

## Research Article

# 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. artemesia* (Merriam 1913) in eastern Idaho. *Urocitellus idahoensis* is endemic to Idaho and has a maximal range area of roughly 29,700 km<sup>2</sup> 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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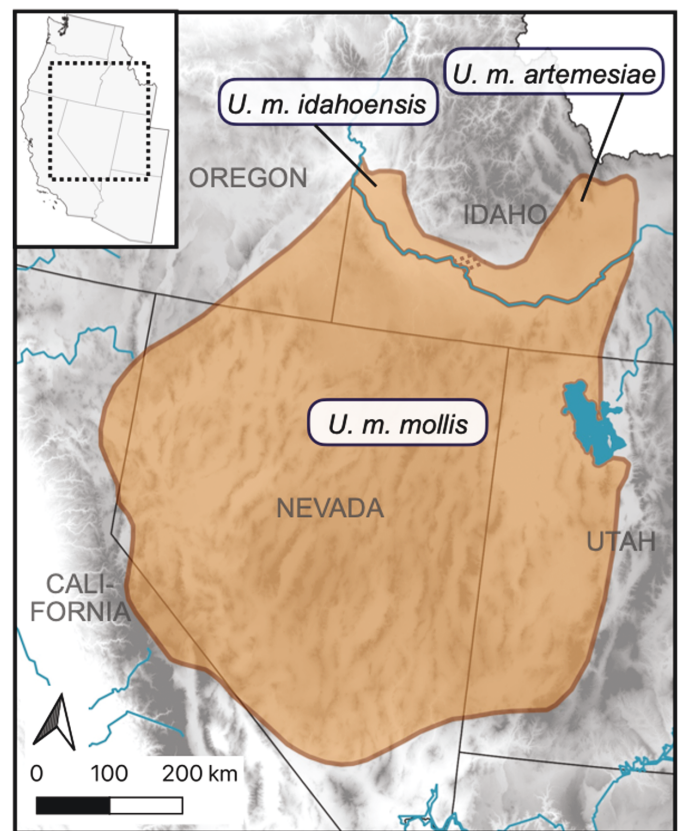
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Database 2023). Recently, Hoisington-Lopez et al. (2012) elevated subspecies within *U. brunneus*, thereby recognizing a sixth species (*U. endemicus*). These sister taxa are minimally diverged genetically (Hoisington-Lopez et al. 2012; McLean et al. 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. artemesiaae* (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. artemesiaae*. He distinguished *U. m. artemesiaae* (as *C. m. artemesiaae*) 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



**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. artemesiaae*, and stippling represents the presumed boundary of the latter 2 subspecies.

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 *artemesiaae*) by Hoffmann et al. (1993).

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 endemism 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 (*Brp*, 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 ( $2 \times \text{BF}$ ), 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 Raftery (1995), with  $2\ln\text{BF}$  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 *Uroditellus*. 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 *Uroditellus*, 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 *Uroditellus* 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://futures.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 trait toolkit ([Guralnick et al. 2016](#)) and republished in the FuTRES v1.0 data snapshot (<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.

