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Research Article

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Paleophylogeography of *Notiosorex* desert shrews with description of a new species

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Abstract

The genus *Notiosorex* is the only group of shrews in North America with adaptations to arid or semiarid zones. The genus was described with a single variable species, *Notiosorex crawfordi*, from which 5 new species have since been distinguished. To date, the phylogenetic relationships of *Notiosorex* species have only been partially analyzed and it is possible that there are still distinct species included within the catch-all of *N. crawfordi*. Here, we use geometric morphometrics on cranial and mandibular characters of the described extant species, 3 fossil species, and a distinctive population of *N. crawfordi* as a proxy for an integrated assessment of phylogenetic relationships of all *Notiosorex* species. Our results indicate that the population from the Altiplano Mexicano is more similar to, yet distinct from, *N. villai* than it is to *N. crawfordi*—we describe it as a new species. We also used the resulting tree to reconstruct phylogeographic history within the genus, which suggests that *Notiosorex* sp. nov., *N. villai*, *N. evotis*, and *N. tataticuli* all diverged allopatrically as populations from the ancestral area that is currently occupied by *N. crawfordi* (and in the deeper past by the fossil species *N. harrisi*), and pushed south into the Gulf Coast, the Altiplano, and Baja California within the last 5 million years following the end of the Miocene.

Key words: arid zones, evolutionary history, fossil, geometric morphometric, shrews.

Paleofilogeografía de las musarañas del desierto *Notiosorex* con descripción de una nueva especie

Resumen

El género *Notiosorex* es el único grupo de musarañas con adaptaciones a zonas áridas y semiáridas en Norteamérica. El género fue descrito con base en una sola especie muy variable, *Notiosorex crawfordi*; desde ese entonces, se han descrito cinco nuevas especies. Hasta la fecha, las relaciones filogenéticas de las especies dentro del género *Notiosorex* solo han sido analizadas parcialmente, y es posible que haya aún mayor número de especies nuevas incluidas dentro del grupo general de *N. crawfordi*. En este estudio, utilizamos morfometría geométrica del cráneo y mandíbula de las especies vivas ya descritas, además de tres especies fósiles, y una población distintiva de *N. crawfordi* del Altiplano Mexicano como un indicador para una evaluación integrada de las relaciones filogenéticas de todas las especies de *Notiosorex*. Nuestros resultados indican que la población del Altiplano Mexicano es más similar y claramente diferenciable de *N. villai* que de *N. crawfordi*, y la describimos como una nueva especie. Utilizamos el árbol filogenético para reconstruir la historia filogeográfica del género, lo que sugiere que esta nueva especie del Altiplano, junto con *N. villai*, *N. evotis* y *N. tataticuli*, todas divergieron de forma alopátrica como poblaciones separadas a partir de la zona ancestral que actualmente ocupa *N. crawfordi* (y en el pasado más antiguo, por la especie fósil *N. harrisi*) y se desplazaron hacia el sur, hacia la costa del Golfo, el Altiplano y Baja California en los últimos 5 millones de años, desde finales del Mioceno.

Palabras clave: fósiles, historia evolutiva, morfometría geométrica, musarañas, zonas áridas.

Within North American desert shrews (*Notiosorex* spp.) some species have undergone geographic expansion processes, while others are restricted to small endemic areas (Camargo et al. 2022). These biogeographic processes are governed by a combination of climate, habitat, and geographical barriers and have consequences for evolution and differentiation of species. The genus consists of

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1 widespread species, *Notiosorex crawfordi*, found in northeastern México, Arizona, New Mexico, and western Texas and adjacent areas—plus 4 more geographically restricted species that are found sympatrically inside the range of *N. crawfordi* or allopatrically to the south in north and central México (Fig. 1; Carraway 2010; Camargo and Álvarez-Castañeda 2020). The genus is characterized by 28 teeth, the anterior of which are lightly tipped with orange—including 3 unicuspid teeth and a third molar that is less than half the size of the second molar—as well as a conspicuous external ear and short tail that is less than half the length of the head and body and is unicolored, matching the dorsal pelage (Coues 1877). *Notiosorex* shrews, distinguished from other shrew genera, possess unique morphological and physiological adaptations that enable them to thrive in inhospitable environments, including a smooth shield structure on their curly overhairs devoid of deep U-shaped notches, traits that contribute to their resilience and ability to endure arid zones (Ducommun et al. 1994).

Based on the fossil record, *Notiosorex* originated between 5 and 7 million years ago (mya) and has widespread fossil occurrences from which 4 extinct species are recognized (Morgan and White 2005; Carraway 2010). *Notiosorex harrisi* is the smallest and geologically oldest of the extinct species and originated in northeastern Arizona during the Hemphillian Land Mammal Age (NALMA) that spans the latest Miocene and earliest Pliocene (Baskin 1979; Carraway 2010). The species is also known from Wisconsin glaciation (last glacial period) and Holocene deposits in New Mexico and the Late Pleistocene and Holocene in southern Chihuahua (Lear and Harris 2007; Carraway 2010). *Notiosorex jacksoni* was large and its teeth were more generalized and less specialized than other fossil species of the genus, with records from the Pliocene in Kansas and

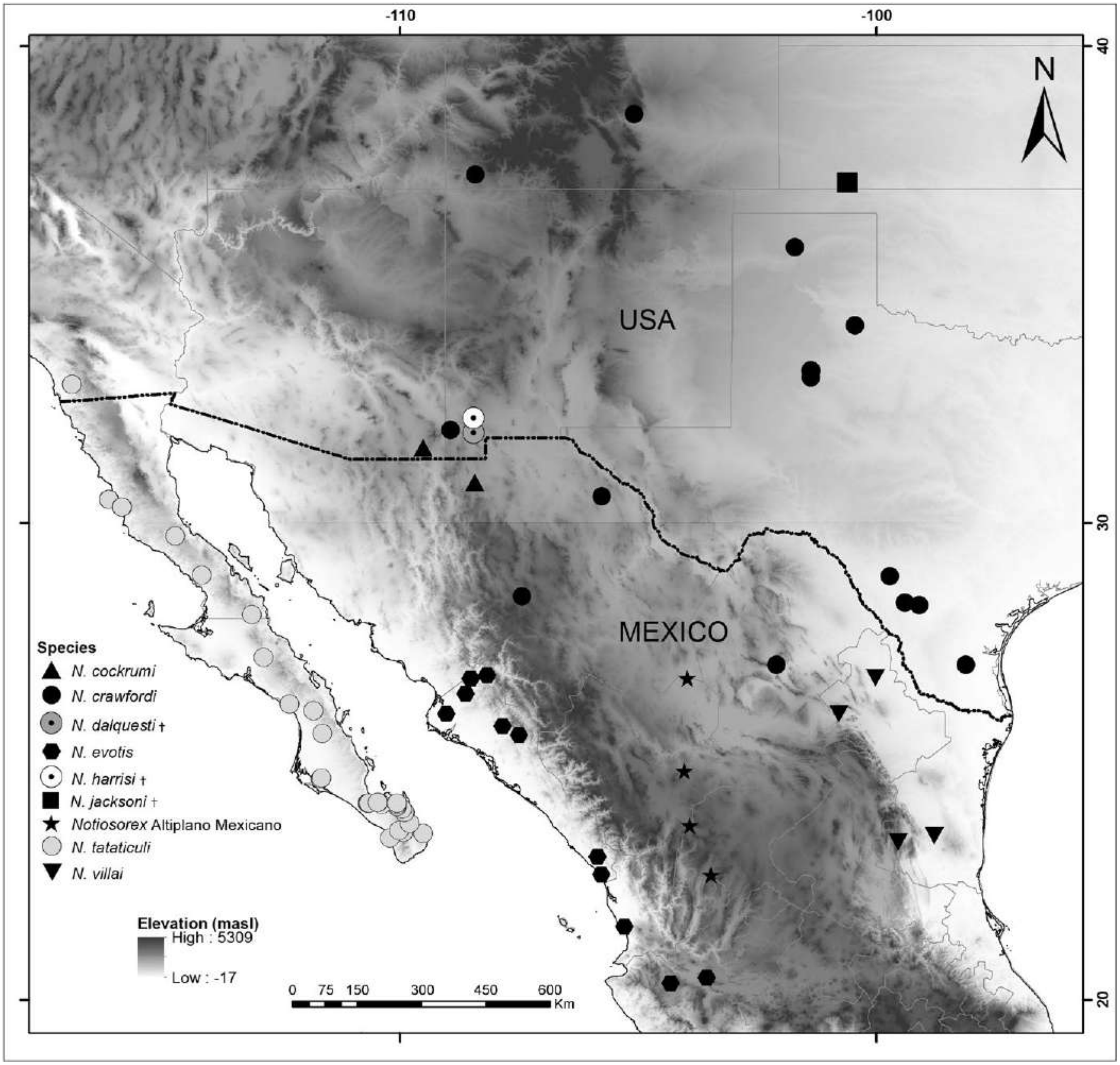

Fig. 1. Distribution map of *Notiosorex* localities included in the paleophylogeographic reconstruction analysis.

Pleistocene in California (Hibbard 1950; Cassiliano 1999). *Notiosorex repenningi* is the largest of the fossil species and is known only from its early Pliocene-type locality in Chihuahua (Lindsay and Jacobs 1985). *Notiosorex dalquesti* is the most recent and widely distributed fossil species with records in Arizona, California, Chihuahua, Kansas, Nevada, New Mexico, Nuevo León, Oklahoma, Texas, and Zacatecas ranging from at least the Late Pleistocene to Holocene (Carraway 2010).

The systematics of *Notiosorex* are still poorly understood. The first taxonomic classifications of the extant species, that were based on cranial characteristics, suggested that all populations across the geographic range should be placed in a single species (*N. crawfordi*) with 2 nominal subspecies (*N. c. crawfordi* and *N. c. evotis*; Coues 1877). In 1877, Merriam (Merriam 1877) added a new species, *Notiosorex gigas*, which was later renamed and transferred to a new genus (*Megasorex*) based on size of the skull, a cranial vault that rises slightly above the face, lack of tooth pigmentation, and distributed in southwest México (Hibbard 1950). Schandalch (1966) described 3 individuals as *N. phillipsi*, differentiated by having only 3 unicuspid teeth in the maxilla instead of the 4 unicuspid teeth typical of *Cryptotis*; however, Choate (1969) reassigned these individuals to *Cryptotis* despite their reduced dentition. Carraway and Timm (2000) elevated the previously recognized subspecies *N. crawfordi evotis* from the coastal plain of México to full species status based on its larger cranium. This species is now recognized to be distributed in Sinaloa, Jalisco, Nayarit, and Michoacán (Camargo et al. 2022). Subsequently, 3 individuals were found in Tamaulipas east of the known range of *N. crawfordi*. They differed in having a glenoid fossa roof that does not extend laterally from the cranium when viewed in dorsal aspect and they were distinguished as a new species, *N. villai* (Carraway and Timm, 2000). *Notiosorex cockrumi* was later distinguished from *N. crawfordi* as a "cryptic species" based on molecular data with a sympatric geographical distribution in Arizona and Sonora (Baker et al. 2003). Molecular analyses found strong differentiation between populations of *N. crawfordi* west and east of the Colorado River, leading to the proposal of those in the western range as a distinct species (*N. tataticuli*; Camargo and Álvarez-Castañeda 2020). *Notiosorex tataticuli* shows pronounced variation within its geographical range and was subdivided into 3 subspecies: *N. t. tataticuli* in Baja California Sur; *N. t. ocanai* in Baja California and California; and *N. t. arroyoi*, endemic to San Martin Island.

In this paper, we assess geographic variation in morphology in *Notiosorex* using geometric morphometrics, which allows us to integrate the analysis of extant and fossil populations. We then compare the phenotypic patterns to what is previously known about molecular differentiation in the extant species to construct a paleophylogeographic scenario of speciation and dispersal in the warm desert environments that emerged in North America at the end of the Cenozoic era. Paleophylogeography integrates information from fossil samples and extant populations using morphometric tree building to reconstruct past ranges, directions of colonization, and the geography of speciation (Polly 2001, 2003a, 2003b). We describe a *Notiosorex* sp. nov. based on new material from Durango in the Altiplano Méxicano that is well-differentiated from other *Notiosorex* species by its size, morphological characteristics, and morphometrics. In doing so, we are using what we fundamentally believe to be a biological species concept (i.e., that a species originates through breakdown in gene flow, often by allopatric or parapatric isolation, that differentiates it from its sibling species; Mayr 1942) but in practice we are recognizing speciation as a consequence of morphometric differentiation and by the potential isolating effects of geographic barriers.

