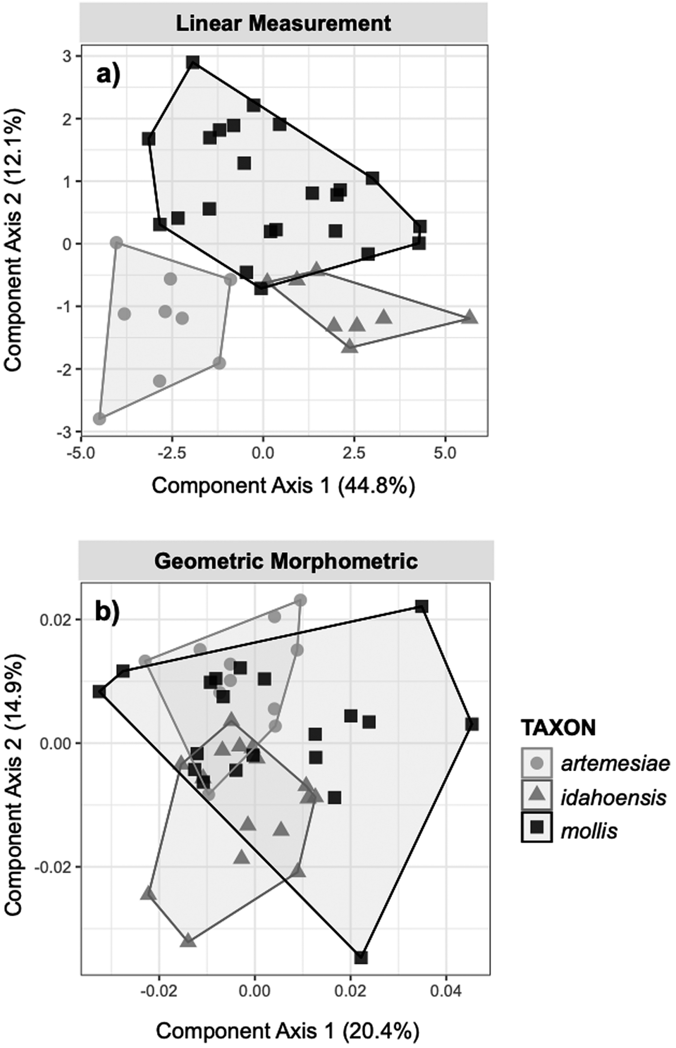

Fig. 4. Principal component analysis of cranial morphology among *U. mollis* sensu lato subspecies based on a) 14 traditional linear measurements and b) 24 two-dimensional geometric morphometric (GMM) landmarks. The GMM data are representative of the ventral cranium only.

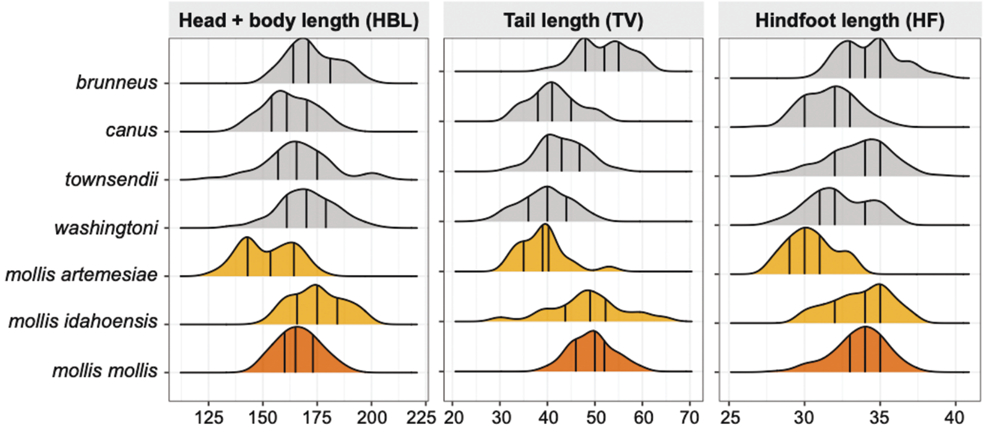

Fig. 5. Ridgeline plots showing distributions of 3 external body measurements in lineages of small-eared *Urocitellus*. Representatives of the *brunneus* and *endemicus* lineages were pooled here due to low sample sizes. *U. mollis artemesiae* and *U. m. idahoensis* represent a single clade (e.g., Fig. 2) but are plotted separately here.

exist among small-eared species, most of them overlap substantially in measurements of HBL, TV, and HF (Fig. 5). External morphology does support recognition of the 2 existing forms within northern *U. mollis* (subspecies *idahoensis* and *artemesiae*), with *idahoensis* being larger in each external metric. However, southern *U. mollis* displays intermediate values between *U. m. idahoensis* and *U. m. artemesiae* for all metrics. External morphological characters therefore do not predict the species-level differences suggested by our nuDNA-based phylogenies, although they do support current delineations at the subspecific level.

Finally, mtDNA data corroborated our major nuDNA-based conclusions but revealed discordant patterns as well. The mtDNA-based phylogeny failed to recover a monophyletic *U. mollis* and is thus in agreement with nuDNA. However, mtDNA trees placed northern *U. mollis* sister to a clade containing southern *U. mollis* and *U. canus* (Harrison et al. 2003; Herron et al. 2004; McLean et al. 2016, 2022), suggesting a closer relationship than in nuDNA trees. Similarly, the average *CytB* distance between northern and southern *U. mollis* was 4.09%, which, while greater than some between-species comparisons in mammals, is lower than most other pairwise species comparisons in the small-eared group (Table 2). Mitochondrial data therefore suggest a closer affinity between northern and southern *U. mollis* than does nuDNA. The cause(s) of this mitonuclear discordance and whether there could be potential hybridization signatures in regions of the nuclear genome beyond UCEs and in taxon pairs beyond those examined by McLean et al. (2022), are important next steps in future work.

Given decisive nuDNA evidence and support from multiple morphological aspects, we re-elevate populations of *U. mollis* sensu lato occurring north of the Snake River (referred to above as "northern *U. mollis*") to their own species, *U. idahoensis* (Merriam 1913), which encompasses 2 subspecies: the larger-bodied *U. i. idahoensis* in the west Snake River Plain and the smaller-bodied *U. i. artemesiae* in the east Snake River Plain (see the Nomenclature section for further descriptive notes and synonymies). We restrict the nomen *U. mollis* (Kennicott 1863) to populations occurring south of the Snake River (referred to above as "southern *U. mollis*") with priority taken from the original type locality ("Camp Floyd, near Fairfield, [Utah County,] Utah") of Kennicott (1863). Our inference that the most recent common ancestor of northern and southern lineages existed early in the history of the small-eared clade (i.e., Fig. 2b) reflects a substantially deeper history of diversification across the Great Basin and Columbia Plateau for the entire group than previously appreciated.

Importance of the Snake River as a physiographic barrier.

Population connectivity for many low-elevation, terrestrial vertebrates is high in the interior Great Basin (Jezkova et al. 2011; Mantooth et al. 2013; Riddle et al. 2014; but see, e.g., Hafner and Upham 2011; Jezkova et al. 2015). This may be due to the general discontinuity of physiographic barriers, including rivers, nearly all of which drain inward rather than transecting basin boundaries. An exception to this pattern is the Snake River, which flows in a generally east-west direction across southern Idaho, thus dissecting the northern Great Basin. The Snake River has been a prominent and persistent landscape feature since the Miocene, draining the Yellowstone hotspot and adjacent regions to the east and encompassing several intermittent paleolakes along its course in Idaho, including Lake Idaho, a large paleolake in the western Snake River Plain (Beranek et al. 2006; Grayson 2011; Staisch et al. 2022). It has remained a major hydrological feature and drained the massive Lake Bonneville as recently as the late Quaternary.

Merriam (1913) described 3 forms (species or subspecies) within the *U. mollis* group from north of the Snake River in Idaho. Howell (1938) and Davis (1939) retained 2 of these as species (*idahoensis* and *artemesiae*). While neither Merriam (1913) nor Howell (1938) elaborated on the possible role of the Snake River as a barrier to dispersal, Davis (1939) wrote extensively about the antiquity of this feature and its role in limiting the movements of Idahoan mammals. He asserted that the Snake River placed greater dispersal limitations on "hibernating, land-dwelling mammals which are closely restricted to a definite home territory and… [are] burrowing" (p. 53). He did not consider the Snake River impermeable to mammals, instead arguing that a species potential to disperse across this feature varied with its breadth, which increases along its course from southeastern to southwestern Idaho.

Citing *Urocitellus* as one example, Davis (1939) hypothesized minimal trans-riverine dispersal in western Idaho where the Snake reaches its greatest breadth, and the distributions of multiple lineages are bounded by it (*U. i. idahoensis* to the north, *U. mollis* to the southeast, and *U. canus vigilis* to the southwest). Conversely, in eastern Idaho, where the Snake River and its tributaries are narrower, he hypothesized higher dispersal and intergradation between lineages north and south of the drainage (e.g., *U. i. artemesiae* and *U. mollis*), respectively. These assertions were based on previous morphology-based concepts of relatedness between lineages (Merriam 1913; Howell 1938), which our nuDNA-based phylogenies did not support. Instead, the new phylogenetic hypotheses presented here support a longstanding role for the Snake River in the diversification of small-eared *Urocitellus* throughout its entire length, likely as a barrier that promoted allopatric speciation or, minimally, reinforced isolation of already-diverged lineages. Further work is needed to test the permeability of the Snake River as a biogeographic barrier for other mammals, which may start with testing for gene flow at landscape scales between populations of *U. mollis* south of the Snake River with those of *U. i. idahoensis* and *U. i. artemesiae* to the north.

Conservation aspects.

Urocitellus idahoensis has a maximal bounded range area of roughly 29,700 km^2 spread across 22 counties in Idaho. This figure is only 7.5% of the total range area of *U. mollis,* as redefined here. However, its distribution within this range polygon is highly discontinuous, and the total area of occupied habitat is likely substantially less. Given the restricted range of *U. idahoensis* and a myriad of possible threats to this taxon, renewed population censuses, monitoring, and assessment of threats are sorely needed. Possible threats faced by *U. idahoensis* include (i) habitat loss and fragmentation, paired with accelerated fire regime; (ii) broader climatic shifts, including changing trends in seasonality, which could affect hibernation phenology; and (iii) human interactions, especially shooting and the application of rodenticide. A fourth threat of intermittent disease outbreaks—especially sylvatic plague—is known to place additional pressure on ground squirrel populations and can compound negative impacts from other threats (U.S. Fish and Wildlife Service 2004; Steenhof et al. 2006; Goldberg et al. 2021; Idaho Department of Fish and Game 2024). Data supporting actual population impacts of any of these factors on *U. idahoensis* are extremely limited, however.