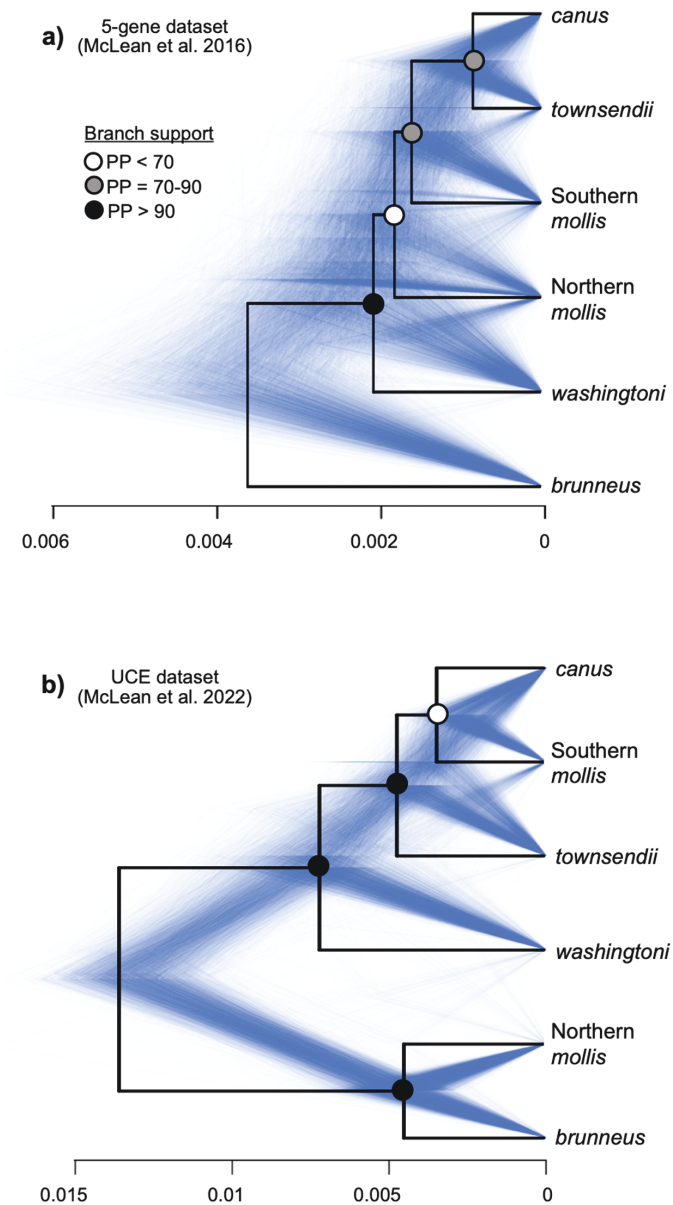
Results  
Species trees and nuDNA-based delimitation.

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



**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.

Table 1. Bayes factor-based tests of species delimitation hypotheses for <i>U. mollis</i> based on nuclear DNA sequence data.		
Model	Marginal L	2lnBF
Five gene data set		
6 spp (northern <i>mollis</i> distinct)	–7,875.92	—
5 spp (northern + southern <i>mollis</i> )	–7,836.72	78.40
Ultraconserved element data set		
6 spp (northern <i>mollis</i> distinct)	–4,135.14	—
5 spp (northern + southern <i>mollis</i> )	–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 *Uroditellus* 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. artemesia*, 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 additional 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 *Uroditellus*. 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. artemesia* lineage had the smallest averages for all measurements. *Uroditellus m. mollis* was typically intermediate for these same measurements.

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

	<i>brunneus</i>	<i>canus</i>	<i>mollis</i> North	<i>mollis</i> South	<i>townsendii</i>	<i>washingtoni</i>
<i>brunneus</i>	0.34 (10)					
<i>canus</i>	5.38	1.18 (8)				
<i>mollis</i> North	6.33	4.23	2.61 (7)			
<i>mollis</i> South	6	2.27	4.09	1.55 (3)		
<i>townsendii</i>	8.68	7.55	8.19	7.75	1.07 (7)	
<i>washingtoni</i>	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.

**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 *Uroditellus*.

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  $\times$  size term (species-specific allometries). See the main text for further details about ANOVA construction.

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

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

Sample sizes in parentheses.