Materials and methods

Material

We examined 207 specimens of *Notiosorex* species: *N. cockrumi* (*n* = 13), *N. crawfordi* (*n* = 83), *N. evotis* (*n* = 18), *N. tataticuli* (*n* = 62), *N. villai* (*n* = 3), and individuals from Altiplano Mexicano (*n* = 9). We included specimens of 3 fossil species: *N. dalquesti* (*n* = 9), *N. harrisi* (*n* = 8), and *N. jacksoni* (*n* = 2; Appendix I). This work does not include the species *N. repenningi* because only 1 incomplete mandible of the holotype is known (Lindsay and Jacobs 1985). Cranial parts of fossil skulls in shrews are typically broken or fragmented records, whereas mandibles are good candidates for the role of morphological markers because they are complex morphological structures well represented in the fossil record due to their durability and small size (Polly 2001). Species nomenclature followed Carraway (2010) and Camargo and Álvarez-Castañeda (2020).

Collection abbreviations are as follows: Centro de Investigaciones Biológicas del Noroeste (CIB); Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango (CRD); Universidad Autónoma de Zacatecas Colección de Vertebrados (CVMZ); The University of Kansas, Natural History Museum (KU); Biodiversity Research and Teaching Collections at Texas A&M University (TCWC); Natural Science Research Laboratory at the Museum of Texas Tech University (TTU); Universidad Autónoma Metropolitana, Unidad Iztapalapa (UAMI); Laboratorio de Paleobiología, Universidad Autónoma de Nuevo León (UANL); University of Michigan Museum of Paleontology (UM); and University of Texas-El Paso Biodiversity Collections (UTEP). Only adults were analyzed and sexual dimorphism was not evaluated because it has been shown to be minimal in desert shrews (Camargo and Álvarez-Castañeda 2020).

Geometric morphometric analyses.

We characterized shape of the mandible in lateral view and the cranium in ventral view using landmark-based geometric morphometrics (Fig. 2A). Landmark coordinates were collected from digital photographs using TPSDig 2.16 (Rohlf 2010). We also collected landmarks from published illustrations of the mandible of *M. gigas* (Armstrong and Jones 1972) for outgroup comparisons. For mandibles, we used 16 landmarks: (1) posteriormost point of lateral curve of alveolus of first incisor; (2) junction between incisor and first antemolar; (3) junction between first and second antemolar; (4) junction between second antemolar and first molar; (5) junction between first and second molar; (6) junction between second and third molar; (7) posteriormost point of third molar; (8) anterior edge of muscular rugosity on coronoid process; (9) posterior point of muscular rugosity on coronoid process; (10) ventralmost point of curvature between coronoid and condylar process; (11) dorsalmost point of condylar process; (12) ventral edge of condyle on condylar process; (13) anteriormost point of curve connecting condylar and angular process; (14) dorsalmost point of curvature between angular process and body of mandible; (15) ventralmost curvature of posterior part of mandibular body; and (16) dorsalmost curvature of central part of mandibular body (Fig. 2A).

Crania were landmarked (Fig. 2B) from a photographic orientation with the palate perpendicular to the photographic plane and the horizontal glenoid fossa parallel to it. We used 19 2-dimensional landmarks modified from Rychlik et al. (2006): (1) dorsal midline of the foramen magnum; (2) ventral midline of the foramen magnum; (3) midline of posterior margin of palate; (4) midline of anterior margin of premaxilla; (5) anterior margin of upper incisor; (6) posterior margin of upper incisor; (7) posterior margin of first antemolar; (8) posterior margin of second antemolar; (9) posteriormost

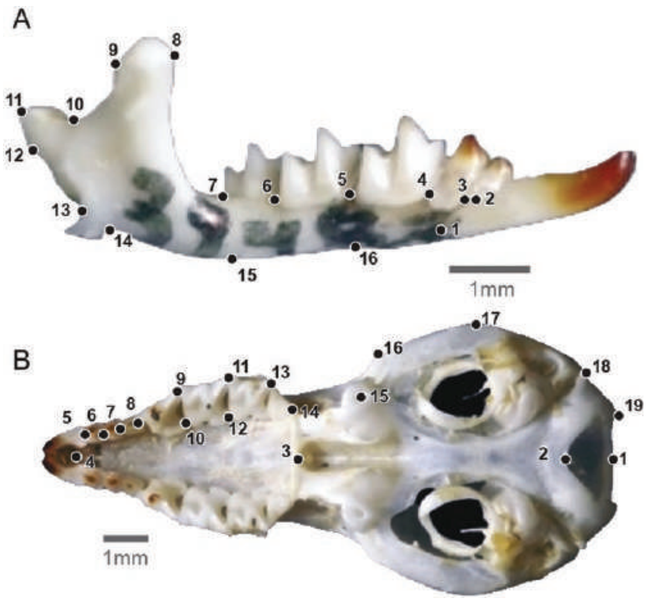

Fig. 2. Landmarks used in geometric morphometric analysis. (A) Jaw of *Notiosorex*. (B) Ventral view of the skull.

point of metastylar blade of upper fourth premolar; (10) posterior margin of fourth antemolar; (11) posteriormost point of metastylar blade of first molar; (12) posteriormost point of hypoconid of first molar; (13) posteriormost point of metastylar blade of second molar; (14) posterior margin of palate at lateral junction of pterygoid process; (15) center of depression in glenoid fossa; (16) anteriormost point of the lateral braincase; (17) lateral point of widest point of braincase; (18) paroccipital process; and (19) lateral edge of foramen magnum.

Landmarks were superimposed using Procrustes GLS fitting to remove the effects of rotation, translation, and size (Rohlf and Slice 1990). Centroid size was calculated as the square root of the summed distances between landmarks of an individual and its own centroid (Bookstein 1997; Zelditch et al. 2012). Procrustes residuals were calculated by subtracting the mean or consensus shape, and principal components analysis (PCA) was performed on the covariance matrix of the residuals (Dryden and Mardia 1998). The resulting principal component (PC) scores were used as shape variables (Dryden and Mardia 1998) for further statistical tests. A pure shape PCA was performed just on the Procrustes coordinates and a second "form" PCA was performed by including centroid size with them.

Statistical tests.

A permutation-based MANOVA was used to assess differences in mean shape among the groups by including all PC scores. Canonical variates analysis (CVA) and discriminant function analysis (DFA) were used to identify which combinations of shape variables best distinguish groups and to classify individuals to groups. Cross-validation was used with DFA to determine the accuracy of identifying individuals based on cranial or mandibular shape.

Geometric morphometrics, statistical analyses, and ordinations were performed with the Paleontological Statistics (PAST) version 4.13 package (Hammer et al. 2001), Geometric Morphometrics for Mathematica version 12.4 package (Polly 2022), and Phylogenetics for Mathematica version 6.8 package (Polly 2023). Additionally, we employed traditional morphometry to compare the morphological measurements of *Notiosorex* species using univariate statistics.

Paleophylogeographic patterns were assessed by building morphometric trees from mandibular shape of fossil and extant species using the maximum likelihood (ML) method for continuous traits with the CONTML module of PHYLIP (Felsenstein 1973; Polly 2003a, 2003b; Caumul and Polly 2005). Because phylogeography traces differentiation between population means, the tree was built using Operational Taxonomic Units made up of the mean shape of samples. A mean shape for each sample was calculated after Procrustes superimposition of the individuals in that sample. The means were then superimposed and analyzed by PCA to generate scores. The PC scores were used as continuous quantitative traits for ML tree construction. We rooted the morphometric tree with *N. harrisi* based on the hypothesis that because of its ancient and widespread fossil distribution, it represents the ancestral morphology and geographic center of the genus (Baskin 1979; Carraway 2010) and because it is our goal to integrate living taxa with the fossil record, which can only be done with morphometric data. We also built an alternative morphometric tree from scores of the *Notiosorex* species plus *M. gigas*—which is considered the closest living relative of *Notiosorex* (Ohdachi et al. 2006)—to explore how outgroup rooting would affect our interpretation. *Megasorex* does not have a fossil record and it is morphologically derived in some ways so it seems less likely to us to represent the ancestral condition than *N. harrisi* as discussed later in the paper, but regardless it represents a viable second hypothesis for establishing morphological and geographic polarity.

The ML mandibular trees were time-scaled (cf. Parham et al. 2012) using first occurrences of *N. harrisi*, *N. dalquesti*, and *N. jacksoni* to constrain the ages of nodes that subtend them (Supplementary Data SD1). Mandible centroid size was mapped onto the time-scaled trees using a Brownian model for ancestral node reconstruction to reconstruct the pattern of evolutionary changes in size (Martins and Hansen 1997). These analyses were done with the Phylogenetics for Mathematica version 6.8 package (Polly 2023).

Results

Mandibular variation.

Mandibular centroid size (CS) showed that the smallest species are *N. villai* (CS = 5.45 to 5.97) and *N. harrisi* (CS = 6.56 to 6.87), while the largest species are *N. evotis* (CS = 12.15 to 12.95) and those of Altiplano Mexicano (CS = 11.11 to 12.7; Fig. 3A). *Megasorex gigas* (CS = 16.5) is considerably larger than all of the *Notiosorex* species. ANOVA on centroid size showed that there are significant differences among extant species ($F = 251$, $P < 0.001$) and all pairs of species were significantly different in size except *N. cockrumi* and *N. tataticuli* ($P = 0.58$). Note that *N. villai* and *M. gigas* were not included in this test because they are represented by only 1 specimen each.

The first 3 PCs of mandible shape explained 63.05% of the variation (PC1 = 39.89%, PC2 = 14.66%, PC3 = 8.5%; Fig. 3B). The broken stick model showed that the first 3 PCs explain more variance than random. Results of the MANOVA based on shape variables indicated that mandibular shape differed among species ($F = 13.97$, $P < 0.001$) with all pairwise comparisons significantly different following Bonferroni correction. The first 3 PCs of form space explained nearly 100% of the variation (Fig. 3C) with PC1 = 99.67%, PC2 = 0.11%, and PC3 = 0.05% (only PC1 had more variance than expected under a broken stick model). The MANOVA on form indicated that mandibular shape and size differed significantly ($F = 244.7$, $P = 0.0001$) including all pairs of species except *N. cockrumi* and *N. tataticuli* (Bonferroni-corrected $P = 0.14$).

The first 2 canonical variate axes of mandibular shape (CV1 and CV2) explain 84.52% (69.12% and 15.40%, respectively) of the variation among the populations relative to variation within populations of *Notiosorex* (Fig. 3D). The major shape changes associated with the first canonical axis are localized in the anterior edge of muscular rugosity on the coronoid process and posterior point of