For example, a well-documented positive feedback loop between the expansion of invasive annual grasses like Cheatgrass (*Bromus tectorum*) and an accelerated fire regime has led to significant sage-steppe landscape conversion in western North America (Knick and Rotenberry 1997; Bradley et al. 2018; Crist et al. 2023). The Snake River Plain is an epicenter of this phenomenon, having experienced widespread conversion from a shrub and forb mosaic dominated primarily by Sagebrush (*Artemisia* spp.) to one of cheatgrass and other exotic annual grasses (Boyte and Wylie 2017), which can directly impact some ground squirrels (Yensen et al. 1992; Steenhof et al. 2006; Lohr et al. 2013; Holbrook et al. 2016). Obligate heterotherms, like all small-eared *Urocitellus,* are vulnerable to food availability in the active and breeding seasons since they emerge in late winter and begin the estivation/hibernation phase in early summer (Davis 1939; Rickart 1987). Changes in forage phenology coupled with potential earlier hibernation emergence due to earlier snowmelt, which has been seen in *U. brunneus* (Goldberg and Conway 2021), may result in suboptimal foraging conditions. Impactful management actions could include enhancing the availability of spring forage through native plant diversity, reduced coverage of invasive grasses, and suppression of accelerated fire regimes.

Negative human interactions could pose additional threats to *U. idahoensis*, driven in part by the proclivity of this species for burrowing in and adjacent to agricultural and ranching lands (Davis 1939; Durrant and Hansen 1954; Rickart 1987). Shooting but not harvesting ground squirrels (thus leaving the carcass on the landscape) is also a popular activity in parts of the range, including on the Morley Nelson Snake River Birds of Prey National Conservation Area in southwest Idaho, where *U. idahoensis* is believed to be relatively abundant (Katzner et al. 2020; Aberg 2023). Additional research is needed to determine the population-level effects of shooting on *U. idahoensis*, especially given the existing estimates of individual ground squirrels killed (Pauli et al. 2019) and the current lack of management focus relative to other *Urocitellus* endemic to Idaho (Idaho Department of Fish and Game 2024).

Finally, disease outbreaks are known to cause temporary reductions in population densities in *U. idahoensis* and other ground-dwelling squirrels. The most notable of these is sylvatic plague, caused by the bacterium *Yersinia pestis,* a pathogen endemic to Eurasia but introduced to the western United States in the early 1900s (Gage and Kosoy 2005; Morelli et al. 2010). Plague persists in animal reservoirs in the western United States and is vectored by infected fleas. Accordingly, this pathogen thrives in social and colonial reservoir species, such as some ground-dwelling sciurids (Biggins and Kosoy 2001; Augustine et al. 2023). Within the range of *U. idahoensis*, few studies have quantified the extent or impact of plague on ground squirrels except in northern populations of the Idaho Ground Squirrel (*U. brunneus*) and in the Columbian Ground Squirrel (*U. columbianus*; Goldberg et al. 2021).

In conclusion, species delimitation integrating multiple DNA sequence and morphological data sets supports specific recognition of the Idaho-endemic taxon *U. idahoensis* (Snake River Plains Ground Squirrel), distinguishing it from *U. mollis* (Piute ground squirrel) south of the Snake River. Our findings sharpen understanding of ground squirrel diversity and distributions in the northern Great Basin and Columbia Plateau ecoregions and reemphasize the importance of the Snake River as a biogeographic barrier that also separates these 2 taxa. This new taxonomy also provides essential knowledge for effective conservation. Given the restricted geographic range of *U. idahoensis*, renewed conservation and landscape connectivity assessments are critical given a combination of potential threats that could place increasingly inflexible constraints on the maintenance of healthy populations. Modeling tools that provide range-wide measures of ecological resilience in the sagebrush biome and resistance to threats could aid in the prioritization of protective or restorative actions (Chambers et al. 2023). Positive outcomes may require paradigm shifts towards adaptive wildlife management encompassing multiple potential threats of changing seasonality, fire regime, human interactions, and disease.

Nomenclature

Family Sciuridae Fischer, 1814

Subfamily Xerinae Murray, 1866

Tribe Marmotini Pocock, 1923

Genus *Urocitellus* Obolenskiy, 1927

Urocitellus idahoensis comb. nov. (Merriam, 1913)

Snake River Plains Ground Squirrel

Urocitellus idahoensis idahoensis *comb. nov*. (Merriam, 1913)

Spermophilus townsendi Merriam, 1891:36. Not *Spermophilus townsendii* Bachman, 1839.

Citellus idahoensis Merriam, 1913:135. Type locality "Payette, at junction of Payette and Snake River, [Payette County,] Idaho," United States.

Citellus mollis idahoensis: Davis, 1939:184. Name combination.

Spermophilus townsendii idahoensis: Hall and Kelson, 1959:336. Name combination.

S[*permophilus*]. *idahoensis*: Nadler, 1968:144. Name combination.

S[*permophilus*]. *m*[*ollis*]. *idahoensis*: Nadler et al., 1982:199. Name combination.

U[*rocitellus*]. *m*[*ollis*]. *idahoensis*: Helgen et al., 2009:297. Name combination.

Holotype

USNM 168290; adult female skin and skull with the following measurements: total length 263 mm, tail length 61 mm, hindfoot length 35 mm. Collected 23 April 1910 by S. G. Jewett.

Urocitellus idahoensis artemesiae comb. nov. (Merriam, 1913)

Citellus mollis artemesiae Merriam, 1913:137. Type locality "Birch Creek, [Clark County,] Idaho," United States.

Citellus mollus [sic] *pessimus* Merriam, 1913:138. Type locality "lower part of Big Lost River, [Butte County,] east central Idaho," United States.

Citellus townsendii artemesiae: Howell, 1938:65. Name combination.

Spermophilus townsendii artemesiae: Hall and Kelson, 1959:336. Name combination.

Spermophilus artemesiae: Rickart, 1989:532. Name combination.

S[*permophilus*]. *m*[*ollis*]. *artemesiae*: Wilson and Ruff, 1999:426. Name combination.

S[*permophilus*]. *mollis artemisiae* Yensen and Sherman, 2001:74. Incorrect subsequent spelling of *Citellus mollis artemesiae* Merriam, 1913.

U[*rocitellus*]. *m*[*ollis*]. *artemesiae*: Helgen et al., 2009:297. Name combination.

Holotype

USNM 23489; adult male skin and skull with the following measurements: total length 188 mm, tail length 43 mm, hindfoot length 31 mm, ear length 3 mm. Collected on 9 August 1890 by V. Bailey and B. H. Dutcher.

General characteristics.

Includes both the smallest (*U. i. artemesiae*) and largest (*U. i. idahoensis*) of the small-eared *Urocitellus* (see Table 5 for specific external measurements and means for both subspecies). As in other small-eared *Urocitellus*, members of the species have a shorter tail (generally <60 mm) and hindfoot length (<39 mm) relative to body size in comparison to the long-eared clade and possess inconspicuous external pinnae. General dorsal color variegated yellowish-brown with pale yellow dappling that is most distinct on rump but extending to shoulders in some individuals. In subspecies *artemesiae*, dappling less distinct (pale markings fewer and smaller), along with in older individuals of *idahoensis*. Individual guard hairs dark gray basally, pale yellow mid-length, and black distally. Lateral and ventral surfaces grayish. Top of nose, outer surfaces of the lower hind legs, and underside of the tail are reddish-brown. Tail with a grayish-black subterminal patch (less distinct in *artemesiae*). The eye ring and anterior edge of the pinna are white. Feet yellowish-white.

Bowing in the zygomatic arches varies in adults, being more outbowed in shorter skulls and inbowed in longer skulls (according to Merriam 1913). Temporal ridges are lyrate, meeting in older individuals near the base of the skull. Postorbital process is long and slender, curving downward towards the tip; supraorbital boundaries are slightly elevated. Cheek teeth are hypsodont and robust. Dental formula is 1/1, 0/0, 2/1, 3/3 = 22. See Table 5 for specific cranial measurements and means for subspecies *idahoensis* and *artemesiae*.

Table 5. External measurements (X ± 1 SD and ranges in millimeters) and measurement ratios (expressed as percentages) of known-age *Urocitellus mollis* sensu lato subspecies.

Measurements	*U. m. artemesiae*	*U. m. idahoensis*	*U. m. mollis*
Length of head and body (HBL)	166.5 ± 5.7 154–174 (15)	180.3 ± 3.1 175–185 (12)	175.5 ± 8.5 156–193 (31)
Length of tail vertebrae (TV)	44.4 ± 4.4 40–53 (14)	53.4 ± 7.5 40–62 (12)	50.4 ± 4.4 45–60 (31)
Length of hind foot (HF)	32.7 ± 0.6 30–33 (15)	36.4 ± 1.3 34–39 (13)	34.2 ± 1.2 32–37 (31)
TV/HBL (%)	27 24–31 (14)	30 23–34 (12)	30 24–38 (31)
HF/HBL (%)	19 19–21 (15)	20 19–22 (12)	20 18–22 (31)

Sample sizes in parentheses.

Comparison

Present comparisons focus only on the formerly conspecific *U. mollis*, *U. i. idahoensis*, and *U. i. artemesiae*. Consistent size differences exist between subspecies *artemesiae* and *idahoensis* in length of head and body (*artemesiae* 166.5 mm ± 5.7, 154 to 174; *idahoensis* 180.3 mm ± 3.1, 175 to 185; Table 5) and length of hind foot (*artemesiae* 32.7 mm ± 0.6, 30 to 33; *idahoensis* 36.4 mm ± 1.3, 34 to 39, Table 5). Based on our sampling, *idahoensis* and *artemesiae* can be reliably distinguished using only some external measures, with *idahoensis* having a larger head and body (i.e., >174 mm) and hind foot length (i.e., >34 mm) on average compared to *artemesiae* (although there is considerable overlap in tail length). *Urocitellus mollis* is intermediate in most external measures. There are also some less consistent distinctions in pelage coloration. A larger data set with more even geographic sampling and accompanying age assignments is needed to determine how reliable these differences are.

Craniodentally, subspecies *idahoensis* is larger than the *artemesiae* lineage and *U. mollis* in all measurements recorded here. Skulls of *idahoensis* are short and broad with relatively wider zygomatic arches, broader braincase, and larger, moderately inflated auditory bullae, whereas *artemesiae* is smaller on average than *idahoensis* in these dimensions. Consistent craniodental measurement differences exist between *artemesiae* and *idahoensis* only in lengths and widths of the auditory bullae and length of the bony palette (Table 4), with *idahoensis* larger in each. However, again, there is considerable overlap of combined *U. idahoensis* with *U. mollis* in individual measurements of the cranium and dentition. These patterns are evident in the ordinations of cranial morphological data as well (Fig. 4), which reveal nearly complete separation of the 2 subspecies *artemesiae* and *idahoensis* along the first component, reflecting the substantial size differences between these taxa but substantial overlap between them on component 2 indicating similarity in shape. In contrast, *U. mollis* overlaps with both *idahoensis* and *artemesiae* on component 1 reflecting its intermediate position with respect to size, whereas it is largely separated from both *U. idahoensis* subspecies on component 2, indicating substantial differences in shape. Principal component 2 is largely a composite of relative (but not absolute) lengths of the bulla, maxillary toothrow, and bony palate. Based on the PCA, *U. idahoensis* has relatively shorter bony palates and larger auditory bullae than *U. mollis*, with longer toothrow proportionate to skull size. Thus, although *idahoensis* and *artemesiae* have distinct size differences, their cranial proportions are more similar, reinforcing their conspecificity.