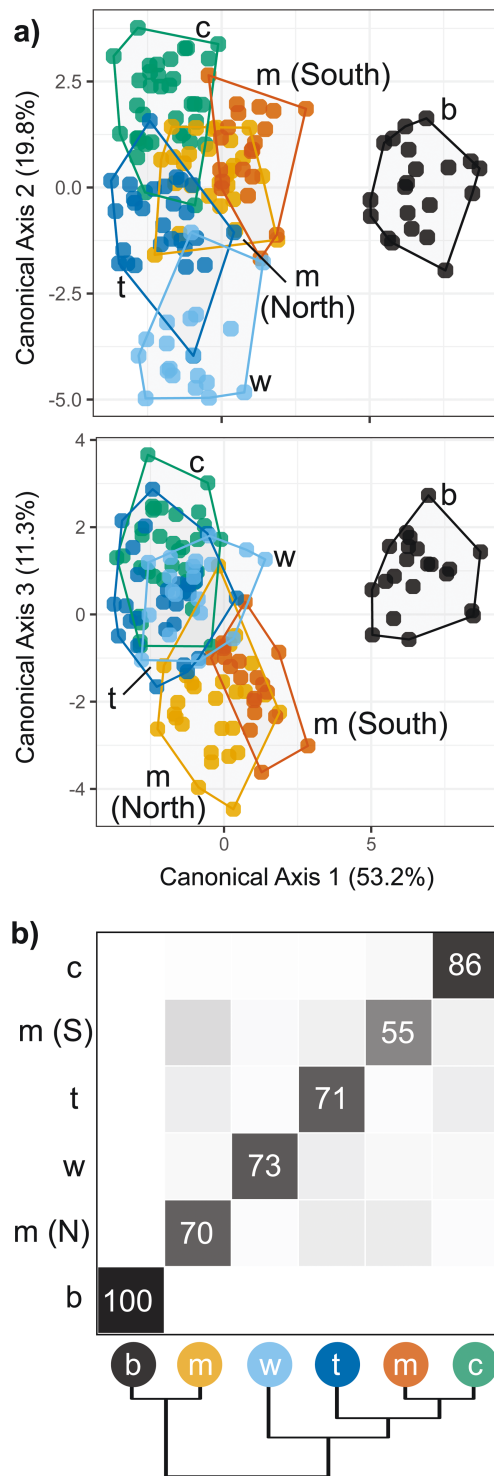
variables of body mass, range area, and extent of prior research and sampling were also predictive of undescribed diversity.

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, paleoceanic, 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 (*colIII*) 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;





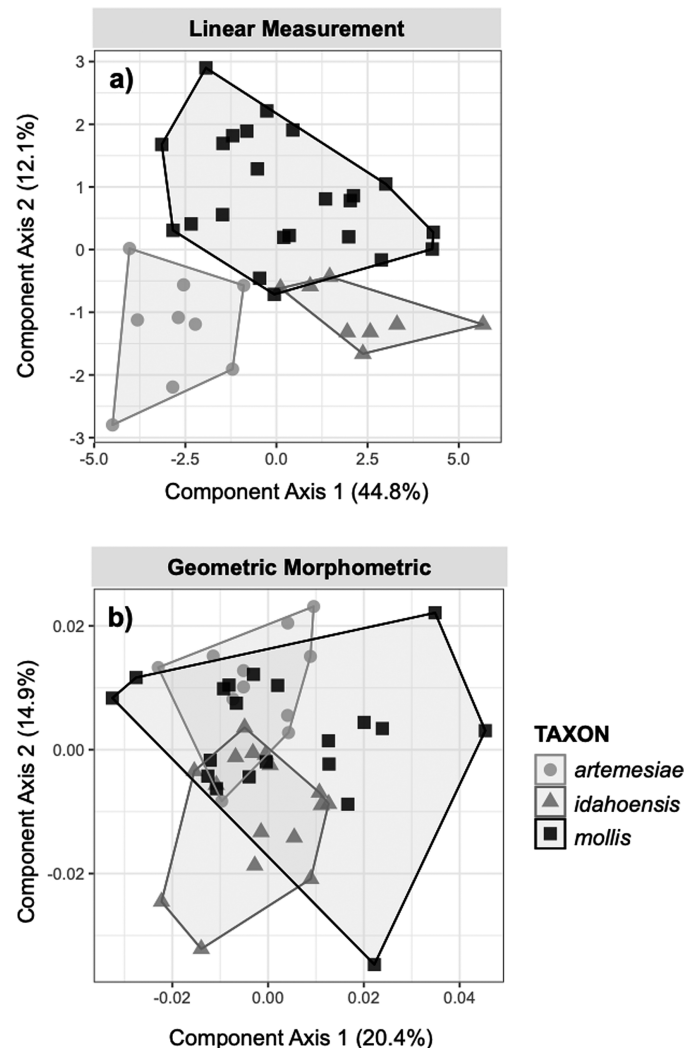
**Fig. 3.** Cranial shape variation in 6 nuclear DNA lineages of small-eared *Urocyon* based on 24 two-dimensional landmarks. a) Plots of group-wide variation from canonical axes 1 and 2 (top), and 1 and 3 (bottom). b) Heatmap of classification accuracies among all pairwise combinations of the 6 genetic 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