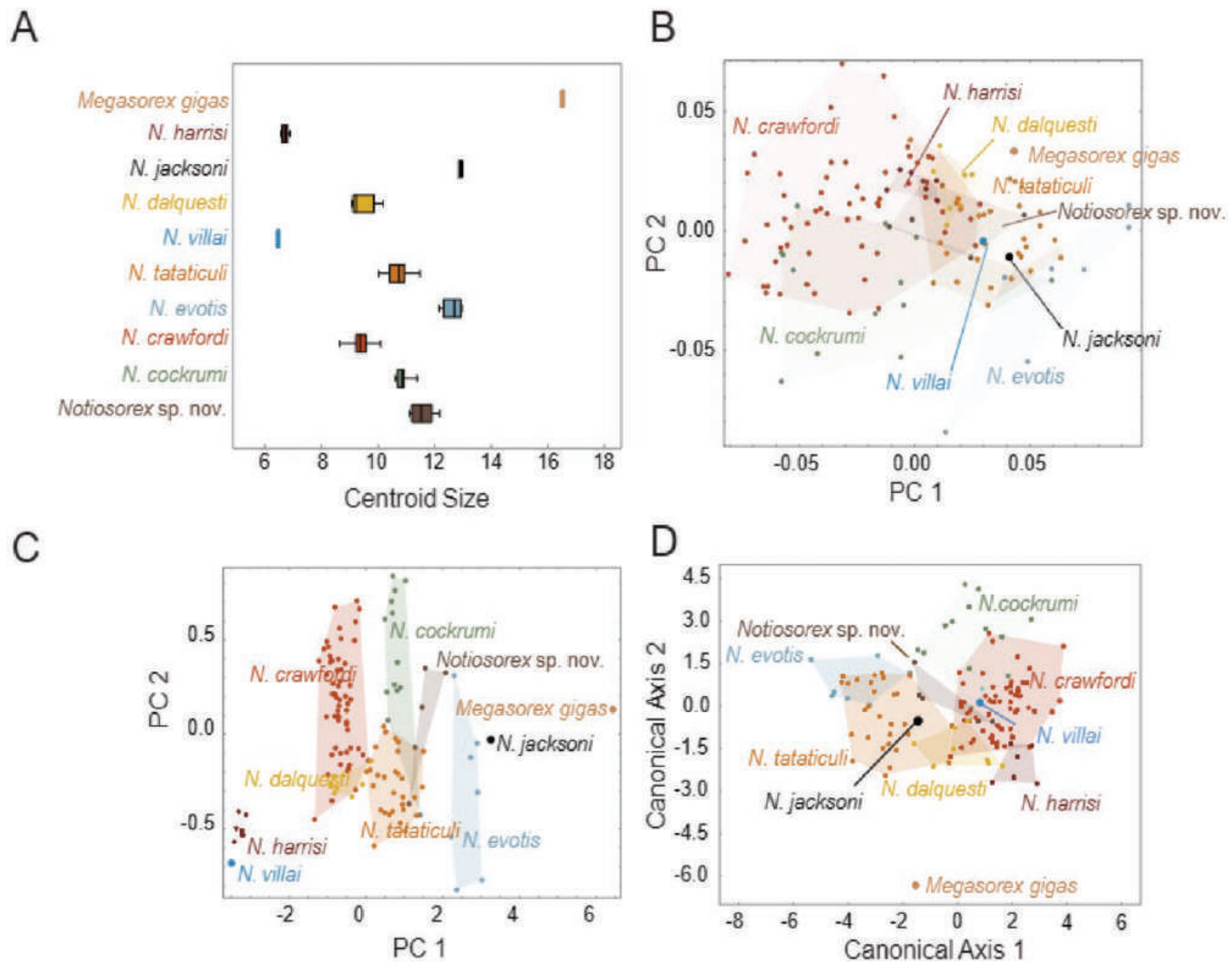

Fig. 3. Mandible results for extant and fossil *Notiosorex* species. (A) Centroid size comparisons. (B) PCA based on shape only. (C) PCA based on form (shape and size). (D) CVA based on shape only.

muscular rugosity on the coronoid process. The second canonical axis describes a minor localized effect in the shape changes that are localized at the posteriormost point of the lateral incisor (posteriormost point of lateral curve of alveolus) and junction between second antemolar and first molar. The DFA on the total shape matrix correctly classified 99.22% of specimens for each species.

Cranium variation.

The smallest species as measured from cranium centroid size (mean and range) are *N. villai* (CS = 14.15, 13.90 to 14.41), *N. cockrumi* (CS = 21.22, 20.16 to 22.30), and *N. crawfordi* (CS = 20.13, 20.14 to 27.55), while the largest species are *N. tataticuli* (CS = 25.44, 20.08 to 30.81), *N. evotis* (CS = 23.32, 21 to 25.61), and the morphological group of Altiplano Mexicano (CS = 22.53, 22.54 to 24.53; Fig. 4A). The permutation-based ANOVA found significant differences in cranium size (*F* = 7.3, $P < 0.001$) with significantly different pairwise sizes based on Tukey's pairwise test between *N. cockrumi* and *N. crawfordi*, and between *N. evotis* and *N. tataticuli*. The Altiplano Méxicano group was not significantly different in cranium size from any other species, nor was *N. crawfordi* from *N. cockrumi*, nor *N. evotis* from *N. tataticuli*. As with mandibles, *N. villai* could not be tested for significant differences because it is represented by a single individual in our sample.

The first 3 PCs of cranium shape explained 40.8% of the variation (PC1 = 19.1%, PC2 = 11.4%, PC3 = 10.4%; Fig. 4B). The broken stick model showed that the first 6 PCs explain more variance than random. There is a reasonable amount of overlap among the cranium shapes in these species, but PC1 tends to separate *N. evotis* and *N. tataticuli* from *N. cockrumi* and *N. crawfordi*. Variation on PC1 is largely related to the relative positions of the center of depression in glenoid fossa, anteriormost point of the lateral braincase, and lateral point of widest point of braincase. PC2 distinguishes specimens from the Altiplano Méxicano and of *N. villai* from the other species of *Notiosorex*. This PC is associated with differences in the relative position in the midline of anterior margin of premaxilla, lateral point of widest point of braincase, and ventral midline of the foramen magnum. Cranium shape was significantly different overall in *Notiosorex* species and the Altiplano Méxicano population (*F* = 7.21, $P < 0.001$) and Bonferroni pairwise tests indicate that all pairs of species are significantly different from each other. In the form-based PCA (shape plus centroid size), *N. villai* is very distinctive but the other species still have broad overlap (Fig. 4C). The MANOVA run on form shape variables was significant, however ($F = 5.0$, $P < 0.001$), and pairwise Bonferroni-corrected tests indicate that the Altiplano Méxicano population is distinct in cranial form from *N. cockrumi* and *N. crawfordi*, and the latter 2 are both distinct from *N. evotis* and *N. tataticuli*.

The first 2 canonical variate axes (CV1 and CV2) explain 57.36% (30.17% and 27.18%, respectively) of the variation among populations relative to variation within populations of *Notiosorex* (Fig. 4D).

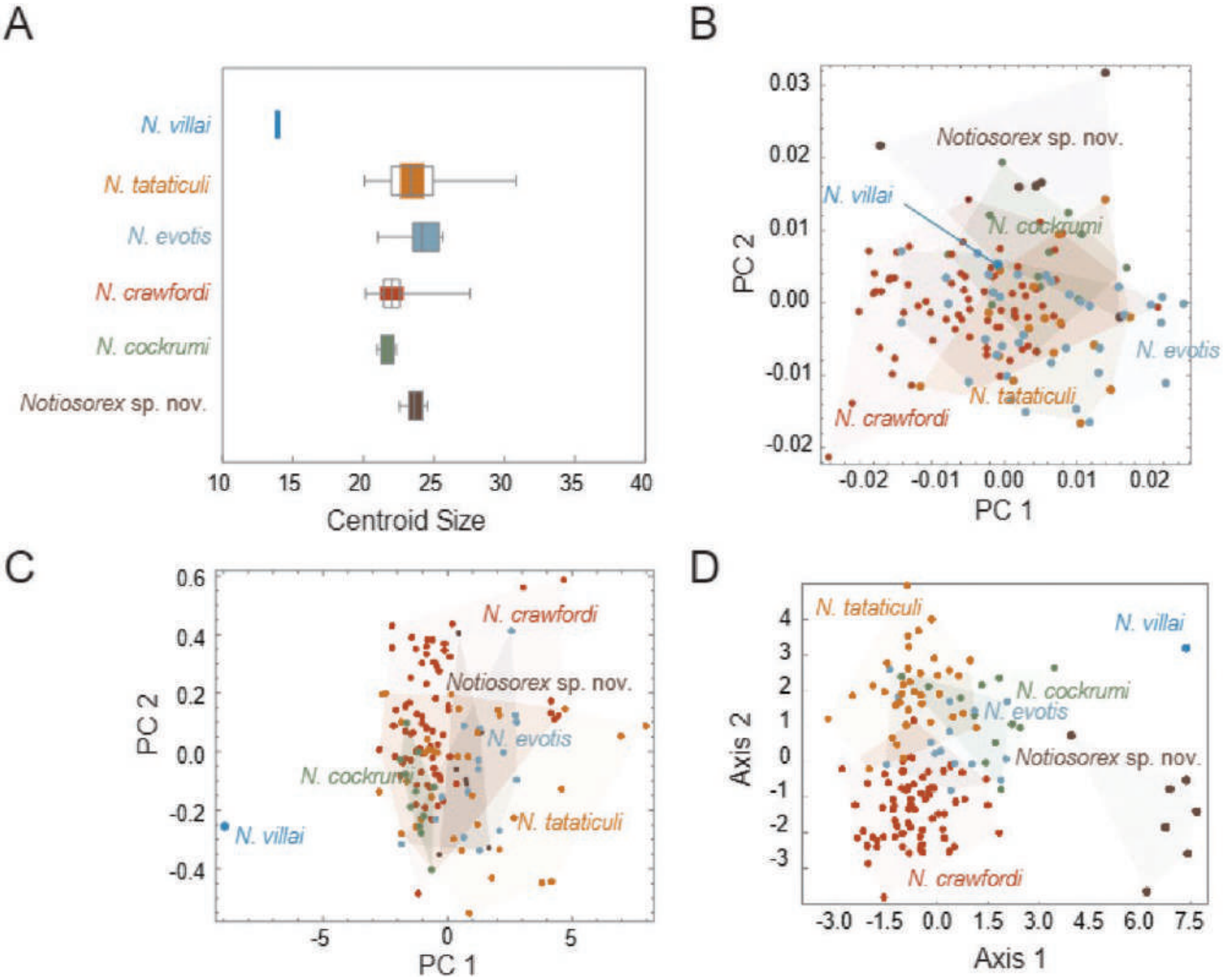

Fig. 4. Cranium results from extant *Notiosorex* species. (A) Centroid size comparisons. (B) PCA based on shape only. (C) PCA based on form (shape and size). (D) CVA based on shape only.

The percentage of specimens correctly classified by DFA from the total cranium shape matrix was 96.48% for each species.

ML trees from mandibular shape.

For paleophylogeographic analysis we constructed a continuous-trait ML analysis of mandible shape using both extant and fossil *Notiosorex* species. We restricted this part of our study to mandibles because all *Notiosorex* fossil species have been described based on their mandibular features and the few available fossil crania are broken (Hibbard 1953; Lindsay and Jacobs 1985; Carraway 2010). We recovered a single fully resolved tree (log likelihood = –208.2) that we rooted with *N. harrisi* because of its very early occurrence in the fossil record (Fig. 5A; Supplementary Data SD1). With this rooting, the timing of the splits of the *N. cockrumi* plus *N. crawfordi* clade and the Altiplano Méxicano population plus *N. villai* clade from the rest of *Notiosorex* are constrained to lie between the first occurrences of *N. harrisi* and *N. jacksoni* at about 5 to 7 mya, whereas the splits of *N. taticuli* and *N. evotis* as well as the speciation events between *N. cockrumi and N. crawfordi* and between *N. villai* and the Altiplano Méxicano shrews would have been sometime after the first occurrence of *N. jacksoni* around 5 Ma, although precisely when is uncertain because none of the 6 species have a fossil record (Supplementary Data SD1). The *N. harrisi* rooting implies that all extant species and *N. dalquesti* have "ghost lineages," an interval of time when a species must logically have existed based on the phylogenetic topology but during which there are no known fossil occurrences (Norell 1992). This rooting also suggests that the ancestral mandible centroid size was 7.88 and there was a general increase in size in most *Notiosorex* clades but a reduction in *N. villai* and to a smaller extent in *N. harrisi* (Fig. 5B; Supplementary Data SD1).