In the original description of *U. idahoensis*, Merriam (1913) mentions the following skull distinctions as compared to topotypical *U. mollis*: "Skull larger and more massive; rostrum and nasals longer; zygomata more spreading throughout; jugal much broader and more massive; maxillary roots of zygomata (viewed from in front) larger, broader, and more massive; anterior frontal region including orbital shelf of frontal, more elevated; upper (superior) face of premaxillary larger and usually reaching farther posteriorly; bullae larger; teeth heavier, the toothrow longer (8.5 mm.)." Most of these characteristics are supported by our analyses based on *idahoensis* having a generally larger size than *U. mollis* (component 1 of PCA, Fig. 4). Key traits mentioned by Merriam (1913) that are corroborated here based on component 2 of our PCA are the larger bullae and longer toothrow, although Merriam does not comment on the full length of the bony palate, which was also an important trait for distinguishing *U. idahoensis* from *U. mollis*.

Merriam (1913) also provided the following description for typical *artemesiae* (which he considered a subspecies of *mollis*): "Skull small, smaller and shorter than in *mollis*; rostrum rather short and slender; zygomata moderately bowed; bullae small—as small as in *canus*; molariform teeth decidedly smaller than in *mollis* (slightly larger than in *canus*). Compared with typical *mollis*, the rostrum is shorter, the zygomata more bowed, the bullae much smaller. Skull very like that of *canus* but zygomata less outstanding anteriorly, braincase slightly less broad posteriorly, and tooth row a little longer; bullae of same size." This aligns with our comparison to *U. mollis* here, but Merriam did not highlight any affinities between *idahoensis* and *artemesiae* in his description. Externally, *artemesiae* does tend to resemble *U. mollis*; however, it shares some key characteristics with *idahoensis*, including the more distinctly dappled pelage (albeit less so than *idahoensis*) and a grayish-black subterminal patch on the tail (again, less distinct than in *idahoensis*). The external similarities between *U. mollis* and *artemesiae*, and less pronounced similarities to *idahoensis*, initially led Merriam to place *artemesiae* as a subspecies of *mollis* while including *idahoensis* as a distinct species, an arrangement followed by only some subsequent authors and not supported here.

Distribution

Endemic to the Snake River Plain in south-central Idaho between the Snake River and the Sawtooth Range, extending from Payette and Canyon counties east to Jefferson and Clark counties. The nominate subspecies, *U. i. idahoensis*, is distributed in the western Snake River Plain, from Payette County east to Elmore County. The subspecies *U. i. artemesiae* is distributed in the eastern Snake River Plain, from Clark County in the east to Gooding County in the west. The exact distributional limit between the 2 subspecies is currently uncertain, although it is likely in Elmore and Gooding counties. The Snake River appears to be a major biogeographic barrier for this species, separating it from *U. mollis* to the south and *U. canus* to the west. The nominate subspecies is also partially sympatric with the *U. brunneus* in Gem and Payette Counties.

Urocitellus mollis (Kennicott, 1863)

Piute Ground Squirrel

Spermophilus mollis Kennicott, 1863:157. Type locality "Camp Floyd, near Fairfield, [Utah County,] Utah," United States.

[*Spermophilus townsendi*] var. *mollis*: Allen, 1874:293. Name combination.

Spermophilus mollis stephensi Merriam, 1898:69. Type locality "Queen Station, near head of Owens Valley, [Esmeralda County,] Nevada," United States.

[*Citellus*] *mollis*: Trouessart, 1904:339. Name combination.

[*Citellus mollis*] *stephensi*: Trouessart, 1904:339. Name combination.

Citellus leurodon Merriam, 1913:136. Type locality "Murphy, [Owyhee County,] in hills of southwestern Idaho west of Snake River," United States.

Citellus mollus Merriam, 1913:138. Incorrect subsequent spelling of *Spermophilus mollis* Kennicott, 1863.

Citellus mollis washoensis Merriam, 1913:138. Type locality "Carson Valley, [Douglas County,] western Nevada," United States.

Citellus townsendii mollis: Howell, 1938:63. Name combination.

Urocitellus mollis: Helgen et al., 2009:297. First use of current name combination.

Holotype

USNM 3777; age and sex unknown, skin and skull with the following measurements: total length 188 mm, tail length 43 mm, hindfoot length 31 mm, ear length 3 mm. Collected on 18 March 1859 by C. S. McCarthy.

General characteristics.

As in other small-eared *Urocitellus*, including *U. idahoensis*, members of the species have a short tail (generally <60 mm) and hindfoot length (<39 mm) relative to body size and possess inconspicuous external pinnae. The general dorsal color is yellowish-gray to medium gray, occasionally with faint pale dappling confined to back and rump. Lateral and ventral pelage grayish-white. Faint reddish-brown on top of nose and above eyes. The dorsal surface of tail bright reddish-brown to dark gray, undersurface reddish-brown or gray. The tail lacks subterminal black spot. The eye ring and anterior edge of the pinna are pale gray or white. Feet grayish- or yellowish-white. General skull morphology is similar to that of *U. idahoensis* described above, but see *Comparison* section below.

Comparison

Despite the consistent size differences that separate subspecies of *U. idahoensis, U. mollis* is intermediate in most external measures and thus external proportions alone do not consistently distinguish it from the former species. The relative tail and hind foot lengths of *U. mollis* are closer to those of *U. i. idahoensis* than *U. i. artemesiae* (Table 5), so these relative lengths combined with geography may serve to distinguish the 2 species. Mean cranial measurements of *U. mollis* are also intermediate in comparison to the smaller *U. i. artemesiae* and larger *U. i. idahoensis* (Tables 4 and 5), and *U. mollis* overlaps with both *idahoensis* and *artemesiae* on principal component 1 reflecting its intermediate position with respect to size. However, the former species is separated from the other taxa on component 2 indicating substantial differences in cranial shape. Component 2 is largely a composite of lengths of the bulla and maxillary toothrow and the length of the bony palate. Based on the PCA, *U. mollis* has relatively longer bony palates, shorter auditory bullae, and a shorter tooth row proportionate to skull size than *U. idahoensis*.

Kennicott's (1863) original description of *U. mollis* focuses primarily on the external appearance of the species, stating: "Form rather stout, with the head small and the muzzle short and compressed. Ears rudimentary, the auricle only about one-twentieth of an inch high, and scarcely distinguishable in dried specimens. Feet rather large with the claws very weak, much compressed and considerably curved. Tail much flattened, the central hairs above and below short and closely appressed, the outer ones longer and distended laterally. The hair clothing and the body are remarkably fine and soft. The upper parts are finely variegated silvery-gray, light yellowish-brown, and black; these colors intimately and uniformly mixed throughout, without any indication of spots whatever. Under parts silvery-gray, with a slight wash of dirty creamy yellow. Tail above yellowish-brown, slightly mixed with black, with a distinct and prominent border and tip of white; beneath reddish-brown within the white border." This description provides few details pertinent to distinguishing *U. mollis* from *U. idahoensis*, but the lack of spots is a key external feature highlighted here. *Urocitellus mollis* can be distinguished from both subspecies of *U. idahoensis* based on subtle pelage traits, including having no dappling (spotting) on their back and not having a subterminal patch on the tail. Both of these traits are less distinct in *U. i. artemesiae*, but are generally still present.

Distribution

Widely distributed throughout much of the Great Basin, including southern Idaho, southeastern Oregon, Nevada, northeastern and east-central California, and the western half of Utah. The northern limit of its distribution is marked by the Snake River, which separates the species from *U. idahoensis* in the north. *U. mollis* may contact *U. canus* in the northeastern portion of its distribution (Cole and Wilson 2009), where the 2 species may be parapatrically distributed in northeastern Nevada, southeastern Oregon, and southwestern Idaho, but more surveys in this region are necessary. In Oregon, *U. mollis* extends at least as far as Malheur County in the northwestern portion of its distribution, although the exact distributional limits where this species meets *U. canus* are uncertain. In the west, the species extends to Lassen and Plumas Counties in northeast California and Mono County, California, in the southeast of its range. In the south, *U. mollis* has been recorded as far as northern Clark County at the north end of the Spring Mountains of Nevada. In Utah, *U. mollis* extends east to Sanpete County and southeast to Iron County and is limited to the west and south of the Great Salt Lake. The species extends north into Idaho at least as far as Bannock County in the northeast and Owyhee County in the northwest.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1. Locations of geometric morphometric landmarks on ventral crania.

Supplementary Data SD2. Raw (nonsuperimposed) geometric morphometric landmark data.

Supplementary Data SD3. Linear measurement data from crania of known-age *Urocitellus mollis*.

Supplementary Data SD4. Extremal measurement data for small-eared *Urocitellus*.

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Author contributions

BSM conceptualized the study; BSM, EAR, RPG, and CJB collected and curated the data; BSM and EAR analyzed and visualized the data; BSM, JAC, and RPG acquired the funding; BSM, CJB, and EAR wrote the original draft; all authors contributed to review and editing of subsequent drafts.

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Conflict of interest

None declared.

Data availability

GenBank accession numbers for genetic data are provided in Appendix I. Raw morphometric data are provided in Supplementary Data files.

References

Aberg MC. 2023. A coupled human and natural systems approach to studying recreation on public lands [doctoral dissertation]. Boise (ID, USA): Boise State University. https://www.proquest.com/docview/2835521427

Adams DC, Collyer ML, Kaliontzopoulou A, Baken EK. 2022. Geomorph: software for geometric morphometric analyses. Version 4.0.4. [Computer software]. https://cran.r-project.org/package=geomorph

Allen JA. 1874. On geographical variation in color among North American squirrels; with a list of the species and varieties of the American Sciuridae occurring north of Mexico. Proceedings of the Boston Society of Natural History 16(1873-1874):276–294. https://www.biodiversitylibrary.org/item/130707

Arbogast BS, Schumacher KI, Kerhoulas NJ, Bidlack AL, Cook JA, Kenagy GJ. 2017. Genetic data reveal a cryptic species of New World flying squirrel: *Glaucomys oregonensis*. Journal of Mammalogy 98(4):1027–1041. https://doi.org/10.1093/jmammal/gyx055

Augustine DJ, Smith JE, Davidson AD, Stapp P. 2023. Burrowing rodents. In: McNew LB, Dahlgren DK, Beck JL, editors. Rangeland wildlife ecology and conservation. Cham (Switzerland): SpringerLink; p.505–548.