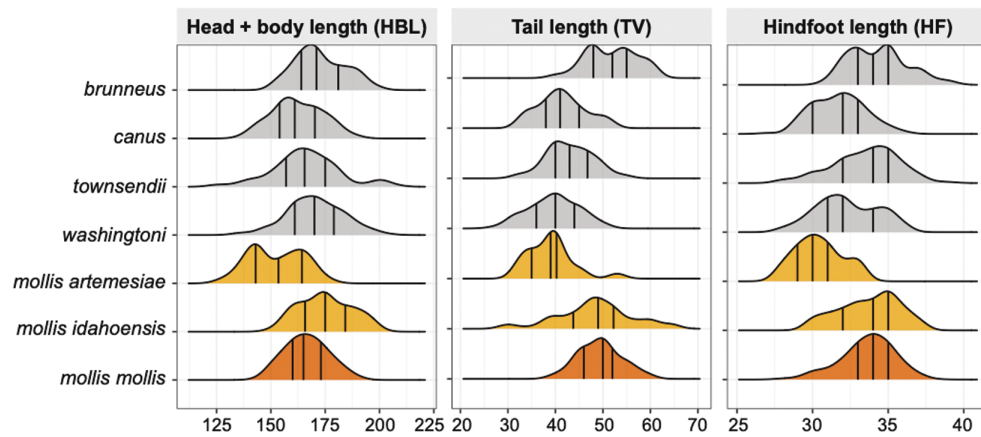
Ground Squirrel) distributed across much of the Great Basin as ecologically defined (Grayson 2011). Nuclear DNA data supported distinct evolutionary histories in *U. mollis* populations occurring north and south of the Snake River in Idaho. We failed to recover these geographic lineages of *U. mollis* 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 *Urocyon*. Representatives of the *brunneus* and *canus* lineages were pooled here due to low sample sizes. *U. mollis artemesiaie* and *U. mollis 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 *artemesiaie*), with *idahoensis* being larger in each external metric. However, southern *U. mollis* displays intermediate values between *U. m. idahoensis* and *U. m. artemesiaie* 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. artemesiaie* 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 *artemesiaie*). 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 *Urocyon* 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. artemesiaie* 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<sup>2</sup> 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 artemesia* comb. nov. (Merriam, 1913)

*Citellus mollis artemesia* Merriam, 1913:137. Type locality “Birch Creek, [Clark County,] Idaho,” United States.

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

*Citellus townsendii artemesia*: Howell, 1938:65. Name combination.

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

*Spermophilus artemesia*: Rickart, 1989:532. Name combination.

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

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

*U*[*rocitellus*]. *m*[*ollis*]. *artemesia*: 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. artemesia*) 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 *artemesia*, 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 *artemesia*). The eye ring and anterior edge of the pinna are white. Feet yellowish-white.

Bowing in the zygomatic arches varies in adults, being more out-bowed 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 *artemesia*.

Comparison

Present comparisons focus only on the formerly conspecific *U. mollis*, *U. i. idahoensis*, and *U. i. artemesia*. Consistent size differences exist between subspecies *artemesia* and *idahoensis* in length of head and body (*artemesia* 166.5 mm ± 5.7, 154 to 174; *idahoensis* 180.3 mm ± 3.1, 175 to 185; Table 5) and length of hind foot (*artemesia* 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 *artemesia* 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 *artemesia* (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 *artemesia* 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 *artemesia* is smaller on average than *idahoensis* in these dimensions. Consistent craniodental measurement differences exist between *artemesia* 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 *artemesia* 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 *artemesia* 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 *artemesia* 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

**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	<i>U. m. artemesia</i>	<i>U. m. idahoensis</i>	<i>U. m. mollis</i>
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.