We also performed a separate outgroup rooting by adding *M. gigas*, the closest relative of *Notiosorex*, to the data set (Ohdachi et al. 2006; Camargo and Álvarez-Castañeda 2020). The best ML tree with *Megasorex* as the root recovered the same topology for *Notiosorex* species but rooted at the branch leading to *N. tataticuli* and *N. evotis* (Supplementary Data SD1). With this rooting, *N. villai* and the Altiplano Méxicano specimens remain sibling species high in the tree, but the rerooted topology places the extinct *N. harrisi* and *N. crawfordi* plus *N. cockrumi* clades in comparatively derived locations. The early first occurrence around 6.7 Ma of *N. harrisi* therefore pushes most of the branching events within *Notiosorex* back into the Miocene resulting in longer ghost lineages than with the *N. harrisi* rooting (Supplementary Data SD1). With the *Megasorex* rooting, the speciation events that produced *N. taticuli* and *N. evotis* would have occurred before 7 Ma, as would divergence of the clade comprised of *N. villai* and the Altiplano Méxicano population (although the 2 could have diverged from each other after 7 Ma). This rooting implies that the ancestral mandible centroid size was 9.95 and

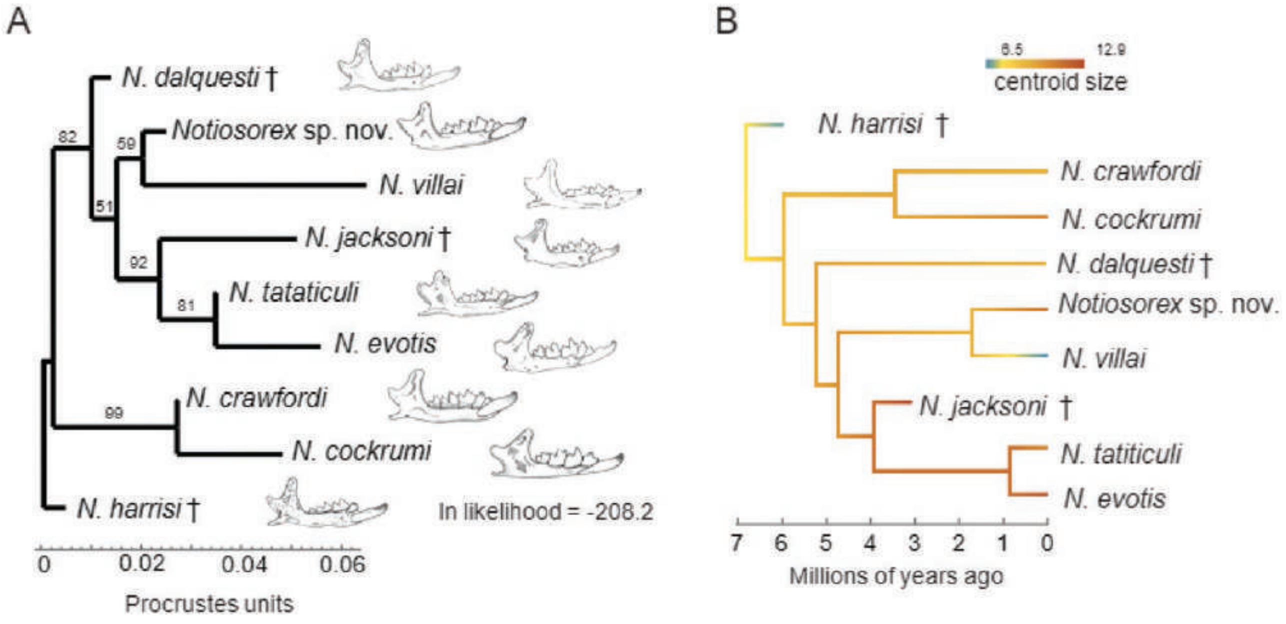

Fig. 5. (A) ML tree based on mandibular characters for extant and fossil species of *Notiosorex*. (B) Centroid size mapped onto the ML tree for mandible shape (see Supplementary Data SD1 for comparison between these trees and those that are rooted with *Megasorex*).

there were parallel size increases in lineages leading to *M. gigas*, *N. tataticuli*, *N. evotis*, *N. jacksoni*, the *N. cockrumi* and *N. crawfordi* clade, and in the Altiplano Méxicano species, but reductions in a paraphyletic portion of the tree where *N. villai*, *N. harrisi*, and *N. dalquesti* are found (Supplementary Data SD1). While the *Megasorex* rooting is not our favored hypothesis, its relative merits and consequences for our interpretations are considered at length in Supplementary Data SD1.

Discussion

Size evolution.

Notiosorex harrisi and *N. villai* are the smallest members of the genus (Figs. 3A and 5B). *Notiosorex villai* previously was known only from the type series (Carraway and Timm 2000); however, we referred an individual (UANL LP-6) collected in the municipality of Nuevo León that had originally been identified as *N. crawfordi* (Rodríguez-Vela 1999) to the species *N. villai* due to its smaller size and similarity in morphometric characteristics with the type series. While these 2 species share small size, they have different shapes and do not group close together on our ML trees (regardless of rooting). This suggests that they evolved small size independently (again regardless of rooting).

Biogeography of the genus *Notiosorex*.

Based on variation in mandibular morphology combined with genetic data currently known from *Notiosorex*, the origin of the genus can be tracked to the upper part of the Miocene in the Sonoran Desert in southwestern United States and northwestern México (Fig. 6A). The first known species is *N. harrisi* (7.0 to 0.08 mya), which probably expanded its distribution over all areas of the warm desert (Hafner and Riddle 2011). *Notiosorex jacksoni* (5.0 to 0.15 mya) has been recorded from the northeastern part of the Chihuahua Desert in the lower Pliocene to the Pleistocene. At the upper part of the Pliocene a wide distribution of *N. dalquesti* (0.15 to 0.08 mya) has been recorded from the Sonoran and Chihuahuan deserts, which is the current range of *N. crawfordi*.

Notiosorex harrisi is the oldest known member of the *Notiosorex* clade, having appeared in the fossil record in the Late Miocene or early Pliocene in northeastern Arizona somewhere between 5 and 7 Ma and we have used it as the preferred root for our paleophylogeographic reconstruction (Fig. 6; Supplementary Data SD1). The oldest records of the genus are closely associated with the initial establishment of the desert and shrubland vegetation types that characterize this region today. Desert and shrubland were becoming fully established in North America in the Late Miocene to Pliocene, 11.6 to 5.0 mya, as were widespread C4 grasslands (Kohn and Fremd 2008; Graham 2011). This period also saw acceleration of tectonic extension that created basin and range topography through northern México resulting in formation of increasingly large lakes in some of the basins (Israde Alcántara et al. 2010). When rooted with *N. harrisi*, the topology of the phylogenetic reconstruction of extant and fossil species of *Notiosorex* suggest that the clade spread southward over the subsequent 4 million years through desert areas as it diversified to occupy its current geographic distribution. Based on its fossil record and the phylogenetic topology, it is likely that *N. harrisi* expanded across most of the southwestern United States and northern México, including over the Sierra Madre Oriental. New geographic barriers developed over the same period, fragmenting the original range, driving speciation, and isolating the extant species in their current ranges.

Notiosorex crawfordi and *N. cockrumi* are the deepest clade to branch after *N. harrisi*. The range of *N. cockrumi* is restricted to the warmest areas of the Sonoran Desert. Based on the fossil records, its range is similar to *N. harrisi* (Fig. 6), with a dissimilar mandibular morphology. Today *N. crawfordi* and *N. cockrumi* are geographically associated, and we found them to be sibling species on our ML trees (regardless of rooting). This suggest that *N. cockrumi* may have evolved from *N. crawfordi*, perhaps sympatrically in the current geographic configuration or allopatrically during some past episode of geographic reorganization and isolation. Baker et al. (2003) called *N. cockrumi* a cryptic species, but our geometric morphometric results show that the 2 species are morphologically quite distinguishable by both cranial and mandibular shape and size, although especially that of the mandible. There are no evident physiographical barriers

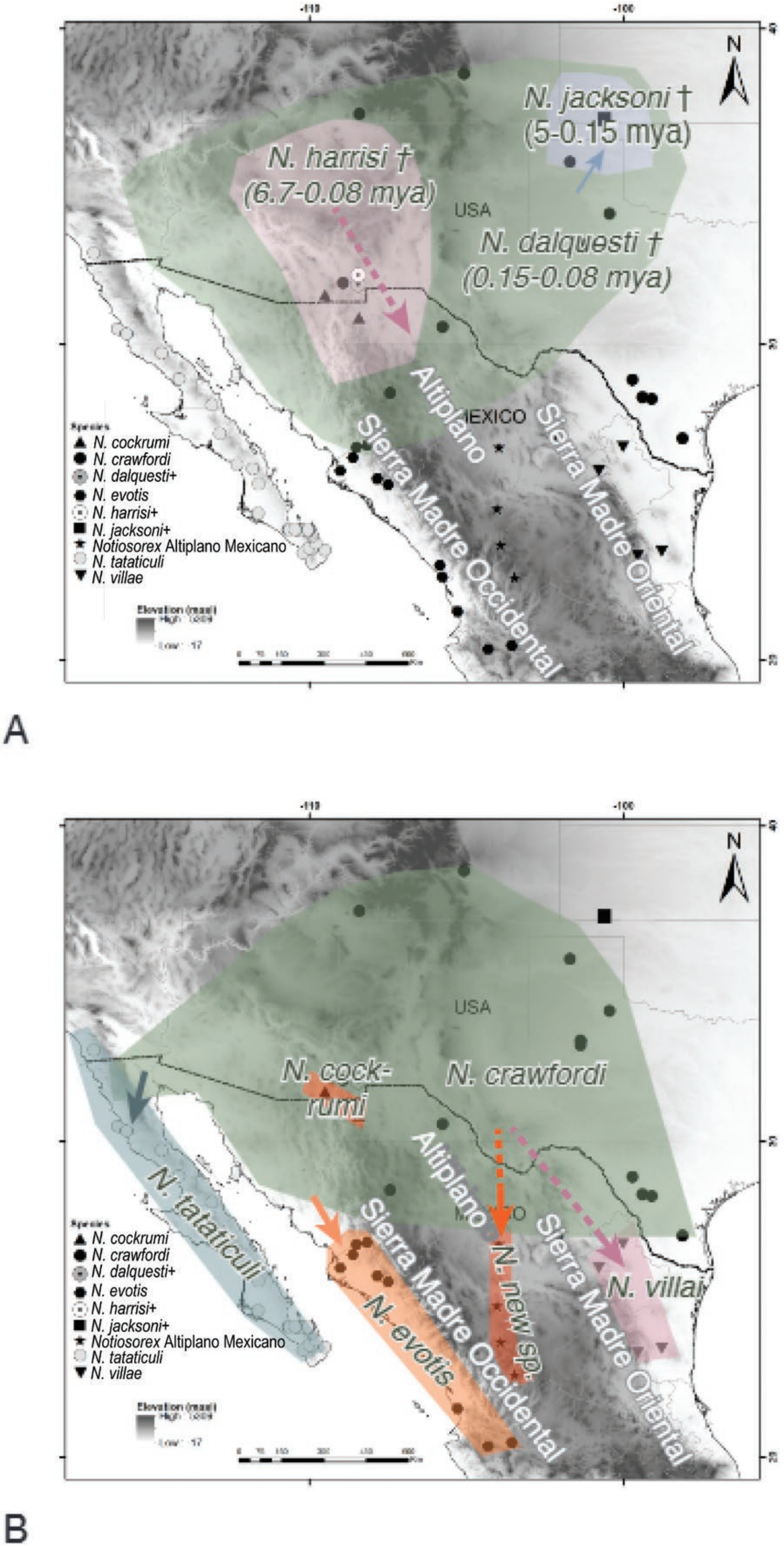

Fig. 6. Paleophylogeography of *Notiosorex*. (A) Approximate ranges of the 3 major extinct taxa based on data from Carraway (2010). *Notiosorex harrisi* (pink), the oldest taxon, has Late Miocene records in northeastern Arizona and later Pleistocene records farther south. *Notiosorex dalquesti* (green) likely represents a speciation from *N. harrisi* with geographic expansion across most of the current range of *N. crawfordi*. *Notiosorex jacksoni* (purple) is first found in the Pliocene at the northeast edge of the range of *N. dalquesti*. Solid arrows represent hypothesized speciation events and broken arrows represent range shifts inferred from fossil record and the ML tree. (B) Phylogeographic divergence of extant *Notiosorex* species based on current ranges, location of fossil taxa, ML tree, and location of biogeographic barriers. *Notiosorex villai* (pink) is morphologically very similar to *N. harrisi* and likely represents a relict offshoot whose

separating *N. cockrumi* from *N. crawfordi*, making it more difficult to establish the boundaries between them. However, the range of *N. cockrumi* extends into warmer and drier climates than that of *N. crawfordi*.

The fossil species *N. dalquesti* is outgroup to the rest of the *Notiosorex* species (Fig. 5A). Fossil occurrences of *N. dalquesti* are distributed widely in Arizona (Mead et al. 1984, 2005; Olsen and Olsen 1984; Emslie 1988; Majors 1993; Czaplewski et al. 1999), California (Jefferson 1991), New Mexico (Findley 1965; Harris 1993), Texas (Logan and Black 1979; Logan 1983), Nevada (Jefferson 1982), Tamaulipas (Dalquest and Roth 1970), and Zacatecas (Jau-Mexia et al. 2000). The most recent record is based on a mandibular fragment (Jau-Mexia et al. 2000) and occurs in the region currently occupied by the new Altiplano Méxicano species. *Notiosorex dalquesti* is much larger than *N. harrisi* (Figs. 3A and 5B) and the 2 have an interesting biogeographic history (Fig. 6A). The first records of *N. harrisi* date from around the end of the Miocene, and although not having been found in the fossil record during the Pliocene, reappeared for a short time in the Late Pleistocene in sympatry with *N. dalquesti* in Arizona (Carraway 2010). Considering that glacial–interglacial cycles began about 2.58 mya and intensified into the Late Pleistocene (Ehlers and Gibbard 2004), it may be that populations of *N. dalquesti* and *N. harrisi* have undergone several processes of expansion and contraction causing population fragmentation and coalescence and associated genetic changes (cf. Excoffier and Ray 2008; Polly et al. 2019). Currently, *N. cockrumi* and *N. crawfordi* are found in sympatric distribution in the same area where these fossil species also coexisted. This region may therefore be an area of *Notiosorex* speciation, but further paleontological and molecular analyses are required to confirm this. Regardless, these data suggest that the ancestor of the *N. dalquesti* clade may have been widely distributed in the Pleistocene before fragmenting into the extinct *N. jacksoni* and extant *N. tataticuli*, *N. evotis*, *N. villai*, and the Altiplano Méxicano population.