Bachman J. 1839. Description of several new species of American quadrupeds. Journal of the Academy of Natural Sciences of Philadelphia 8(1):57–74. https://www.biodiversitylibrary.org/item/79280

Badgley C. 2010. Tectonics, topography, and mammalian diversity. Ecography 33(2):220–231. https://doi.org/10.1111/j.1600-0587.2010.06282.x

Badgley C, Smiley TM, Finarelli JA. 2014. Great Basin mammal diversity in relation to landscape history. Journal of Mammalogy 95(6):1090–1106. https://doi.org/10.1644/13-mamm-s-088

Baken EK, Collyer ML, Kaliontzopoulou A, Adams DC. 2021. Geomorph v4.0 and gmShiny: enhanced analytics and a new graphical interface for a comprehensive morphometric experience. Methods in Ecology and Evolution 12(12):2355–2363. https://doi.org/10.1111/2041-210x.13723

Baker RJ, Bradley RD. 2006. Speciation in mammals and the genetic species concept. Journal of Mammalogy 87(4):643–662. https://doi.org/10.1644/06-MAMM-F-038R2.1

Balk MA, Deck J, Emery KF, Walls RL, Reuter D, LaFrance R, Arroyo-Cabrales J, Barrett P, Blois J, Boileau A, *et al.* 2022. A solution to the challenges of interdisciplinary aggregation and use of specimen-level trait data. iScience 25(10):105101. https://doi.org/10.1016/j.isci.2022.105101

Beranek LP, Link PK, Fanning CM. 2006. Miocene to Holocene landscape evolution of the western Snake River Plain region, Idaho: using the SHRIMP detrital zircon provenance record to track eastward migration of the Yellowstone hotspot. Geological Society of America Bulletin 118(9–10):1027–1050. https://doi.org/10.1130/b25896.1

Biggins DE, Kosoy MY. 2001. Influences of introduced plague on North American mammals: implications from ecology of plague in Asia. Journal of Mammalogy 82(4):906–916. https://doi.org/10.1644/1545-1542(2001)082<0906:ioipon>2.0.co;2

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Computational Biology 10(4):e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Boyte SP, Wylie BK. 2017. Estimates of herbaceous annual cover in the sagebrush ecosystem. (May 1, 2017). Sioux Falls (SD, USA): U.S. Geological Survey Data Release. https://doi.org/10.5066/F7445JZ9

Bradley BA, Curtis CA, Fusco EJ, Abatzoglou JT, Balch JK, Dadashi S, Tuanmu MN. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20(6):1493–1506. https://doi.org/10.1007/s10530-017-1641-8

Bryant D, Bouckaert R, Felsenstein J, Rosenberg NA, Roychoudhury A. 2012. Inferring species trees directly from biallelic genetic markers: bypassing gene trees in a full coalescent analysis. Molecular Biology and Evolution 29(8):1917–1932. https://doi.org/10.1093/molbev/mss086

Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018. How many species of mammals are there? Journal of Mammalogy 99(1):1–14. https://doi.org/10.1093/jmammal/gyx147

Chambers JC, Brown JL, Bradford JB, Doherty KE, Crist MR, Schlaepfer DR, Urza AK, Short KC. 2023. Combining resilience and resistance with threat-based approaches for prioritizing management actions in sagebrush ecosystems. Conservation Science and Practice 5(11):e13021. https://doi.org/10.1111/csp2.13021

Cole FR, Wilson DE. 2009. *Urocitellus canus* (Rodentia: Sciuridae). Mammalian Species (834):1–8. https://doi.org/10.1644/834.1

Colella JP, Frederick LM, Talbot SL, Cook JA. 2021. Extrinsically reinforced hybrid speciation within Holarctic ermine (*Mustela* spp.) produces an insular endemic. Diversity and Distributions 27(4):747–762. https://doi.org/10.1111/ddi.13234

Collyer ML, Adams DC. 2021. RRPP: linear model evaluation with randomized residuals in a permutation procedure. Version 1.1.2. [Computer software] (https://cran.r-project.org/package=RRPP).

Crist MR, Belger R, Davies KW, Davis DM, Meldrum JR, Shinneman DJ, Remington TE, Welty J, Mayer KE. 2023. Trends, impacts, and cost of catastrophic and frequent wildfires in the sagebrush biome. Rangeland Ecology and Management 89(July 2023):3–19. https://doi.org/10.1016/j.rama.2023.03.003

Davis WB. 1939. The Recent Mammals of Idaho. Caldwell (ID, USA): The Caxton Printers, Ltd.

Durrant SD, Hansen RM. 1954. Distribution patterns and phylogeny of some western ground squirrels. Systematic Zoology 3(2):82–85. https://doi.org/10.2307/2411841

Felsenstein J. 1989. PHYLIP – phylogeny inference package. Version 3.2. Cladistics 5:164–166.

Fischer G. 1814. Zoognosia. Volumen III. Quadrupeda reliqua. Ceti. Monotrymata. Moscow (Russia): Nicolai Sergeidis Vsevolozsky.

Gage KL, Kosoy MY. 2005. Natural history of plague: perspectives from more than a century of research. Annual Review of Entomology 50(2005):505–528. https://doi.org/10.1146/annurev.ento.50.071803.130337

Grayson D. 2011. The Great Basin: a natural prehistory. Berkeley and Los Angeles (CA, USA): University of California Press.

Goldberg AR, Conway CJ. 2021. Hibernation behavior of a federally threatened ground squirrel: climate change and habitat selection implications. Journal of Mammalogy 102(2):574–587. https://doi.org/10.1093/jmammal/gyab021

Goldberg AR, Conway CJ, Biggins DE. 2021. Effects of experimental flea removal and plague vaccine treatments on survival of northern Idaho ground squirrels and two coexisting sciurids. Global Ecology and Conservation 26(April 2021):e01489. https://doi.org/10.1016/j.gecco.2021.e01489

Guralnick RP, Balk MA, Deck J, Emery K, Davis E, Sewnath N, Bernor R, Walls R. 2022. FuTRES (Functional Trait Resource for Environmental Studies) data store archival copy – 5/21/2022, Version 1.0. [accessed 5 Dec 2023]. Zenodo. https://doi.org/10.5281/zenodo.6569644

Guralnick RP, Zermoglio PF, Wieczorek J, LaFrance R, Bloom D, Russell L. 2016. The importance of digitized biocollections as a source of trait data and a new VertNet resource. Database 2016(2016):baw158. https://doi.org/10.1093/database/baw158

Hafner JC, Upham NS. 2011. Phylogeography of the dark kangaroo mouse, *Microdipodops megacephalus*: cryptic lineages and dispersal routes in North America's Great Basin. Journal of Biogeography 38(6):1077–1097. https://doi.org/10.1111/j.1365-2699.2010.02472.x

Hall ER, Kelson KR. 1959. The mammals of North America. 1st ed. New York (NY, USA): Ronald Press Co.

Harrison RG, Bogdanowicz SM, Hoffmann RS, Yensen E, Sherman PW. 2003. Phylogeny and evolutionary history of the ground squirrels (Rodentia: Marmotinae). Journal of Mammalian Evolution 10(3):249–276. https://doi.org/10.1023/b:jomm.0000015105.96065.f0

Helgen KM, Cole FR, Helgen LE, Wilson DE. 2009. Generic revision in the Holarctic ground squirrel genus *Spermophilus*. Journal of Mammalogy 90(2):270–305. https://doi.org/10.1644/07-mamm-a-309.1

Herrera ND, Bell KC, Callahan CM, Nordquist E, Sarver BAJ, Sullivan J, Demboski JR, Good JM. 2022. Genomic resolution of cryptic species diversity in chipmunks. Evolution 76(9):2004–2019. https://doi.org/10.1111/evo.14546

Herron MD, Castoe TA, Parkinson CL. 2004. Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilus*). Molecular Phylogenetics and Evolution 31(3):1015–1030. https://doi.org/10.1016/j.ympev.2003.09.015

Hoffmann RS, Anderson CG, Thorington RW, Heaney LR. 1993. Family Sciuridae. In: Wilson DE, Reeder DM., editors. Mammal species of the world: a taxonomic and geographic reference. 2nd ed. Washington (DC, USA): Smithsonian Institution Press; p. 419–466.

Hoisington-Lopez JL, Waits LP, Sullivan J. 2012. Species limits and integrated taxonomy of the Idaho ground squirrel (*Urocitellus brunneus*): genetic and ecological differentiation. Journal of Mammalogy 93(2):589–604. https://doi.org/10.1644/11-mamm-a-021.1

Holbrook JD, Arkle RS, Rachlow JL, Vierling KT, Pilliod DS, Wiest MM. 2016. Occupancy and abundance of predator and prey: implications of the fire-cheatgrass cycle in sagebrush ecosystems. Ecosphere 7(6):e01307. https://doi.org/10.1002/ecs2.1307

Howell AH. 1928. Descriptions of six new North American ground squirrels. *Proceedings of the Biological Society of Washington* 41:211–214. https://doi.org/10.5281/zenodo.13446982

Howell AH. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. North American Fauna 56:1–256. https://doi.org/10.3996/nafa.56.0001

Idaho Department of Fish and Game. 2024. Idaho State wildlife action plan. 2023 rev. ed. Boise (ID, USA): Idaho Department of Fish and Game. https://idfg.idaho.gov/

Jezkova T, Jaeger JR, Oláh-Hemmings V, Jones KB, Lara-Resendiz RA, Mulcahy DG, Riddle BR. 2015. Range and niche shifts in response to past climate change in the desert horned lizard *Phrynosoma platyrhinos*. Ecography 39(5):437–448. https://doi.org/10.1111/ecog.01464

Jezkova T, Olah-Hemmings V, Riddle BR. 2011. Niche shifting in response to warming climate after the last glacial maximum: inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (*Dipodomys microps*). Global Change Biology 17(11):3486–3502. https://doi.org/10.1111/j.1365-2486.2011.02508.x

Kass RE, Raftery AE. 1995. Bayes factors. Journal of the American Statistical Association 90(430):773–795. https://doi.org/10.2307/2291091

Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular Biology and Evolution 30(4):772–780. https://doi.org/10.1093/molbev/mst010

Katzner TE, Carlisle JD, Poessel SA, Thomason EC, Pauli BP, Pilliod DS, Belthoff JR, Heath JA, Parker KJ, Warner KS, *et al*. 2020. Illegal killing of nongame wildlife and recreational shooting in conservation areas. Conservation Science and Practice 2(11):e279. https://doi.org/10.1111/csp2.279

Kays RW, Wilson DE. 2010. Mammals of North America. 2nd ed. Princeton (NJ, USA): Princeton University Press.