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. artemesia* 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.

*Uroditellus 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 mollis* 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.

*Uroditellus 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 *Uroditellus*, 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. artemesia* (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. artemesia* 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. *Uroditellus 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. artemesia*, 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 *Urocyon mollis*.

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

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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.

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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	KFFK000000000	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	KFFK000000000	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	KFFK100000000	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		KFFK100000000	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	KFFK100000000	McLean et al. (2016)   McLean et al. (2022)
Ucanus_EY966	Urocitellus	canus	vigilis	Idaho	Owyhee	USNM	Uncataloged	EY	966	OR813776		KFFKH000000000	McLean et al. (2022)   Harrison et al. (2003)
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	Uroctellus	canus	vigilis	Idaho	Owyhee			EY	968	AF157889			Harrison et al. (2003)
Uidahoenisis_MSB152485	Uroctellus	idahoenisis	artemesiae	Idaho	Butte	MSB	152485	NK	145662	KX278528	KX278604, KX290213, KX278648, KX290258	KFJB000000000	McLean et al. (2016)   McLean et al. (2022)
Uidahoenisis_MSB152846	Uroctellus	idahoenisis	artemesiae	Idaho	Butte	MSB	152846	NK	145739	KX278579			McLean et al. (2016)
Uidahoenisis_MSB152352	Uroctellus	idahoenisis	artemesiae	Idaho	Butte	MSB	152352	NK	147596	KX278529	KX278605, KX290214, KX278649, KX290259		McLean et al. (2016)
Uidahoenisis_MSB71991	Uroctellus	idahoenisis	idahoenisis	Idaho	Ada	MSB	71991	NK	30724	KX278569		KFJA000000000	McLean et al. (2016)   McLean et al. (2022)
Uidahoenisis_MSB89149	Uroctellus	idahoenisis	idahoenisis	Idaho	Ada	MSB	89149	NK	5929	KX278552	KX278634, KX290243, KX278678, KX290257	KFIZ000000000	McLean et al. (2016)   McLean et al. (2022)
Uidahoenisis_EY1068	Uroctellus	idahoenisis	idahoenisis	Idaho	Ada			EY	1068	AF157880			Harrison et al. (2003)
Uidahoenisis_EY1067	Uroctellus	idahoenisis	idahoenisis	Idaho	Ada			EY	1067	AF157949			Harrison et al. (2003)
Umollis_EY1129a	Uroctellus	mollis	mollis	Idaho	Owyhee	USNM	Uncataloged	EY	1129a	AF157920	KX278597, KX290206, KX278641, KX290250	KFY000000000	Harrison et al. (2003)   McLean et al. (2016)   McLean et al. (2022)
Umollis_EY1130a	Uroctellus	mollis	mollis	Idaho	Owyhee	USNM	Uncataloged	EY	1130a	AF157938	KX278598, KX290207, KX278642, KX290251	KFX000000000	Harrison et al. (2003)   McLean et al. (2016)
Umollis_MVZ224858	Uroctellus	mollis	mollis	California	Mono	MVZ	224858			KX278535	KX278616, KX290225, KX278660, KX290270		McLean et al. (2016)
Umollis_MSB47928	Uroctellus	mollis	mollis	Nevada	White Pine	MSB	47928					KFKA000000000	McLean et al. (2022)
Utownsendii_EY1160a	Uroctellus	townsendii	nancyae	Washington	Kittitas	USNM	Uncataloged	EY	1160a	AF157933	KX278596, KX290205, KX278640, KX290249	KFJL000000000	Harrison et al. (2003)   McLean et al. (2016)   McLean et al. (2022)
Utownsendii_EY1159	Uroctellus	townsendii	nancyae	Washington	Kittitas			EY	1159	AF157932			Harrison et al. (2003)
Utownsendii_EY1162	Uroctellus	townsendii	townsendii	Washington	Yakima			EY	1162	AF157934			Harrison et al. (2003)
Utownsendii_EY1164	Uroctellus	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	KFJ1000000000	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		KFJ000000000	McLean et al. (2016)   McLean et al. (2022)