Notiosorex evotis and *N. tataticuli*, *N. villai*, and the Altiplano Mexicano population are present in allopatric areas with strong geographical barriers that limit dispersal between them, but the northern parts of their ranges are contiguous with the southern range of *N. crawfordi* (Fig. 6). *Notiosorex evotis* has a range on the coastal plain of México isolated by the Sierra Madre Occidental, restricted to the Planicie Costera del Pacifico. The range of *N. tataticuli* is restricted to the east by the Colorado River, extending to the Lower California Desert, which serves as a geographic barrier that likely contributes to the speciation process in desert shrews (Camargo and Álvarez-Castañeda 2020). *Notiosorex villai* has a restricted range to the eastern side of the Sierra Madre Occidental and the Altiplano Méxicano population to its western side. The Sierra Madre Oriental is likely to have formed the barrier that promoted the process of isolation and speciation that gave rise to these 2 groups. We hypothesize that these 4 groups originated from taxa living farther north and became isolated during the Plio-Pleistocene as they pushed south between the geographic barriers of the Gulf of California, the Sierra Madre Occidental, the Sierra Madre Oriental, and on the Altiplano Central—isolated from Texas by the Río Bravo (Fig. 6). This hypothesized scenario would explain the branching pattern in our mandibular tree, the current geographic distributions of the species, and their phylogeographic relationships to the fossil *Notiosorex* species.

Notiosorex jacksoni is the sibling species to *N. tataticuli* and *N. evotis* (Fig. 5A). It is the largest species in the genus (Figs. 4A and 5B) and its records date back to the early Pliocene, 4.1 mya. It occurred in Kansas (Hibbard 1950), Texas (Dalquest 1978), and California (Repenning 1967). (Carraway 2010) grouped *N. evotis* with *N. jacksoni*, a relationship that we also recovered (Fig. 5A). *Notiosorex evotis* and *N. tataticuli* are the largest of the extant species and they group together based on mandibular shape. Hibbard (1950) mentions that the other fossil taxa found at the type locality of *N. jacksoni* currently have a more southern distribution.

Therefore, we suggest that *N. jacksoni* could be the direct ancestor of *N. evotis* and *N. tataticuli*. This suggests that their clade (Fig. 6) originated north of its current distribution in the Pliocene and was pushed southward along with other descendants of *N. harrisi* and *N. dalquesti* during the climatic and vegetative reorganization of North America through the early Quaternary. This is compatible with the fact that *Notiosorex* populations of southernmost California have recently been recognized as *N. tataticuli*, which may have speciated as it became isolated on Baja California (Camargo and Álvarez-Castañeda 2020). In our scenario, *N. evotis*, *N. cockrumi*, and the Altiplano Méxicano population would have diverged on the mainland side of the Gulf of California, with the latter 2 speciating through isolation by the barrier of the Sierra Madre Occidental.

Cranial and mandibular morphologies show that the population from the Altiplano Central is different from *N. crawfordi*, with which it has heretofore been considered conspecific, as well as from all other *Notiosorex* species. Furthermore, it is more similar to *N. villai* than to *N. crawfordi* (Fig. 5A). In addition, its range is isolated by mountain ranges from *Notiosorex* species to its east (*N. villai*) and west (*N. evotis*), and by the rivers Conchos and Bravo from species to the north (*N. crawfordi*). These barriers isolate the Altiplano Méxicano shrews from dispersal and gene flow from other *Notiosorex* groups (Camargo et al. 2022). Based on this evidence, we consider the Altiplano Méxicano population to be a new species, which we formally describe below.

Relationships among fossil species.

Notiosorex harrisi persisted past the end of the last glaciation before becoming extinct in approximately the same geographic area currently occupied by *N. crawfordi* as indicated by fossils from Wisconsonian and Holocene deposits of New Mexico and from a Pleistocene/Holocene record from southern Chihuahua (Carraway 2010). The precise relationship between *N. harrisi* and extant *N. crawfordi* deserves further attention in future studies because they occupy broadly overlapping geographic areas with very little time between the last occurrence of *N. harrisi* about 1,300 years ago and now. Until recently, both *N. harrisi* and *N. dalquesti* fossil specimens had been considered to belong to *N. crawfordi*, but Carraway demonstrated that they were distinct in size, features, and morphometrics (Carraway 2010). Whether *N. crawfordi* has a deep origin and persisted in parallel with *N. harrisi* without a known fossil record or whether *N. harrisi* underwent rapid postglacial evolution to become the *N. crawfordi* we see today deserves further consideration with techniques like ancient DNA sequencing. The difference would change some aspects of our tree topology (Fig. 5A) but would not substantially alter our paleophylogeographic interpretation (Fig. 6). The precise evolutionary relationship between *N. harrisi* and *N. jacksoni* also deserves further investigation because there is a long gap in the occurrences of *N. harrisi* during the period when *N. jacksoni* occurs, which picks up again just after extinction of the

range was displaced toward the Gulf Coastal plain. *Notiosorex crawfordi* (green) is likely to be anagenetic descendant of *N. dalquesti* and occupies roughly the same geographic range. *Notiosorex tataticuli* (gray), *N. evotis* (light orange), *N. cockrumi* (dark orange), and the new Altiplano Mexicano species (dark orange) originated by speciation from *N. dalquesti*/*N. crawfordi* and are separated by geographic barriers of the Gulf of California and the Sierra Madre Occidental and Oriental.

latter (Carraway 2010). These species also have broadly overlapping ranges in the southwest United States and northern México, suggesting either that they are actually the same lineage with substantial morphological change over time, that their relative abundances changed dramatically affecting the likelihood that one or the other is preserved in the fossil record, or that they had as yet undocumented geographic range changes that shifted them between the broad geographic range from which they are both known and a different, perhaps much smaller, geographic location with a poorer fossil record. The first and the third of these scenarios would require substantial changes to our paleophylogeographic reconstruction, but the second would not. Addressing these outstanding questions is outside the scope of our present study.

Systematic biology.

The assessment of qualitative characters, reinforced by multivariate analyses of morphometry and paleophylogeny of most of the known species of *Notiosorex* desert shrews of mandibular and cranial phylogeny are presented herein. They demonstrate that an evolutionary process can be detected, by comparing morphologies separated by long stretches of phylogenetic position, and indicate that the Altiplano Méxicano populations deserve recognition as a distinct species.

Family Soricidae Fischer, 1814
Subfamily Soricinae Fischer, 1814
Tribe Notiosoricini Reumer, 1984
Genus *Notiosorex* Coues, 1877

Notiosorex carrawayae, new species
Carraway's Desert Shrew; musaraña desértica del Altiplano Mexicano

Holotype

CIB 31482, an adult female collected by A. Maeda-Martínez and prepared by Issac Camargo (original number 986) on 20 December 2016, at Peñón Blanco, Durango, México; 24.7101°N, −104.0311°W, 1,677 m a.s.l. The specimen consists of a standard museum study skin with accompanying cranium, mandibles, and skeleton, housed at Centro de Investigaciones Biológicas del Noroeste; all body parts are in good condition (Fig. 7).

Paratypes (n = 6)

Three adult females, 1 adult male, and 3 adults with no sex assignment, all from 17 km E, 28 km N Ceballos, Durango (26.7393°N, −103.9641°W; UAMI 801, 1222, 1607, 1859 to 1861).

Diagnosis

Notiosorex carrawayae can be distinguished by its upper third unicuspid that is U-shaped. It has an elongated skull and the upper incisor is thick with a reddish tip. The skull and mandibular size are larger, skull is more globular, and mandibular higher and longer than other known species. It is not grayish like other *Notiosorex* species (Fig. 8); the coat of *N. carrawayae* ranges from yellowish brown (10YR/5/4/) to light yellowish brown (10YR/6/4), whereas other species are grayish with the exception of the insular subspecies *N. tataticuli ocanai* which has a dark brown coloration.

Notiosorex carrawayae is characterized by a wider skull at the depression in glenoid fossa and at the posterior margin of the palate at the lateral junction of the pterygoid process. The molars are larger than those of *N. crawfordi*, and braincase extends to the anteriormost point of the lateral braincase. The jaw is deeper and its molars are taller and broader than *N. crawfordi*. Incisors, and first and second molar more pigmented at the tip than other species of *Notiosorex*. Based on our morphometric analysis, the phylogenetic position of *N. carrawayae* is likely to be sister species *N. villai*, although *N. carrawayae* is larger and has larger teeth. The analyzed morphometric measurements among *Notiosorex* species are found in Table S2.

Fig. 7. Holotype of the *Notiosorex carrawayae* from Peñón Blanco, Durango, México (CIB 31482).

Measurements of the holotype in mm.

External measurements: total length = 67; tail length = 23; foot length = 6; ear length = 5; and weight = 3.2 g. Craniodental measurements: rostral breadth = 6.29; least interorbital breadth = 3.96; condylobasal length = 16.75; breadth across between second upper molar = 5.00; length of fourth upper premolar to third molar = 4.16; palatal length = 7.32; length of unicuspid toothrow = 1.99; length of first unicuspid to third molar = 6.08; length of coronoid process–posterior point of upper condylar facet = 2.48; height of coronoid process = 3.68; height of coronoid valley = 2.44; height of articular condyle = 2.78; length of mandible = 7.11; length of coronoid process–ventral point of lower condylar facet = 3.2; length of the lower tooth row = 4.05; length of lower canine = 0.73; length of lower fourth premolar = 1.1; length of lower first molar = 1.48; length of lower second molar = 1.6; length of lower third molar = 1.01; length

Fig. 8. Carraway's desert shrew (*Notiosorex carrawayae*).

from upper articular condyle to posterior edge of lower third molar = 3.49; and depth of dentary at first lower third molar = 0.94.

Measurements of the holotype and 6 paratypes (mean and range).

External measurements: total length 77.75 (67 to 84); tail length 26 (23 to 29); foot length 17 (5 to 19); ear length 5 (5); and weight (3 to 3.2 g). Craniodental measurements: rostral breadth 5.80 (4.84 to 6.77); least interorbital breadth 3.69 (3.43 to 3.96); condylobasal length 16.37 (16.0 to 16.75); breadth across between second upper molar 4.61 (4.22 to 5.0); length of fourth premolar to third molar 4.14 (4.1 to 4.19); palatilar length 6.63 (6.0 to 7.27); length of unicuspid toothrow 2.03 (1.84 to 2.23); length of first unicuspid to third molar 6.26 (6.05 to 6.47); length of coronoid process–posterior point of upper condylar facet 2.44 (2.33 to 2.56); height of coronoid process 3.71 (3.63 to 3.79); height of coronoid valley 2.32 (2.2 to 2.44); height of articular condyle 2.66 (2.55 to 2.78); length of mandible 7.09 (7 to 7.19); length of coronoid process–ventral point of lower condylar facet 3.27 (3.1 to 3.45); length of the lower tooth row 4.03 (4.01 to 4.06); length of lower canine 0.84 (0.73 to 0.96); length of lower fourth premolar 1.15 (1 to 1.3); length of lower first molar 1.52 (1.48 to 1.57); length of lower second molar 1.57 (1.54 to 1.6); length of lower third molar 1.12 (1.01 to 1.23); length from upper articular condyle to posterior edge of lower third molar 3.37 (3.16 to 3.58); and depth of dentary at lower first molar 1.19 (0.94 to 1.45).

Morphological comparison.