Kays R, Lasky M, Allen ML, Dowler RC, Hawkins MTR, Hope AG, Kohli BA, Mathis VL, McLean BS, Olson LE, *et al*. 2022. Which mammals can be identified from camera traps and crowdsourced photographs? Journal of Mammalogy 103(4):767–775. https://doi.org/10.1093/jmammal/gyac021

Kennicott R. 1863. Descriptions of four new species of *Spermophilus*, in the collections of the Smithsonian Institution. Proceedings of the Academy of Natural Sciences of Philadelphia 15:157–158. https://www.biodiversitylibrary.org/part/84767

Knick ST, Rotenberry JT. 1997. Landscape characteristics of disturbed shrubsteppe habitats in southwestern Idaho (USA). Landscape Ecology 12(1997):287–297. https://doi.org/10.1023/A:1007915408590

Leaché AD, Fujita MK, Minin VN, Bouckaert RR. 2014. Species delimitation using genome-wide SNP data. Systematic Biology 63(4):534–542. https://doi.org/10.1093/sysbio/syu018

Lohr K, Yensen E, Munger JC, Novak SJ. 2013. Relationship between habitat characteristics and densities of southern Idaho ground squirrels. The Journal of Wildlife Management 77(5):983–993. https://doi.org/10.1002/jwmg.541

Malaney JL, Demboski JR, Cook JA. 2017. Integrative species delimitation of the widespread North American jumping mice (Zapodinae). Molecular Phylogenetics and Evolution 114(September 2017):137–152. https://doi.org/10.1016/j.ympev.2017.06.001

Mammal Diversity Database. 2023. Mammal Diversity Database v1.11 [Data Set]. Zenodo. https://doi.org/10.5281/zenodo.7830771

Mantooth SJ, Hafner DJ, Bryson RW, Riddle BR. 2013. Phylogeographic diversification of antelope squirrels (*Ammospermophilus*) across North American deserts. Biological Journal of the Linnean Society 109(4):949–967. https://doi.org/10.1111/bij.12084

McLean BS, Bell KC, Allen JM, Helgen KM, Cook JA. 2019. Impacts of inference method and data set filtering on phylogenomic resolution in a rapid radiation of ground squirrels (Xerinae: Marmotini). Systematic Biology 68(2):298–316. https://doi.org/10.1093/sysbio/syy064

McLean BS, Bell KC, Cook JA. 2022. SNP-based phylogenomic inference in Holarctic ground squirrels (*Urocitellus*). Molecular Phylogenetics and Evolution 169(April 2022):107396. https://doi.org/10.1016/j.ympev.2022.107396

McLean BS, Helgen KM, Goodwin HT, Cook JA. 2018. Trait-specific processes of convergence and conservatism shape ecomorphological evolution in ground-dwelling squirrels. Evolution 72(3):473–489. https://doi.org/10.1111/evo.13422

McLean BS, Jackson DJ, Cook JA. 2016. Rapid divergence and gene flow at high latitudes shape the history of Holarctic ground squirrels (*Urocitellus*). Molecular Phylogenetics and Evolution 102(September 2016):174–188. https://doi.org/10.1016/j.ympev.2016.05.040

Merriam CH. 1891. Results of a biological reconnaissance of south central Idaho, south of latitude 45° and east of the thirty-eighth meridian, made during the summer of 1890, with annotated lists of the mammals and birds, and descriptions of new species. North American Fauna 5:1–30. https://doi.org/10.3996/nafa.5.0001

Merriam CH. 1898. Descriptions of six new ground squirrels from the western United States. Proceedings of the Biological Society of Washington 12(March 1898):69–71. http://doi.org/10.5281/zenodo.13441805

Merriam CH. 1913. Six new ground squirrels of the *Citellus mollis* group from Idaho, Oregon, and Nevada. Proceedings of the Biological Society of Washington 26(May 1913):135–138. https://doi.org/10.5281/zenodo.13676614

Mills KK, Everson KM, Hildebrandt KB, Brandler OV, Steppan SJ, Olson LE. 2023. Ultraconserved elements improve resolution of marmot phylogeny and offer insights into biogeographic history. Molecular Phylogenetics and Evolution 184(July 2023):107785. https://doi.org/10.1016/j.ympev.2023.107785

Morelli G, Song Y, Mazzoni CJ, Eppinger M, Roumagnac P, Wagner DM, Feldkamp M, Kusecek B, Vogler AJ, Li Y, *et al*. 2010. *Yersinia pestis* genome sequencing identifies patterns of global phylogenetic diversity. Nature Genetics 42(12):1140–1143. https://doi.org/10.1038/ng.705

Murray A. 1866. The geographical distribution of mammals. London (UK): Day and Son.

Nadler CF. 1966. Chromosomes and systematics of American ground squirrels of the subgenus *Spermophilus*. Journal of Mammalogy 47(4):579–596. https://doi.org/10.2307/1377889

Nadler CF. 1968. The serum proteins and transferrins of the ground squirrel subgenus *Spermophilus*. Comparative Biochemistry and Physiology 27(2):487–503. https://doi.org/10.1016/0010-406x(68)90246-6

Nadler CF. 1968. The chromosomes of *Spermophilus townsendi* (Rodentia: Sciuridae) and report of a new subspecies. Cytogenetics 7(2):144–157. https://doi.org/10.1159/000129978

Nadler CF, Hoffmann RS, Vorontsov NN, Koeppl JW, Deutsch L, Sukernik RI. 1982. Evolution in ground squirrels: II. Biochemical comparisons in Holarctic populations of *Spermophilus*. Zeitschrift für Säugetierkunde 47A(4):198–215. https://www.biodiversitylibrary.org/part/191595

Nadler CF, Lyapunova EA, Hoffmann RS, Vorontsov NN, Shaitarova LL, Borisov YM. 1984. Chromosomal evolution in holarctic ground squirrels (*Spermophilus*). II: Giemsa-band homologies of chromosomes and the tempo of evolution. Zeitschrift für Säugetierkunde 49(2):78–90. https://www.biodiversitylibrary.org/part/191696

Obolenskiy S. 1927. A preliminary review of the Palaearctic sousliks (*Citellus* and *Spermophilopsis*). Compe Rendu de l'Academie des Sciences de l'USSR 12:188–193.

Padial JM, Miralles A, De la Riva I, Vences M. 2010. The integrative future of taxonomy. Frontiers in Zoology 7(2010):16. https://doi.org/10.1186/1742-9994-7-16

Paradis E, Schliep K. 2019. Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35(3):526–528. https://doi.org/10.1093/bioinformatics/bty633

Parsons DJ, Pelletier TA, Wieringa JG, Duckett DJ, Carstens BC. 2022. Analysis of biodiversity data suggests that mammal species are hidden in predictable places. Proceedings of the National Academy of Sciences of the United States of America 119(14):e2103400119. https://doi.org/10.1073/pnas.2103400119

Pauli BP, Sun ER, Tinkle ZK, Forbey JS, Demps KE, Heath JA. 2019. Human habitat selection: using tools from wildlife ecology to predict recreation in natural landscapes. Natural Areas Journal 39(2):142–149. https://doi.org/10.3375/043.039.0202

Phuong MA, Lim MCW, Wait DR, Rowe KC, Moritz C. 2014. Delimiting species in the genus *Otospermophilus* (Rodentia: Sciuridae), using genetics, ecology, and morphology. Biological Journal of the Linnean Society 113(4):1136–1151. https://doi.org/10.1111/bij.12391

Pocock RI. 1923. The classification of the Sciuridæ. Proceedings of the Zoological Society of London 93(2):209–246. https://doi.org/10.1111/j.1096-3642.1923.tb02184.x

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5):901–904. https://doi.org/10.1093/sysbio/syy032

Reeder DM, Helgen KM, Wilson DE. 2007. Global trends and biases in new mammal species discoveries. Occasional Papers of the Museum of Texas Tech University 269:1–35.

Rickart EA. 1987. *Spermophilus townsendii*. Mammalian Species 268:1–6. https://doi.org/10.2307/0.268.1

Rickart EA. 1989. Variation in renal structure and urine concentrating capacity among ground squirrels of the *Spermophilus townsendii* complex (Rodentia: Sciuridae). Comparative Biochemistry and Physiology 92(4):531–534. https://doi.org/10.1016/0300-9629(89)90360-5

Rickart EA, Hoffmann RS, Rosenfield M. 1985. Karyotype of *Spermophilus townsendii artemesiae* (Rodentia: Sciuridae) and chromosomal variation in the *Spermophilus townsendii* complex. Mammalian Chromosomes Newsletter 26(3-4):94–102.

Riddle BR, Jezkova T, Eckstut ME, Oláh-Hemmings V, Carraway LN. 2014. Cryptic divergence and revised species taxonomy within the Great Basin pocket mouse, *Perognathus parvus* (Peale, 1848), species group. Journal of Mammalogy 95(1):9–25. https://doi.org/10.1644/12-mamm-a-252

Rohlf FJ. 2006. tpsDig. Version 2.10. [Computer software]. Stony Brook (NY, USA): Department of Ecology and Evolution, State University of New York https://www.sbmorphometrics.org/

Schlager S. 2017. Morpho and Rvcg – shape analysis in R. In: Zheng G, Li S, Szekely G, editors. Statistical shape and deformation analysis. London (UK): Academic Press; p. 217–256.

Schliep KP. 2011. Phangorn: phylogenetic analysis in R. Bioinformatics 27(4):592–593. https://doi.org/10.1093/bioinformatics/btq706

Sikes RS, The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97(3):663–688. https://doi.org/10.1093/jmammal/gyw078

Staisch LM, O'Connor JE, Cannon CM, Holm-Denoma C, Link PK, Lasher J, Alexander JA. 2022. Major reorganization of the Snake River modulated by passage of the Yellowstone Hotspot. Bulletin of the Geological Society of America 134(7-8):1834–1844. https://doi.org/10.1130/b36174.1

Steenhof K, Yensen E, Kochert MN, Gage KL. 2006. Populations and habitat relationships of Piute ground squirrels in southwestern Idaho. Western North American Naturalist 66(4):482–491. https://doi.org/10.3398/1527-0904(2006)66[482:pahrop]2.0.co;2

Thorington RW, Hoffmann RS. 2005. Family Sciuridae. In: Wilson DE, Reeder DM, editors. Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Baltimore (MD, USA): The Johns Hopkins University Press; p. 754–818.

Thorington RW, Koprowski JL, Steele ML, Whatton JF. 2012. Squirrels of the world. Baltimore (MD, USA): The Johns Hopkins University Press.

Tinwari V, Kashikar A. 2019. Outlier detection. Version 0.1.0. [Computer software]. https://cran.r-project.org/package=OutlierDetection.

Trouessart E-L. 1904. Catalogus mammalium tam viventium quam fossilium. Berlin (Germany): R. Friedlander and Sohn.

U.S. Fish and Wildlife Service. 2004. Species assessment and listing priority assignment form. *Spermophilus brunneus endemicus*, southern Idaho ground squirrel. Boise (ID, USA): U.S. Fish and Wildlife Service. https://downloads.regulations.gov/FWS-HQ-ES-2015-0143-0022/content.pdf

Wickham H. 2016. ggplot2: elegant graphics for data analysis. New York (NY, USA): Springer-Verlag.

Wilke CO. 2024. ggridges: Ridgeline plots in ggplot2." Version 0.5.6. [Computer software]. https://cran.r-project.org/package=ggridges

Wilson DE, Ruff S. 1999. The Smithsonian book of North American Mammals. Washington (DC, USA): Smithsonian Institution Press.