Utownsendii_UWBM32803	Urocitellus	townsendii		Washington	Yakima	UWBM	32803					KFJ1000000000	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		KFJE000000000	McLean et al. (2016)   McLean et al. (2022)
Uwashingtoni_EY1156a	Urocitellus	washingtoni		Washington		USNM	Uncataloged	EY	1156a	KX278587		KFJD000000000	McLean et al. (2016)   McLean et al. (2022)
Uwashingtoni_UWBM82235	Urocitellus	washingtoni		Washington	Douglas	UWBM	82235	TNL	454	KX278542	KX278623, KX290232, KX278667, KX290277	KFJC000000000	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
UrbbrKUM45922	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45922	Female	Adult	Geometric morphometric
UrbbrKUM45923	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45923	Female	Adult	Geometric morphometric
UrbbrKUM45925	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45925	Female	Adult	Geometric morphometric
UrbbrKUM45926	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45926	Female	Adult	Geometric morphometric
UrbbrKUM45929	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45929	Male	Adult	Geometric morphometric
UrbbrKUM45930	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45930	Female	Adult	Geometric morphometric
UrbbrKUM45932	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45932	Female	Adult	Geometric morphometric
UrbbrKUM45936	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45936	Female	Adult	Geometric morphometric
UrbbrKUM45937	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45937	Male	Adult	Geometric morphometric
UrbbrKUM45938	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	45938	Female	Adult	Geometric morphometric
UrbbrKUM130612	Urocitellus	brunneus	brunneus	Idaho	Adams	KU	130612	Female	Adult	Geometric morphometric
UrbbrUSNM202410	Urocitellus	brunneus	brunneus	Idaho	Valley	USNM	202410	Female	Adult	Geometric morphometric
UrbbrUSNM265911	Urocitellus	brunneus	brunneus	Idaho	Valley	USNM	265911	Male	Adult	Geometric morphometric
UrbbrUSNM265913	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
UrmooidMSB70152	Urocitellus	idahoensis	idahoensis	Idaho		MSB	70152	Male	Adult	Geometric morphometric
UrmooidMSB70158	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	Esmeralda	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	Female	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	nancyae	Washington	Benton	KU	131552	Male	Adult	Geometric morphometric
UrtonaKUM131553	Urocitellus	townsendii	nancyae	Washington	Benton	KU	131553	Female	Adult	Geometric morphometric
UrtonaKUM131556	Urocitellus	townsendii	nancyae	Washington	Benton	KU	131556	Male	Adult	Geometric morphometric
UrtonaKUM131557	Urocitellus	townsendii	nancyae	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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UrwaUSNM:206743	Urocitellus	washingtoni		Oregon	[Umatilla?]	USNM	206743	Male	Adult	Geometric morphometric
UrwaUSNM:78577	Urocitellus	washingtoni		Oregon	[Umatilla?]	USNM	78577	Female	Adult	Geometric morphometric
UrwaUSNM:79393	Urocitellus	washingtoni		Oregon	[Morrow?]	USNM	79393	Female	Adult	Geometric morphometric
UrwaUSNM:79270	Urocitellus	washingtoni		Oregon	[Morrow?]	USNM	79270	Male	Adult	Geometric morphometric
UrwaUSNM:79251	Urocitellus	washingtoni		Oregon	[Morrow?]	USNM	79251	Male	Adult	Geometric morphometric
UrwaUSNM:79252	Urocitellus	washingtoni		Oregon	[Morrow?]	USNM	79252	Female	Adult	Geometric morphometric
UrwaUSNM:78393	Urocitellus	washingtoni		Oregon	[Umatilla?]	USNM	78393	Female	Adult	Geometric morphometric
UrwaUSNM:78576	Urocitellus	washingtoni		Oregon	[Umatilla?]	USNM	78576	Male	Adult	Geometric morphometric
UrwaUSNM:78189	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

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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