Notiosorex carrawayae is allopatric to the other species of *Notiosorex* and can be found in proximity to the ranges of *N. crawfordi*, *N. evotis*, and *N. villai*. *Notiosorex carrawayae* can be differentiated from *N. crawfordi* by its color, larger size, craniodental measurements, and univariate summary statistics (mean ± standard error and range, in mm): rostral breadth *N. carrawayae* 5.71 ± 0.30 (4.84 to 6.77) versus *N. crawfordi* 4.84 ± 0.01 (4.4 to 5.2); palatilar length 7.35 ± 0.18 (6.0 to 7.27) versus 6.79 ± 0.02 (6.2 to 7.3); length of unicuspid toothrow 2.08 ± 0.13 (1.84 to 2.23) versus 1.88 ± 0.01 (1.5 to 2.2); length of first unicuspid to third molar 6.18 ± 0.15 (6.05 to 6.47) versus 6.03 ± 0.05 (5.1 to 6.8); length of coronoid process–posterior point of upper condylar facet 2.46 ± 0.03 (2.33 to 2.56) versus 3.3 ± 0.02 (2.7 to 3.9); height of coronoid process 3.69 ± 0.06 (3.63 to 3.79) versus 4.02 ± 0.01 (3.4 to 4.6); length of mandible 7.12 ± 0.06 (7.0 to 7.19) versus 7.04 ± (6.4 to 7.7); length of lower first molar 1.52 ± 0.03 (1.48 to 1.57) versus 1.44 ± 0.01 (1.1 to 1.6); length of first unicuspid 1.56 ± 0.02 (1.54 to 1.6) versus 1.36 ± 0.01 (1.2 to 1.5); and length of lower third molar 1.28 ± 0.07 (1.01 to 1.23) versus 0.98 ± 0.01 (0.9 to 1; Supplementary Data SD2). The measurements of the Zacatecas specimens are slightly different from those that are presented in the work of Carraway and Timm (Álvarez-Cordoba et al. 2020).

The skull of *N. carrawayae* can be differentiated in shape from *N. crawfordi* mainly by the midline of the anterior margin of the premaxilla, posterior margin of second antemolar, posteriormost point of metastylar blade of upper fourth premolar, posterior margin of fourth antemolar, posteriormost point of metastylar blade of upper first molar, and posteriormost point of hypoconid of upper first molar. The shape of the jaw of *N. carrawayae* is different from *N. crawfordi* at anterior edge of muscular rugosity on coronoid process, posterior point of muscular rugosity on coronoid process, junction between first and second molar, junction between second and third molar, junction between incisor and first antemolar, and dorsalmost curvature of central part of mandibular body (Supplementary Data SD2; Fig. 9B).

The morphological distinction of *N. crawfordi* from other *Notiosorex* shrews is best seen in its more rounded skull, globose braincase, and by its generally smaller skull dimensions, although it is not as small as *N. villai*. *Notiosorex crawfordi* is distinguished by its jaw shape and measurements, with lower toothrow shorter excluding the first incisor, length of the upper molariform teeth reduced, and the general shape having a sigmoidal curve (Fig. 9A).

In ventral view *N. carrawayae* can be differentiated from *N. crawfordi* because the third molar is U-shaped, whereas in *N. crawfordi* it is V-shaped. The skull of *N. carrawayae* is more flattened when viewed from the ventral view, the upper incisor thicker with the tip more pigmented, and a longer palate and larger skull (Fig. 9A).

Notiosorex carrawayae can be differentiated from *N. evotis* by shape of the skull including increase in size of the braincase and paroccipital process. Morphometric differences (in mm) are: length of fourth upper premolar to third molar in *N. carrawayae* 4.13 ± 0.03 (4.1 to 4.19) versus *N. evotis* 4.47 ± 0.27 (4.08 to 4.68); length of first unicuspid to third molar 6.18 ± 0.15 (6.05 to 6.47) versus 6.69 ± 0.25 (6.39 to 6.97); length of coronoid process–posterior point of upper condylar facet 2.46 ± 0.03 (2.33 to 2.56) versus 3.52 ± 0.03 (3.48 to 3.54); height of coronoid process 3.69 ± 0.06 (3.63 to 3.79) versus 4.09 ± 0.12 (3.92 to 4.16); length of coronoid process–ventral point of lower condylar facet 3.30 ± 0.14 (3.1 to 3.45) versus 3.61 ± 0.09 (3.49 to 3.7); length of the lower tooth row 4.03 ± 0.17 (4.01 to 4.06) versus 4.59 ± 0.01 (4.58 to 4.6); length of lower canine 0.86 ± 0.07 (0.73 to 0.96) versus 0.47 ± 0.01 (0.45 to 0.47); length of the fourth lower premolar 1.08 ± 0.04 (1 to 1.3) versus 0.73 ± 0.02 (0.71 to 0.75); length of lower second molar 1.56 ± 0.02 (1.54 to 1.6) versus 1.28 ± 0.08 (1.24 to 1.39); length of lower third molar 1.28 ± 0.07 (1.01 to 1.23) versus 0.99 ± 0.02 (0.97 to 1.0); and length from upper articular condyle to posterior edge of lower third molar 3.4 ± 0.14 (3.16 to 3.58) versus 4.6 ± 0.11 (4.49 to 4.7; Supplementary Data SD2).

Notiosorex carrawayae can be differentiated from *N. villai* in shape of the dentition. Though both species are grouped in the highest values of the genus for molars based on CVA1, the molars of *N. carrawayae* are larger. Morphometric differences (in mm) are: condylobasal length 16.36 ± 0.15 (16 to 16.75) versus 17.11 ± 0.08 (16.9 to 17.2); length of fourth upper premolar to third molar 4.13 ± 0.03 (4.1 to 4.19) versus 4.6 ± 0.02 (4.4 to 4.7); length of lower first molar 1.52 ± 0.03 (1.48 to 1.57) versus 1.45 ± 0.01 (1.1 to 1.5) and length of lower second molar 1.56 ± 0.02 (1.54 to 1.6) versus 1.4 ± 0.06 (1.4 to 1.4; Supplementary Data SD2). Furthermore, *N. villai* can be distinguished by the roof of the glenoid fossa not extending laterally from the cranium when the skull is viewed from dorsal view (Carraway and Timm 2000).

Geographic distribution.

Notiosorex carrawayae is known from south of the Conchos River in Durango and Zacatecas south through Hidalgo and México City (Fig. 10). There are additional records of *Notiosorex* in Hidalgo; however, we could not examine this material because some specimens are known to have been lost (TTU 24185, Stuhler JD, Department of Integrative Biology, University of Wisconsin–Madison, Madison, WI, USA, personal communication, September 2021) and others were not found (Álvarez and González-Ruiz 2001). *Notiosorex* was found in grasslands in the lowlands and patches of scrub at higher altitudes, and on rocky substrate from México City (Márquez-Villalba et al. 2022).

Ecology

The holotype was collected in Peñón Blanco, Durango, in an area with water springs that is drained by the Río Peñón Blanco which is one of the main tributaries of the Nazas River (Roldán-Quintana et al. 2009). The first record of *N. carrawayae* in Durango (24.4145°N, −105.3339°W) was documented at 130 km NE of the holotype locality in arid grassland with scattered catclaw (*Acacia greggii*), and mesquite (*Prosopis* spp.) on the east-facing foothills of the Sierra Madre Occidental in northwestern Durango. Other mammals taken in the same area were *Chaetodipus hispidus*, *Chaetodipus nelsoni*, *Baiomys taylori*, *Onychomys torridus*, *Sigmodon fulviventer*, and *Sigmodon ochrognathus* (Baker 1966).

Four more desert shrew records from Durango were documented from 4,312 trap-nights using gallon-sized pitfall traps; however, none were captured in Sherman live traps across 12,000 trap-nights in mixed desert and brush habitats—the specimens were recovered 19 km east of the type locality. Vegetation was dominated by prickly pear (*Opuntia* spp.), creosote bush (*Laria tridentata*), black bush (*Acacia* spp.), mesquite (*Prosopis* spp.), and catclaw (*Acacia greggii*). Mammalian species from the locality are: *Chaetodipus hispidus*, *Dipodomys nelsoni*, *Sigmodon hispidus*, *S. fulviventer fulviventer*, *S. ochrognathus*, *Neotoma goldmani*, *Taxidea taxus*, *Mustela frenata*, and *Tayassu tajacu* (Petersen 1976).

Notiosorex habitat in Zacatecas is riparian vegetation surrounded by desert scrub (Alvarez-Cordoba 2020). In México City the dominant vegetation included shrubby stonecrop (*Sedum praealtum*), nolina (*Nolina parviflora*), broomstick tree (*Pittocaulon praecox*), white Tepozan (*Buddleia cordata*), Tepozan (*B. parviflora*), woollyjoint pricklypear (*Opuntia tormentosa*), and huizache (*Acacia farnesiana*; Márquez-Villalba et al. 2022).

Etymology

The specific epithet is in honor of Leslie Carraway, a mammalian researcher who contributed to the biological, taxonomic, and fossil knowledge of mammals, mainly shrews in North America. Her research contributions have been the basis for the knowledge of this family.

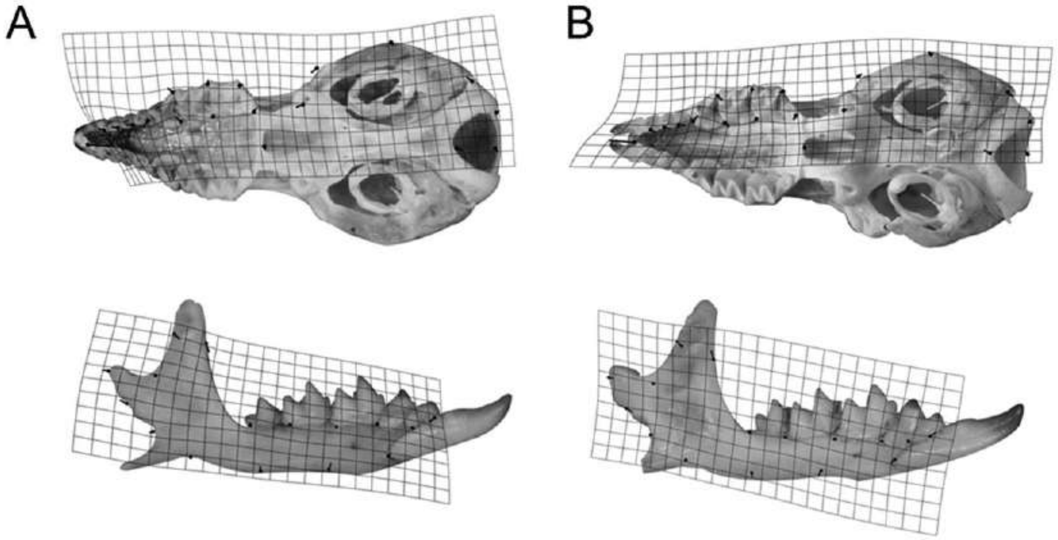

Fig. 9. Deformation grids showing the difference from the *Notiosorex* mean of *N. crawfordi* (A) and populations of *N. carrawayae* (B).