Yensen E. 1991. Taxonomy and distribution of the Idaho ground squirrel, *Spermophilus brunneus*. Journal of Mammalogy 72(3):583–600. https://doi.org/10.2307/1382142

Yensen E, Quinney DL, Johnson K, Timmerman K, Steenhof K. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. American Midland Naturalist 128(2):299–312. https://doi.org/10.2307/2426464

Yensen E. 2019. *Urocitellus nancyae*. The IUCN red list of threatened species 2019: e.T116989724A116989738 [accessed 22 Dec 2023] https://www.iucnredlist.org/species/116989724/116989738.

Yensen E, Sherman PW. 2001. Demise of the small-eared ground squirrels (Abstracts from the Symposium on Conservation Biology of Ground Squirrels and the Shrub-Steppe Ecosystem). Journal of the Idaho Academy of Science 37(1):74–77.

Appendix I

Specimens examined for molecular analysis.

sample Code	Genus	specific Epithet	subspecific epithet	state Province	County	institution Code	catalog Number	tissue Identifier	tissue Number	GenBank Accessions mtDNA	GenBank Accessions nuDNA_5gene	GenBank accessions nuDNA_UCEs	Citations
Ubrunneus_EY978	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	USNM	Uncataloged	EY	978	AF157884	KX278603, KX290211, KX278647, KX290256	KFKK00000000	Harrison et al. (2003) | McLean et al. (2016) | McLean et al. (2022)
Ubrunneus_EY980	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams			EY	980	AF157952			Harrison et al. (2003)
Ubrunneus_ CS-A0102-Ubb27	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams				CS-A0102-Ubb27	JQ679203			Hoisington-Lopez et al. (2012)
Ubrunneus_ ChS-0946-Ubb38	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams				ChS-0946-Ubb38	JQ679271			Hoisington-Lopez et al. (2012)
Ubrunneus_ RV-175-Ubb40	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Valley				RV-175-Ubb40	JQ679274			Hoisington-Lopez et al. (2012)
Ubrunneus_EY974	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Payette	USNM	Uncataloged	EY	974	AF157886	KX278601, KX290209, KX278645, KX290254	KFKM00000000	Harrison et al. (2003) | McLean et al. (2016) | McLean et al. (2022)
Ubrunneus_EY975	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Payette	USNM	Uncataloged	EY	975	AF157883	KX278602, KX290210, KX278646, KX290255	KFKL00000000	Harrison et al. (2003) | McLean et al. (2016) | McLean et al. (2022)
Ubrunneus_ CP-D0402-Ube11	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Payette				CP-D0402-Ube11	JQ679146			Hoisington-Lopez et al. (2012)
Ubrunneus_ MC-MC005-Ube13	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Washington				MC-MC005-Ube13	JQ679154			Hoisington-Lopez et al. (2012)
Ubrunneus_ SB-D0378-Ube21	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Gem				SB-D0378-Ube21	JQ679177			Hoisington-Lopez et al. (2012)
Ucanus_MSB110676	*Urocitellus*	*canus*	*canus*	Nevada	Humboldt	MSB	110676			KX278559		KFKJ00000000	McLean et al. (2016) | McLean et al. (2022)
Ucanus_MSB110677	*Urocitellus*	*canus*	*canus*	Nevada	Humboldt	MSB	110677			KX278558			McLean et al. (2016)
Ucanus_MSB110678	*Urocitellus*	*canus*	*canus*	Nevada	Humboldt	MSB	110678			KX278557			McLean et al. (2016)
Ucanus_EY963	*Urocitellus*	*canus*	*vigilis*	Idaho	Owyhee	USNM	Uncataloged	EY	963	KX278526	KX278599, KX290212, KX278643, KX290252		McLean et al. (2016)
Ucanus_EY964	*Urocitellus*	*canus*	*vigilis*	Idaho	Owyhee	USNM	Uncataloged	EY	964	KX278527	KX278600, KX290208, KX278644, KX290253	KFKI00000000	McLean et al. (2016) | McLean et al. (2022)
Ucanus_EY966	*Urocitellus*	*canus*	*vigilis*	Idaho	Owyhee	USNM	Uncataloged	EY	966	OR813776		KFKH00000000	McLean et al. (2022)
Ucanus_EY965	*Urocitellus*	*canus*	*vigilis*	Idaho	Owyhee			EY	965	AF157888			Harrison et al. (2003)

sample Code	Genus	specific Epithet	subspecific epithet	state Province	County	institution Code	catalog Number	tissue Identifier	tissue Number	GenBank Accessions mtDNA	GenBank Accessions nuDNA_5gene	GenBank accessions nuDNA_UCEs	Citations
Ucanus_EY968	*Urocitellus*	*canus*	*vigilis*	Idaho	Owyhee			EY	968	AF157889			Harrison et al. (2003)
Uidahoensis_MSB152485	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Butte	MSB	152485	NK	145662	KX278528	KX278604, KX290213, KX278648, KX290258	KFJB00000000	McLean et al. (2016) | McLean et al. (2022)
Uidahoensis_MSB152846	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Butte	MSB	152846	NK	145739	KX278579			McLean et al. (2016)
Uidahoensis_MSB152352	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Butte	MSB	152352	NK	147596	KX278529	KX278605, KX290214, KX278649, KX290259		McLean et al. (2016)
Uidahoensis_MSB71991	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Ada	MSB	71991	NK	30724	KX278569		KFJA00000000	McLean et al. (2016) | McLean et al. (2022)
Uidahoensis_MSB89149	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Ada	MSB	89149	NK	5929	KX278552	KX278634, KX290243, KX278678, KX290257	KFIZ00000000	McLean et al. (2016) | McLean et al. (2022)
Uidahoensis_EY1068	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Ada			EY	1068	AF157880			Harrison et al. (2003)
Uidahoensis_EY1067	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Ada			EY	1067	AF157949			Harrison et al. (2003)
Umollis_EY1129a	*Urocitellus*	*mollis*	*mollis*	Idaho	Owyhee	USNM	Uncataloged	EY	1129a	AF157920	KX278597, KX290206, KX278641, KX290250	KFJY00000000	Harrison et al. (2003) | McLean et al. (2016) | McLean et al. (2022)
Umollis_EY1130a	*Urocitellus*	*mollis*	*mollis*	Idaho	Owyhee	USNM	Uncataloged	EY	1130a	AF157938	KX278598, KX290207, KX278642, KX290251	KFJX00000000	Harrison et al. (2003) | McLean et al. (2016)
Umollis_MVZ224858	*Urocitellus*	*mollis*	*mollis*	California	Mono	MVZ	224858			KX278535	KX278616, KX290225, KX278660, KX290270		McLean et al. (2016)
Umollis_MSB47928	*Urocitellus*	*mollis*	*mollis*	Nevada	White Pine	MSB	47928					KFKA00000000	McLean et al. (2022)
Utownsendii_EY1160a	*Urocitellus*	*townsendii*	*nancyae*	Washington	Kittitas	USNM	Uncataloged	EY	1160a	AF157933	KX278596, KX290205, KX278640, KX290249	KFJL00000000	Harrison et al. (2003) | McLean et al. (2016) | McLean et al. (2022)
Utownsendii_EY1159	*Urocitellus*	*townsendii*	*nancyae*	Washington	Kittitas			EY	1159	AF157932			Harrison et al. (2003)
Utownsendii_EY1162	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima			EY	1162	AF157934			Harrison et al. (2003)
Utownsendii_EY1164	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima			EY	1164	AF157935			Harrison et al. (2003)

sample Code	Genus	specific Epithet	subspecific epithet	state Province	County	institution Code	catalog Number	tissue Identifier	tissue Number	GenBank Accessions mtDNA	GenBank Accessions nuDNA_5gene	GenBank accessions nuDNA_UCEs	Citations
Utownsendii_ UWBM78329	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	UWBM	78329	JEB	814	KX278537	KX278618, KX290227, KX278662, KX290272	KFJI00000000	McLean et al. (2016) | McLean et al. (2022)
Utownsendii_ UWBM78316	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	UWBM	78316	JEB	801	KX278538	KX278619, KX290228, KX278663, KX290273		McLean et al. (2016)
Utownsendii_ EY1163a	*Urocitellus*	*townsendii*		Washington	Yakima	USNM	Uncataloged	EY	1163a	KX278565		KFJK00000000	McLean et al. (2016) | McLean et al. (2022)
Utownsendii_ UWBM32803	*Urocitellus*	*townsendii*		Washington	Yakima	UWBM	32803					KFJJ00000000	McLean et al. (2022)
Uwashingtoni_ EY1157	*Urocitellus*	*washingtoni*		Washington	Grant			EY	1157	AF157937			Harrison et al. (2003)
Uwashingtoni_ EY1158	*Urocitellus*	*washingtoni*		Washington	Grant	USNM	Uncataloged	EY	1158	AF157936	KX278639, KX290248, KX278683, KX290292		Harrison et al. (2003) | McLean et al. (2016)
Uwashingtoni_ EY1155a	*Urocitellus*	*washingtoni*		Washington		USNM	Uncataloged	EY	1155a	KX278576		KFJE00000000	McLean et al. (2016) | McLean et al. (2022)
Uwashingtoni_ EY1156a	*Urocitellus*	*washingtoni*		Washington		USNM	Uncataloged	EY	1156a	KX278587		KFJD00000000	McLean et al. (2016) | McLean et al. (2022)
Uwashingtoni_ UWBM82235	*Urocitellus*	*washingtoni*		Washington	Douglas	UWBM	82235	TNL	454	KX278542	KX278623, KX290232, KX278667, KX290277	KFJC00000000	McLean et al. (2016) | McLean et al. (2022)
Uwashingtoni_ UWBM82234	*Urocitellus*	*washingtoni*		Washington	Douglas	UWBM	82234	AKW	154	KX278562			McLean et al. (2016)

Appendix II

Specimens examined for craniometric analysis.

sampleCode	Genus	specific Epithet	subspecific Epithet	state Province	County	institution Code	catalog Number	Sex	age Class	Inclusive data set
UrbrbrKUM45922	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45922	Female	Adult	Geometric morphometric
UrbrbrKUM45923	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45923	Female	Adult	Geometric morphometric
UrbrbrKUM45925	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45925	Female	Adult	Geometric morphometric
UrbrbrKUM45926	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45926	Female	Adult	Geometric morphometric
UrbrbrKUM45929	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45929	Male	Adult	Geometric morphometric
UrbrbrKUM45930	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45930	Female	Adult	Geometric morphometric
UrbrbrKUM45932	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45932	Female	Adult	Geometric morphometric
UrbrbrKUM45936	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45936	Female	Adult	Geometric morphometric
UrbrbrKUM45937	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45937	Male	Adult	Geometric morphometric
UrbrbrKUM45938	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	45938	Female	Adult	Geometric morphometric
UrbrbrKUM130612	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Adams	KU	130612	Female	Adult	Geometric morphometric
UrbrbrUSNM202410	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Valley	USNM	202410	Female	Adult	Geometric morphometric
UrbrbrUSNM265911	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Valley	USNM	265911	Male	Adult	Geometric morphometric
UrbrbrUSNM265913	*Urocitellus*	*brunneus*	*brunneus*	Idaho	Valley	USNM	265913	Male	Adult	Geometric morphometric
UrbrenKUM45940	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Washington	KU	45940	Male	Adult	Geometric morphometric
UrbrenKUM45942	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Washington	KU	45942	Female	Adult	Geometric morphometric
UrbrenKUM45943	*Urocitellus*	*brunneus*	*endemicus*	Idaho	Washington	KU	45943	Female	Adult	Geometric morphometric
UrbrenUSNM201726	*Urocitellus*	*brunneus*	*endemicus*	Idaho	[Washington?]	USNM	201726	Male	Adult	Geometric morphometric
UrbrenUSNM201727	*Urocitellus*	*brunneus*	*endemicus*	Idaho	[Washington?]	USNM	201727	Male	Adult	Geometric morphometric
UrbrenUSNM201728	*Urocitellus*	*brunneus*	*endemicus*	Idaho	[Washington?]	USNM	201728	Male	Adult	Geometric morphometric
UrbrenUSNM201730	*Urocitellus*	*brunneus*	*endemicus*	Idaho	[Washington?]	USNM	201730	Male	Adult	Geometric morphometric
UrcacaKUM133131	*Urocitellus*	*canus*	*canus*	Nevada	Washoe	KU	133131	Female	Adult	Geometric morphometric
UrcacaUSNM80283	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	80283	Female	Adult	Geometric morphometric
UrcacaUSNM80284	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	80284	Female	Adult	Geometric morphometric
UrcacaUSNM80285	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	80285	Female	Adult	Geometric morphometric
UrcacaUSNM80286	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	80286	Female	Adult	Geometric morphometric
UrcacaUSNM89183	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	89183	Male	Adult	Geometric morphometric
UrcacaUSNM89184	*Urocitellus*	*canus*	*canus*	Oregon	[Crook?]	USNM	89184	Female	Adult	Geometric morphometric
UrcacaUSNM204832	*Urocitellus*	*canus*	*canus*	Oregon	[Deschutes?]	USNM	204832	Male	Adult	Geometric morphometric
UrcacaUSNM204834	*Urocitellus*	*canus*	*canus*	Oregon	[Deschutes?]	USNM	204834	Male	Adult	Geometric morphometric
UrcacaUSNM204835	*Urocitellus*	*canus*	*canus*	Oregon	[Deschutes?]	USNM	204835	Female	Adult	Geometric morphometric
UrcacaUSNM204837	*Urocitellus*	*canus*	*canus*	Oregon	[Deschutes?]	USNM	204837	Male	Adult	Geometric morphometric
UrcacaUSNM206850	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	206850	Female	Adult	Geometric morphometric
UrcacaUSNM207175	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207175	Male	Adult	Geometric morphometric

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UrcacaUSNM207176	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207176	Female	Adult	Geometric morphometric
UrcacaUSNM207177	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207177	Male	Adult	Geometric morphometric
UrcacaUSNM207182	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207182	Male	Adult	Geometric morphometric
UrcacaUSNM207173	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207173	Male	Adult	Geometric morphometric
UrcacaUSNM207178	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207178	Male	Adult	Geometric morphometric
UrcacaUSNM207180	*Urocitellus*	*canus*	*canus*	Oregon	[Jefferson?]	USNM	207180	Female	Adult	Geometric morphometric
UrcaviKUM131473	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131473	Female	Adult	Geometric morphometric
UrcaviKUM131476	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131476	Male	Adult	Geometric morphometric
UrcaviKUM131478	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131478	Female	Adult	Geometric morphometric
UrcaviKUM131480	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131480	Female	Adult	Geometric morphometric
UrcaviKUM131486	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131486	Female	Adult	Geometric morphometric
UrcaviKUM131487	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131487	Male	Adult	Geometric morphometric
UrcaviKUM131490	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131490	Male	Adult	Geometric morphometric
UrcaviKUM131492	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131492	Male	Adult	Geometric morphometric
UrcaviKUM131498	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131498	Male	Adult	Geometric morphometric
UrcaviKUM131499	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131499	Female	Adult	Geometric morphometric
UrcaviKUM131501	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131501	Male	Adult	Geometric morphometric
UrcaviKUM131504	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131504	Female	Adult	Geometric morphometric
UrcaviKUM131507	*Urocitellus*	*canus*	*vigilis*	Oregon	Malheur	KU	131507	Female	Adult	Geometric morphometric
UrcaviUSNM168363	*Urocitellus*	*canus*	*vigilis*	Oregon	[Malheur?]	USNM	168363	Female	Adult	Geometric morphometric
UrcaviUSNM168364	*Urocitellus*	*canus*	*vigilis*	Oregon	[Malheur?]	USNM	168364	Female	Adult	Geometric morphometric
UrcaviUSNM168484	*Urocitellus*	*canus*	*vigilis*	Oregon	[Malheur?]	USNM	168484	Male	Adult	Geometric morphometric
UrcaviUSNM168485	*Urocitellus*	*canus*	*vigilis*	Oregon	[Malheur?]	USNM	168485	Male	Adult	Geometric morphometric
UrmoarUSNM23926	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23926	Female	Adult	Geometric morphometric
UrmoarUSNM23927	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23927	Male	Adult	Geometric morphometric
UrmoarUSNM23929	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23929	Male	Adult	Geometric morphometric
UrmoarUSNM23931	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23931	Male	Adult	Geometric morphometric
UrmoarUSNM23932	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23932	Male	Adult	Geometric morphometric
UrmoarUSNM23933	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23933	Male	Adult	Geometric morphometric
UrmoarUSNM243551	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	243551	Male	Adult	Geometric morphometric
UrmoarUSNM266540	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	[Clark?]	USNM	266540	Female	Adult	Geometric morphometric
UrmoarUSNM23333	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23333	Male	Adult	Geometric morphometric
UrmoarUSNM23490	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23490	Male	Adult	Geometric morphometric
UrmoarUSNM23930	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho		USNM	23930	Male	Adult	Geometric morphometric
UrmoidMSB70152	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho		MSB	70152	Male	Adult	Geometric morphometric
UrmoidMSB70158	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho		MSB	70158	Female	Adult	Geometric morphometric

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UrmoidMSB70162	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho		MSB	70162	Female	Adult	Geometric morphometric
UrmoidMSB70167	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho		MSB	70167	Female	Adult	Geometric morphometric
UrmoidUSNM168287	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Payette?]	USNM	168287	Female	Adult	Geometric morphometric
UrmoidUSNM168288	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Payette?]	USNM	168288	Female	Adult	Geometric morphometric
UrmoidUSNM168357	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Payette?]	USNM	168357	Male	Adult	Geometric morphometric
UrmoidUSNM168359	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Payette?]	USNM	168359	Female	Adult	Geometric morphometric
UrmoidUSNM179649	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Canyon?]	USNM	179649	Female	Adult	Geometric morphometric
UrmoidUSNM201733	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Washington?]	USNM	201733	Male	Adult	Geometric morphometric
UrmoidUSNM201734	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Washington?]	USNM	201734	Female	Adult	Geometric morphometric
UrmoidUSNM398289	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Ada	USNM	398289	Female	Adult	Geometric morphometric
UrmoidUSNM168510	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Canyon?]	USNM	168510	Female	Adult	Geometric morphometric
UrmoidUSNM168511	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Canyon?]	USNM	168511	Male	Adult	Geometric morphometric
UrmoidUSNM169582	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Elmore?]	USNM	169582	Male	Adult	Geometric morphometric
UrmoidUSNM169581	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	[Elmore?]	USNM	169581	Male	Adult	Geometric morphometric
UrmomoKUM6072	*Urocitellus*	*mollis*	*mollis*	Nevada	Esmerelda	KU	6072	Male	Adult	Geometric morphometric
UrmomoKUM6712	*Urocitellus*	*mollis*	*mollis*	Idaho	Bannock	KU	6712	Female	Adult	Geometric morphometric
UrmomoKUM46060	*Urocitellus*	*mollis*	*mollis*	Nevada	Elko	KU	46060	Female	Adult	Geometric morphometric
UrmomoKUM46061	*Urocitellus*	*mollis*	*mollis*	Nevada	Elko	KU	46061	Female	Adult	Geometric morphometric
UrmomoKUM46062	*Urocitellus*	*mollis*	*mollis*	Nevada	Elko	KU	46062	Female	Adult	Geometric morphometric
UrmomoKUM46063	*Urocitellus*	*mollis*	*mollis*	Nevada	Elko	KU	46063	Female	Adult	Geometric morphometric
UrmomoKUM77590	*Urocitellus*	*mollis*	*mollis*	Nevada	Churchill	KU	77590	Male	Adult	Geometric morphometric
UrmomoKUM131469	*Urocitellus*	*mollis*	*mollis*	Idaho	Cassia	KU	131469	Female	Adult	Geometric morphometric
UrmomoKUM131470	*Urocitellus*	*mollis*	*mollis*	Idaho	Cassia	KU	131470	Male	Adult	Geometric morphometric
UrmomoKUM131471	*Urocitellus*	*mollis*	*mollis*	Idaho	Cassia	KU	131471	Female	Adult	Geometric morphometric
UrmomoKUM131529	*Urocitellus*	*mollis*	*mollis*	Idaho	Cassia	KU	131529	Male	Adult	Geometric morphometric
UrmomoKUM131537	*Urocitellus*	*mollis*	*mollis*	Idaho	Cassia	KU	131537	Male	Adult	Geometric morphometric
UrmomoUSNM22584	*Urocitellus*	*mollis*	*mollis*	Utah	[Utah?]	USNM	22584	Female	Adult	Geometric morphometric
UrmomoUSNM29366	*Urocitellus*	*mollis*	*mollis*	Nevada		USNM	29366	Female	Adult	Geometric morphometric
UrmomoUSNM29361	*Urocitellus*	*mollis*	*mollis*	Nevada		USNM	29361	Male	Adult	Geometric morphometric
UrmomoUSNM66378	*Urocitellus*	*mollis*	*mollis*	California	Lassen	USNM	66378	Female	Adult	Geometric morphometric
UrmomoUSNM29370	*Urocitellus*	*mollis*	*mollis*	California		USNM	29370	Male	Adult	Geometric morphometric
UrmomoUSNM29496	*Urocitellus*	*mollis*	*mollis*	California		USNM	29496	Male	Adult	Geometric morphometric
UrmomoUSNM29896	*Urocitellus*	*mollis*	*mollis*	California		USNM	29896	Male	Adult	Geometric morphometric
UrmomoUSNM22585	*Urocitellus*	*mollis*	*mollis*	Utah	[Utah?]	USNM	22585	Male	Adult	Geometric morphometric
UrtonaKUM131564	*Urocitellus*	*townsendii*	*nancyae*	Washington	Benton	KU	131564	Male	Adult	Geometric morphometric
UrtonaKUM131568	*Urocitellus*	*townsendii*	*nancyae*	Washington	Benton	KU	131568	Female	Adult	Geometric morphometric