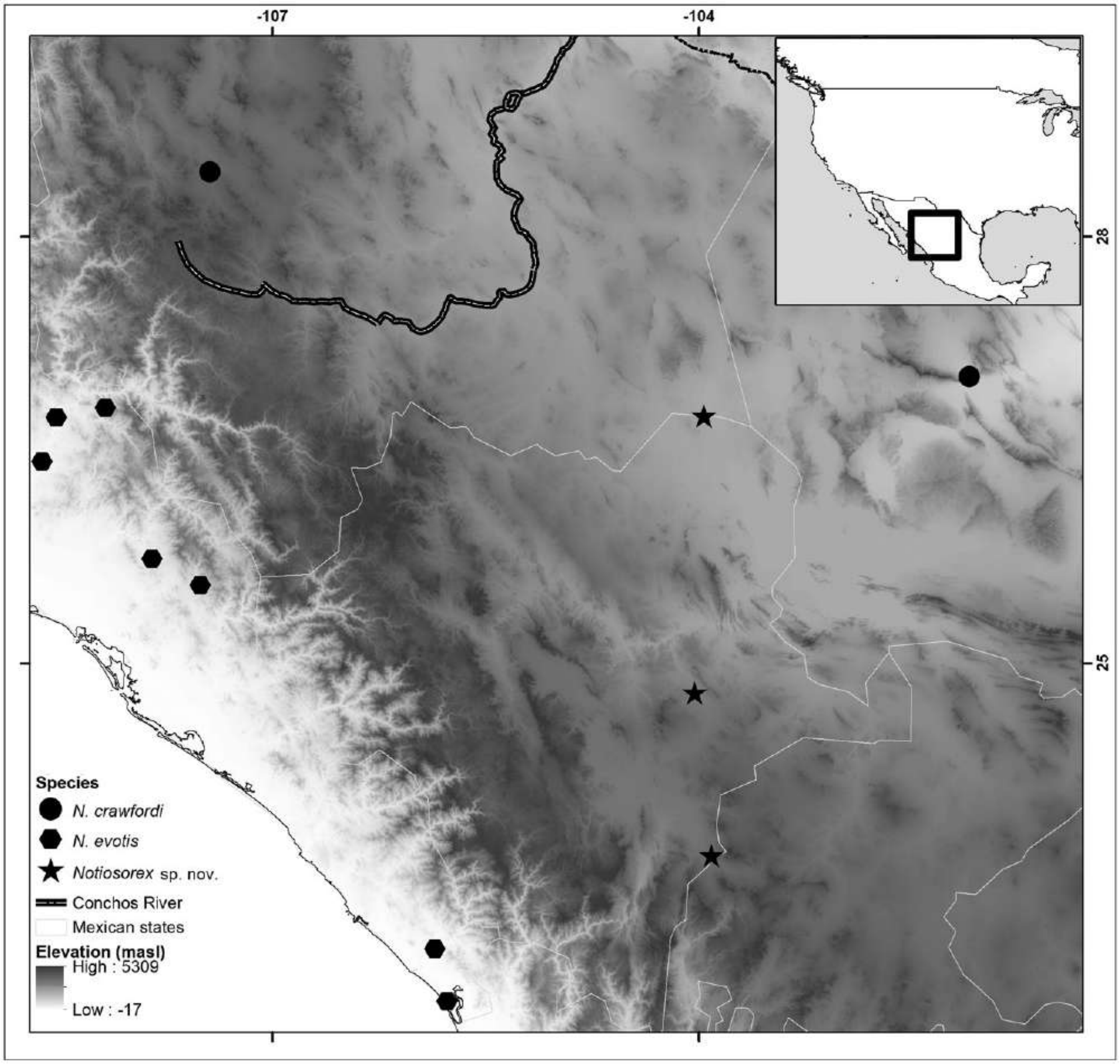

Fig. 10. Localities for the new species *Notiosorex carrawayae* from the Altiplano Mexicano (star). Localities for *N. crawfordi* (black dots) and *N. evotis* (rhombus) are also shown. The black lines indicate the course of the Conchos River which could be the graphic barrier that divides the populations south of its distribution. Areas shaded in lighter gray indicate lower elevations.

Supplementary data

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

Supplementary Data SD1.—Comparison of alternative tree rooting with *Notiosorex harrisi* and *Megasorex gigas*.

Supplementary Data SD2.—Morphometric measurements of the *Notiosorex* species and *N. carrawayae* paratypes.

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Author contributions

IC: conceptualization, data curation, formal analysis, funding acquisition, visualization, methodology, software, supervision, validation, writing—review and editing, writing—original draft, writing—review and editing; PDP conceptualization, data curation, methodology, resources, software, supervision, validation, writing—review and editing; STA-C: conceptualization, funding acquisition, supervision, validation, writing—review and editing; JDS: data curation, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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Conflict of interest

None declared.

Data availability

Data and code may be available upon request.

References

Álvarez T, González-Ruíz N. 2001. Nuevos registros de *Notiosorex crawfordi* (Insectivora: Soricidae) para México. Acta Zoológica Mexicana 84:175–177. https://doi.org/10.21829/azm.2001.84841841

Álvarez-Córdova F, Rosas-Valdez R, Martínez-Salazar EA. 2020. A new record and phylogenetic position of *Notiosorex crawfordi* (Eulipotyphla, Soricidae) with distribution in Zacatecas, Mexico, using mitochondrial DNA. Mammalia 84(4):407–412. https://doi.org/10.1515/mammalia-2018-0190

Armstrong DM, Jones JK. 1972. *Megasorex gigas*. Mammalian Species 16(16):1–2. https://doi.org/10.2307/3503846

Baker RH. 1966. Further notes on the mammals of Durango, Mexico. Journal of Mammalogy 47(2):344–345. https://doi.org/10.2307/1378144

Baker RJ, O'Neill MB, McAliley LR. 2003. A new species of desert shrew *Notiosorex* based on nuclear and mitochondrial sequence data. Occasional Papers, Museum of Texas Tech University 222:1–12. https://doi.org/10.5962/bhl.title.157011

Baskin JA. 1979. Small mammals of the Hemphillian age White Cone local fauna, northeastern Arizona. Journal of Paleontology 53(3):695–708. https://www.jstor.org/stable/1304006

Bookstein FL. 1997. Morphometric tools for landmark data. Cambridge (UK): Cambridge University Press.

Camargo I, Álvarez-Castañeda ST. 2020. A new species and subspecies of the desert shrew (*Notiosorex*) from the Baja California peninsula and California. Journal of Mammalogy 101(3):872–886. https://doi.org/10.1093/jmammal/gyaa045

Camargo I, Álvarez-Castañeda ST, Polly PD, Stuhler JD, Maldonado JE. 2022. Molecular phylogenetic and taxonomic status of the large-eared desert shrew *Notiosorex evotis* (Eulipotyphla: Soricidae). Journal of Mammalogy 103(6):1422–1430. https://doi.org/10.1093/jmammal/gyac069

Carraway LN. 2010. Fossil history of *Notiosorex* (Soricomorpha: Soricidae) shrews with descriptions of new fossil species. Western North American Naturalist 70(2):144–163. https://doi.org/10.3398/064.070.0202

Carraway LN, Timm RM. 2000. Revision of the extant taxa of the genus *Notiosorex* (Mammalia: Insectivora: Soricidae). Proceedings of the Biological Society of Washington 113(1):302–318. http://hdl.handle.net/1808/9913

Cassiliano ML. 1999. Biostratigraphy of Blancan and Irvingtonian mammals in the Fish Creek-Vallecito Creek section, southern California, and a review of the Blancan-Irvingtonian boundary. Journal of Vertebrate Paleontology 19(1):169–186. https://doi.org/10.1080/02724634.1999.10011131

Caumul R, Polly PD. 2005. Comparative phylogenetic and environmental components of morphological variation: skull, mandible and molar shape in marmots (*Marmota*, Rodentia). Evolution 59(11):2460–2472. https://doi.org/10.1111/j.0014-3820.2005.tb00955.x

Choate JR. 1969. Taxonomic status of the shrew, *Notiosorex* (*Xenosorex*) *phillipsii* Schaldach, 1966 (Mammalia: Insectivora). Proceedings of the Biological Society of Washington 82:469–476. https://www.biodiversitylibrary.org/page/34549969

Coues E. 1877. Precursory notes on American insectivorous mammals, with description of a new species. Bulletin of the United States Geologic and Geographical Survey of the Territories 3:631–653. http://resource.nlm.nih.gov/101688968

Czaplewski NJ, Mead JI, Bell CJ, Peachey WD, Ku TL. 1999. Papago springs cave revisited, part II: vertebrate paleofauna. Occasional Papers of the Oklahoma Museum of Natural History 5:1–41.

Dalquest WW. 1978. Early blancan mammals of the beck ranch local fauna of Texas. Journal of Mammalogy 59(2):269–298. https://doi.org/10.2307/1379912

Dalquest WW, Roth E. 1970. Late Pleistocene mammals from a cave in Tamaulipas, Mexico. The Southwestern Naturalist 15(2):217–230. https://doi.org/10.2307/3670350

Dryden IL, Mardia KV. 1998. Statistical analysis of shape. Biometrika 76(2):271–281. https://doi.org/10.1093/biomet/76.2.271

Ducommun MA, Jeanmaire-Besancon F, Vogel P. 1994. Shield morphology of curly overhair in 22 genera of Soricidae (Insectivora, Mammalia). Revue Suisse de Zoologie 101(3):623–643. https://www.biodiversitylibrary.org/partpdf/79920.

Ehlers J, Gibbard PL. 2004. Quaternary glaciations—extent and chronology: part II: North America. Amsterdam (The Netherlands): Elsevier Science.

Emslie SD. 1988. Vertebrate paleontology and taphonomy of caves in Grand Canyon, Arizona. National Geographic Research 4(1):128–142.

Excoffier L, Ray N. 2008. Surfing during population expansions promotes genetic revolutions and structuration. Trends in Ecology and Evolution 23(7):347–351. https://doi.org/10.1016/j.tree.2008.04.004

Felsenstein J. 1973. Maximum-likelihood estimation of evolutionary trees from continuous characters. American Journal of Human Genetics 25(5):471–492.

Findley JS. 1965. Shrews from Hermit Cave, Guadalupe Mountains, New Mexico. Journal of Mammalogy 46(2):206–210. https://doi.org/10.2307/1377840

Graham A. 2011. The age and diversification of terrestrial New World ecosystems through Cretaceous and Cenozoic time. American Journal of Botany 98(3):336–351. https://doi.org/10.3732/ajb.1000353

Hammer O, Harper DAT, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4(1):1–9.

Harris AH. 1993. Quaternary vertebrates of New Mexico. Bulletin-New Mexico Museum of Natural History and Science 2:179–198.

Hafner D. Riddle B. 2011. Boundaries and barriers of North American warm deserts: An evolutionary perspective. In: Upchurch P, McGowan AJ, Slater CSC, editors. Palaeogeography and Palaeobiogeography: Biodiversity in Space and Time. Boca de Raton, (FL, USA): CRC Press.

Hibbard CW. 1950. Mammals of the Rexroad formation from Fox Canyon, Kansas. Contributions from the Museum of Paleontology of Michigan 8(6):113–192.

Hibbard CW. 1953. The insectivores of the Rexroad fauna, upper Pliocene of Kansas. Journal of Paleontology 27(1):21–32.

Israde Alcántara I, Velázquez-Durán R, Lozano García MS, Bischoff J, Domínguez Vázquez G, Garduño Monroy VH. 2010. Evolución Paleolimnológica del Lago Cuitzeo, Michoacán durante el Pleistoceno-Holoceno. Boletín de la Sociedad Geológica Mexicana 62(3):345–357.

Jau-Mexia N, Polaco O, Arroyo-Cabrales J. 2000. New mammals for the Pleistocene of Zacatecas, Mexico. Current Research in the Pleistocene 17:124–125.

Jefferson GT. 1982. Late Pleistocene vertebrates from a Mormon Mountain cave in southern Nevada. Bulletin of the Southern California Academy of Sciences 81(3):121–127. https://doi.org/10.3160/0038-3872-81.3.121

Jefferson GT. 1991. A catalogue of Late Quaternary vertebrates from California. Part two: mammals. Natural History Museum of Los Angeles County Technical Reports 7(5):1–129.

Kohn MJ, Fremd TJ. 2008. Miocene tectonics and climate forcing of biodiversity, western United States. Geology 36(10):783–786. https://doi.org/10.1130/g24928a.1

Lear LL, Harris AH. 2007. Holocene fauna of Big Manhole Cave, Eddy County, New Mexico. Southwestern Naturalist 52(1):110–115. https://doi.org/10.1894/0038-4909(2007)52[110:hfobmc]2.0.co;2

Lindsay EH, Jacobs LL. 1985. Pliocene small mammal fossils from Chihuahua, Mexico. Paleontologica Mexicana 51:1–59.

Logan LE. 1983. Paleoecological implications of the mammalian fauna of Lower Sloth Cave, Guadalupe Mountains, Texas. National Speleological Society, Bulletin 45:3–11.

Logan LE, Black CC. 1979. The Quaternary vertebrate fauna of Upper Sloth Cave, Guadalupe Mountains National Park, Texas. In: Genoways HH, Baker RJ, editors. Biological investigations in the Guadalupe Mountains National Park Service Proceedings and Transactions Series 4:141–158.

Majors CP. 1993. Preliminary report on a Late Pleistocene vertebrate assemblage from Bonita, San Diego County, California. PaleoBios 15(4):63–77.

Márquez-Villalba GL, Martínez-Coronel M, Rivera-Tellez D, Galeana-Barrera LE, Pérez-Hernández RB. 2022. First record of the desert shrew *Notiosorex crawfordi* in México City. Therya Notes 3(3):153–157. https://doi.org/10.12933/therya_notes-22-88

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. The American Naturalist 149(4):646–667. https://www.jstor.org/stable/2463542

Mayr E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. New York (NY, USA): Columbia University Press.