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UrtonaKUM131569	*Urocitellus*	*townsendii*	*nancyae*	Washington	Benton	KU	131569	Male	Adult	Geometric morphometric
UrtonaKUM131578	*Urocitellus*	*townsendii*	*nancyae*	Washington	Yakima	KU	131578	Female	Adult	Geometric morphometric
UrtonaKUM131579	*Urocitellus*	*townsendii*	*nancyae*	Washington	Yakima	KU	131579	Female	Adult	Geometric morphometric
UrtonaKUM131582	*Urocitellus*	*townsendii*	*nancyae*	Washington	Yakima	KU	131582	Female	Adult	Geometric morphometric
UrtonaKUM131583	*Urocitellus*	*townsendii*	*nancyae*	Washington	Yakima	KU	131583	Male	Adult	Geometric morphometric
UrtonaKUM131552	*Urocitellus*	*townsendii*	*nancyeae*	Washington	Benton	KU	131552	Male	Adult	Geometric morphometric
UrtonaKUM131553	*Urocitellus*	*townsendii*	*nancyeae*	Washington	Benton	KU	131553	Female	Adult	Geometric morphometric
UrtonaKUM131556	*Urocitellus*	*townsendii*	*nancyeae*	Washington	Benton	KU	131556	Male	Adult	Geometric morphometric
UrtonaKUM131557	*Urocitellus*	*townsendii*	*nancyeae*	Washington	Benton	KU	131557	Male	Adult	Geometric morphometric
UrtotoKUM131584	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131584	Male	Adult	Geometric morphometric
UrtotoKUM131586	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131586	Male	Adult	Geometric morphometric
UrtotoKUM131587	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131587	Female	Adult	Geometric morphometric
UrtotoKUM131590	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131590	Male	Adult	Geometric morphometric
UrtotoKUM131593	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131593	Female	Adult	Geometric morphometric
UrtotoKUM131595	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131595	Female	Adult	Geometric morphometric
UrtotoKUM131596	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131596	Female	Adult	Geometric morphometric
UrtotoKUM131602	*Urocitellus*	*townsendii*	*townsendii*	Washington	Benton	KU	131602	Female	Adult	Geometric morphometric
UrtotoKUM131605	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	KU	131605	Male	Adult	Geometric morphometric
UrtotoKUM131608	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	KU	131608	Female	Adult	Geometric morphometric
UrtotoKUM131612	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	KU	131612	Female	Adult	Geometric morphometric
UrtotoKUM131614	*Urocitellus*	*townsendii*	*townsendii*	Washington	Yakima	KU	131614	Female	Adult	Geometric morphometric
UrtotoUSNM235736	*Urocitellus*	*townsendii*	*townsendii?*	Washington	Yakima	USNM	235736	Female	Adult	Geometric morphometric
UrtotoUSNM235737	*Urocitellus*	*townsendii*	*townsendii?*	Washington	Yakima	USNM	235737	Female	Adult	Geometric morphometric
UrtotoUSNM235735	*Urocitellus*	*townsendii*	*townsendii?*	Washington	Yakima	USNM	235735	Male	Adult	Geometric morphometric
UrtotoUSNM89320	*Urocitellus*	*townsendii*	*townsendii?*	Washington	Klickitat	USNM	89320	Male	Adult	Geometric morphometric
UrtotoUSNM89319	*Urocitellus*	*townsendii*	*townsendii?*	Washington	Klickitat	USNM	89319	Male	Adult	Geometric morphometric
UrwaKUM53130	*Urocitellus*	*washingtoni*		Washington	Walla Walla	KU	53130	Female	Adult	Geometric morphometric
UrwaKUM53131	*Urocitellus*	*washingtoni*		Washington	Walla Walla	KU	53131	Female	Adult	Geometric morphometric
UrwaKUM131679	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131679	Male	Adult	Geometric morphometric
UrwaKUM131680	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131680	Male	Adult	Geometric morphometric
UrwaKUM131681	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131681	Female	Adult	Geometric morphometric
UrwaKUM131686	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131686	Female	Adult	Geometric morphometric
UrwaKUM131695	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131695	Male	Adult	Geometric morphometric
UrwaKUM131696	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131696	Male	Adult	Geometric morphometric
UrwaKUM131698	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131698	Male	Adult	Geometric morphometric
UrwaKUM131701	*Urocitellus*	*washingtoni*		Washington	Franklin	KU	131701	Male	Adult	Geometric morphometric

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UrwaUSNM206743	*Urocitellus*	*washingtoni*		Oregon	[Umatilla?]	USNM	206743	Male	Adult	Geometric morphometric
UrwaUSNM78577	*Urocitellus*	*washingtoni*		Oregon	[Umatilla?]	USNM	78577	Female	Adult	Geometric morphometric
UrwaUSNM79393	*Urocitellus*	*washingtoni*		Oregon	[Morrow?]	USNM	79393	Female	Adult	Geometric morphometric
UrwaUSNM79270	*Urocitellus*	*washingtoni*		Oregon	[Morrow?]	USNM	79270	Male	Adult	Geometric morphometric
UrwaUSNM79251	*Urocitellus*	*washingtoni*		Oregon	[Morrow?]	USNM	79251	Male	Adult	Geometric morphometric
UrwaUSNM79252	*Urocitellus*	*washingtoni*		Oregon	[Morrow?]	USNM	79252	Female	Adult	Geometric morphometric
UrwaUSNM78393	*Urocitellus*	*washingtoni*		Oregon	[Umatilla?]	USNM	78393	Female	Adult	Geometric morphometric
UrwaUSNM78576	*Urocitellus*	*washingtoni*		Oregon	[Umatilla?]	USNM	78576	Male	Adult	Geometric morphometric
UrwaUSNM78189	*Urocitellus*	*washingtoni*		Oregon	[Umatilla?]	USNM	78189	Male	Adult	Geometric morphometric
MVZ:Mamm:67346	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67346	Female	Adult	Linear measurement
MVZ:Mamm:67347	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67347	Male	Adult	Linear measurement
MVZ:Mamm:67348	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67348	Female	Adult	Linear measurement
MVZ:Mamm:67349	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67349	Female	Adult	Linear measurement
MVZ:Mamm:67351	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67351	Female	Adult	Linear measurement
MVZ:Mamm:67352	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67352	Male	Adult	Linear measurement
MVZ:Mamm:67353	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	MVZ	67353	Male	Adult	Linear measurement
UMNH:Mamm:8948	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Jerome	UMNH	8948	Female	Adult	Linear measurement
UMNH:Mamm:28295	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28295	Female	Adult	Linear measurement
UMNH:Mamm:28296	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28296	Female	Adult	Linear measurement
UMNH:Mamm:28297	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28297	Female	Adult	Linear measurement
UMNH:Mamm:28298	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28298	Female	Adult	Linear measurement
UMNH:Mamm:28299	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28299	Female	Adult	Linear measurement
UMNH:Mamm:28300	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28300	Male	Adult	Linear measurement
UMNH:Mamm:28301	*Urocitellus*	*idahoensis*	*artemesiae*	Idaho	Bingham	UMNH	28301	Male	Adult	Linear measurement
MVZ:Mamm:67309	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67309	Female	Adult	Linear measurement
MVZ:Mamm:67310	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67310	Male	Adult	Linear measurement
MVZ:Mamm:67311	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67311	Female	Adult	Linear measurement
MVZ:Mamm:67312	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67312	Female	Adult	Linear measurement
MVZ:Mamm:67280	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67280	Male	Adult	Linear measurement
MVZ:Mamm:67281	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67281	Male	Adult	Linear measurement
MVZ:Mamm:67282	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67282	Male	Adult	Linear measurement
MVZ:Mamm:67283	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67283	Male	Adult	Linear measurement
MVZ:Mamm:67284	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67284	Male	Adult	Linear measurement
MVZ:Mamm:67295	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67295	Male	Adult	Linear measurement
MVZ:Mamm:67296	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	MVZ	67296	Female	Adult	Linear measurement
UMNH:Mamm:28254	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Elmore	UMNH	28254	Female	Adult	Linear measurement

sampleCode	Genus	specific Epithet	subspecific Epithet	state Province	County	institution Code	catalog Number	Sex	age Class	Inclusive data set
UMNH:Mamm:28302	*Urocitellus*	*idahoensis*	*idahoensis*	Idaho	Payette	UMNH	28302	Female	Adult	Linear measurement
UMNH:Mamm:28128	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28128	Female	Adult(1)	Linear measurement
UMNH:Mamm:28129	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28129	Female	Adult(1)	Linear measurement
UMNH:Mamm:28130	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28130	Male	Adult(1)	Linear measurement
UMNH:Mamm:28131	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28131	Female	Adult(1)	Linear measurement
UMNH:Mamm:28172	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28172	Male	Adult(1)	Linear measurement
UMNH:Mamm:28173	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28173	Male	Adult(1)	Linear measurement
UMNH:Mamm:28404	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28404	Female	Adult(1)	Linear measurement
UMNH:Mamm:28408	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28408	Female	Adult(1)	Linear measurement
UMNH:Mamm:28409	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28409	Male	Adult(1)	Linear measurement
UMNH:Mamm:28415	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28415	Male	Adult(1)	Linear measurement
UMNH:Mamm:28126	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28126	Female	Adult(2)	Linear measurement
UMNH:Mamm:28134	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28134	Male	Adult(2)	Linear measurement
UMNH:Mamm:28148	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28148	Female	Adult(2)	Linear measurement
UMNH:Mamm:28162	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28162	Female	Adult(2)	Linear measurement
UMNH:Mamm:28310	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28310	Female	Adult(2)	Linear measurement
UMNH:Mamm:28314	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28314	Male	Adult(2)	Linear measurement
UMNH:Mamm:28319	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28319	Female	Adult(2)	Linear measurement
UMNH:Mamm:28320	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28320	Male	Adult(2)	Linear measurement
UMNH:Mamm:28399	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28399	Male	Adult(2)	Linear measurement
UMNH:Mamm:28452	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28452	Female	Adult(2)	Linear measurement
UMNH:Mamm:28121	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28121	Male	Adult(3)	Linear measurement
UMNH:Mamm:28123	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28123	Female	Adult(3)	Linear measurement
UMNH:Mamm:28149	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28149	Female	Adult(3)	Linear measurement
UMNH:Mamm:28323	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28323	Female	Adult(3)	Linear measurement
UMNH:Mamm:28414	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28414	Female	Adult(3)	Linear measurement
UMNH:Mamm:28456	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28456	Female	Adult(3)	Linear measurement
UMNH:Mamm:28457	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28457	Female	Adult(3)	Linear measurement
UMNH:MAMM:28383	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28383	Female	Adult(4)	Linear measurement
UMNH:Mamm:28412	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28412	Female	Adult(4)	Linear measurement
UMNH:Mamm:28331	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28331	Female	Adult(5)	Linear measurement
UMNH:Mamm:28324	*Urocitellus*	*mollis*	*mollis*	Utah	Tooele	UMNH	28324	Female	Adult(6)	Linear measurement