Mead JI, Czaplewski NJ, Agenbroad LD. 2005. Rancholabrean (Late Pleistocene) mammals and localities of Arizona. In: McCord RD, editor. Vertebrate paleontology of Arizona, Mesa Southwest Museum Bulletin 11:139–180.

Mead JI, Roth EL, Van Devender TR, Steadman DW. 1984. The Late Wisconsinan vertebrate fauna from Deadman Cave, southern Arizona. Transactions of the San Diego Society of Natural History 20(14):247–276. https://doi.org/10.5962/bhl.part.29007

Merriam CH. 1877. Descriptions of five new shrews from Mexico, Guatemala, and Colombia. Proceedings of the Biological Society of Washington 11:227–230.

Morgan GS, White RS Jr. 2005. Miocene and Pliocene vertebrates from Arizona. In: Heckert AG, Lucas SG, editors. Vertebrate paleontology in Arizona. Albuquerque (NM, USA): New Mexico Museum of Natural History and Science Bulletin; p.114–135.

Norell MA. 1992. The effect of phylogeny on temporal diversity and evolutionary tempo. In: Novacek MJ, Wheeler QD, editors. Extinction and phylogeny. New York (NY, USA): Columbia University Press; p. 89–118.

Olsen JW, Olsen SJ. 1984. Zooarcheological analysis of small vertebrates from Stanton's Cave, Arizona. In: Euler RC, editor. The archaeology, geology, and paleontology of Stanton's Cave; Grand Canyon National Park, Arizona. Grand Canyon Natural History Association Monograph 6. (AZ, USA): Grand Canyon Association; p. 47–57.

Ohdachi SD, Hasegawa M, Iwasa MA, Vogel P, Oshida T, Lin L-K, Abe H. 2006. Molecular phylogenetics of soricid shrews (Mammalia) based on mitochondrial cytochrome b gene sequences: with special reference to the Soricinae. Journal of Zoology 270:177–191. https://doi.org/10.1111/j.1469-7998.2006.00125.x

Parham JF, Donoghue PC, Bell CJ, Calway TD, Head JJ, Holroyd PA, Inoue JG, Irmis RB, Joyce WG, Ksepka DT, *et al.* 2012. Best practices for justifying fossil calibrations. Systematic Biology 61(2):346–359. https://doi.org/10.1093/sysbio/syr107

Petersen MK. 1976. Noteworthy range extensions of some mammals in Durango, Mexico. The Southwestern Naturalist 21(1):139–142. https://doi.org/10.2307/3670339

Polly PD. 2001. On morphological clocks and paleophylogeography: towards a timescale for *Sorex* hybrid zones. In: Hendry AP, Kinnison MT, editors. Microevolution rate, pattern, process. Dordrecht (The Netherlands): Cambridge University Press; p. 339–357.

Polly PD. 2003a. Paleophylogeography: the tempo of geographic differentiation in marmots (*Marmota*). Journal of Mammalogy 84(2):369–384. https://doi.org/10.1644/1545-1542(2003)084<0369:pttogd>2.0.co;2

Polly PD. 2003b. Paleophylogeography of *Sorex araneus*: molar shape as a morphological marker for fossil shrews. Mammalia 67(2):233–243. https://doi.org/10.1515/mamm.2003.67.2.233

Polly PD. 2022. Geometric morphometrics for Mathematica. Version 12.4. https://github.com/pdpolly/Morphometrics-for-Mathematica

Polly PD. 2023. Phylogenetics for Mathematica. Version 6.8. https://github.com/pdpolly/Phylogenetics-for-Mathematica

Polly PD, Wójcik JM, Searle JB, Zima J. 2019. Geometric morphometric tests for phenotypic divergence between chromosomal races. In: Searle JB, Polly PD, Zima J, editors. Shrews, chromosomes and speciation. Cambridge: Cambridge University Press; p. 336–364.

Repenning CA. 1967. Subfamilies and genera of the Soricidae. Geological Survey Professional Paper 565:1–74.

Rodríguez-Vela H. 1999. *Notiosorex crawfordi* (Coues, 1877) en el matorral desértico de Nuevo León, México. Vertebrata Mexicana 5:5–8.

Rohlf FJ. 2010. TpsDig2 v2.16. Stony Brook (NY, USA): Department of Ecology and Evolution, State University of New York. http://life.bio.sunysb.edu/morph/

Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Biology 39(1):40. https://doi.org/10.2307/2992207

Roldán-Quintana J, Mcdowell F, Delgado Granados H, Valencia-Moreno M. 2009. East-west variations in age, chemical and isotopic composition of the Laramide batholith in southern Sonora, Mexico. Revista Mexicana de Ciencias Geologicas 26(2):543–563.

Rychlik L, Ramalhinho G, Polly PD. 2006. Response to environmental factors and competition: skull, mandible and tooth shapes in Polish water shrews (*Neomys*, Soricidae, Mammalia). Journal of Zoological Systematics and Evolutionary Research 44(4):339–351. https://doi.org/10.1111/j.1439-0469.2006.00374.x

Zelditch ML, Swiderski DL, Sheets HD. 2012. Geometric morphometrics for biologists: a primer. 2nd ed. London (UK): Academic Press.

Appendix I

Notiosorex specimens used in geometric morphometrics analyses.

Notiosorex carrawayae (*n* = 9): Durango: Peñón Blanco (24.7908°N, –104.0292°W; CIB 31482), 3.2 km N, 1.3 km W Súchil (23.6468°N, –103.9110°W; CRD 787), 17 km E, 28 km N Ceballos (26.7393°N, –103.9641°W; UAMI 801, 1222, 1607, 1859 to 1860). Zacatecas: Tlalticoaloya, Susticacán (26.6055°N, –103.1604°W; CVZM 252, 253).

Notiosorex cockrumi (*n* = 13): Arizona: Leslie Canyon National Wildlife Refuge (31.5612°N, –109.5074°W; TTU 82981 to 82984, 82986 to 82988, 82991, 82993, 82994, 83502, 83504, 83505).

Notiosorex crawfordi (*n* = 83): United States: Colorado: Phantom Canyon, Eightmile Creek (38.5669°N, –105.0900°W; KU 125350, 125360, 125261), Mesa Verde National Park; Museum (37.2983°N, –108.4150°W; KU 105109). New Mexico: 7.5 mi W of Animas; 0.5 mi N Hwy 9; Antelope Pass (31.9448°N, –108.9319°W; KU 145525, 145258). Texas: Alice, La Copita Ranch (27.0214°N, –98.126°W; TCWC 53283, 63458); Chaparral WMA (28.3260°N, –99.4075°W; TTU 88236 to 88241, 88259 to 88264, 97880 to 97893, 98009, 98152, 98240, 98282, 98305 to 98312, 98314 to 98322, 97885); 1 mi SE Post (33.1829°N, –101.3690°W; TTU 7025 to 7027, 8177, 8602, 8605 to 8609, 8611, 8613, 8684, 8685, 8693, 9305, 11970); 10.0 mi S Post (33.0460°N, –101.3769°W; TTU 35743); Ranch Post, Jack Lotts (33.1930°N, –101.3809°W; TCWC 40000, 41913, 48634, 48635); La Salle Co, Drift Fence No. 94 (28.2744°N, –99.1036°W; TTU 98558); Zavala (28.8801°N, –99.7232°W; TTU 93323). MEXICO: Chihuahua: 2 km W Minaca (28.4548°N, –107.4366°W; KU 109475); 3.5 Mi E of Los Lamentos (30.5537°N, –105.7656°W; KU 764889). Coahuila: 3 mi NW of Cuatro Cienegas (27.0166°N, –102.0975°W; KU 51572).

Notiosorex dalquesti (*n* = 9) New Mexico: Howell Ridge Cave (31.8873°N, –108.4524°N; UTEP 32 to 519); Dry Cave, Balcony Room (32.3723°N, –104.4815°W; UTEP 12 to 141, 12 to 294); Big Manhole Cave (32.2028°N, –104.4858°W; UTEP 120 to 150, 120 to 260, 120 to 337, 120 to 650, 120 to 740, 120 to 1311).

Notiosorex evotis (*n* = 18): Sinaloa: 5.6 km N, 3 km W Villa Union (23.2418°N, –108.5155°W; CIB 27875 Topotype); 19 km W Choix (26.7257°N, –108.5155°W; CIB 27876 to 27878, 28196, 29201); El Fuerte (26.4161°N, –108.6172°W; KU 75184); 10 km S, 38 km E of Sinaloa (25.7321°N, –107.8440°W; KU 125477); El Rosario (22.9902°N, –105.8569°W; KU 90581); 20 km N, 5 km E of Badiraguato (25.5461°N, –107.5047°W; KU 96419, 98889); 1 mi S of El Cajon (26.7958°N, –108.1723°W; KU 100319); 5 mi NW of El Carrizo (25.9933°N, –109.0217°W; KU 105409); Isla Palmito Del Verde; 6 mi NW of Teacapan (22.62133°N, –105.77076°W; KU 98880). Jalisco: 6.41 km NW, Soyatlán del Oro (20.3400°N, –104.3200°W; CIB 29625); 21 mi SW of Guadalajara (20.4603°N, –103.5621°W; KU 42583, 42584). Nayarit: San Blas (21.5312°N, –105.2861°W; CIB 31460).

Notiosorex harrisi (*n* = 8): New Mexico: Harris' Pocket, Dry Cave (32.3723°N, –104.4815°W; UTEP 3 to 31, 6 to 5810); Howell's Ridge Cave (31.8873°N, –108.4524°W; UTEP 32 to 35); Shelter Cave (32.1883°N, –106.6078°W; UTEP 54 to 127); U-Bar Cave (31.4744°N, –108.4336°W; UTEP 5689-86-17, 5689-133-33, 5689-153-61); Big Manhole Cave (32.2028°N, –108.4524°W; UTEP 120 to 366).

Notiosorex jacksoni (*n* = 2): Kansas: Fox Canyon Quarry (37.0458°N, –100.5527°W; UM 24358 to 24359).

Notiosorex tataticuli arroyoi (*n* = 11): Baja California: Isla San Martín (30.4974°N, –116.1132°W; CIB 24050 to 24054, 32011 to 32016 Paratypes).

Notiosorex tataticuli ocanai (*n* = 10): United States: California: Lakeside; Head of Wildcat Canyon (32.9061°N, –116.883°W; KU 92627); Mint Canyon; 14805 Sierra Highway (34.4781°N, –118.3884°W; KU 160254). MEXICO: Baja California: 22.5 km S San Quintín (30.3333°N, –115.8333°W; CIB 27880 Paratype, CIB 27881 Holotype, CIB 27882 Paratype, CIB 32017 to CIB 32019 Paratypes); 1 km SE Cataviña (29.7259°N, –114.7134°W; CIB 27883); 2.6 km S Punta Prieta (28.9044°N, –114.1563°W; CIB 27884).

Notiosorex tataticuli tataticuli (*n* = 41): Baja California Sur: El Sauzal. 24 km S, 4 km E San Ignacio (27.1742°N, –112.868°W; CIB 31745); 6 km S, 16 km E San Juanico (26.2047°N, –112.318°W; CIB 27498); 6 km S, 16 km E San Juanico (26.204°N, –112.318°W; CIB 27872); San José de Comondú (26.059°N, –111.821°W; CIB 9846 to 9848); 28 km N, 52 km W, Las Pocitas (24.648°N, –111.647°W; CIB 18893); 5 km N, 30 km W Santa Rita (24.635°N, –111.666°W; CIB 24055); 12.2 km S, 15.2 km W Santa Rita (24.635°N, –111.666°W; CIB 24056); El Comitán, 17.5 km W La Paz (24.1384°N, –110.467°W; CIB 27874, CIB 27502); 7 km N, 4.5 km W El Sargento (24.125°N, –110.651°W; CIB 29345); 3.9 km N, 6.5 km W El Sargento (24.124°N, –110.060°W; CIB 23270); 7.1 km N, 4.7 km W El Sargento (24.123°N, –110.065°W; CIB 23979); 4 km N, 6.6 km W El Sargento (24.1195°N, –110.067°W; CIB 23981 Holotype, CIB 31573 Paratype, CIB 23980 to 23983 Paratypes, CIB 25225 to 25226 Paratypes), 7 km N, 4.5 km W El Sargento (24.1195°N, –110.650°W; CIB 27563 to 27567, CIB 27873, CIB 27886 Paratypes); 3.9 km N, 6.5 km W El Sargento (24.119°N, –110.065°W; CIB 23984, CIB 29341 to 29344 Paratypes); 3 km S, 8.7 km W La Paz (24.098°N, –110.383°W; CIB 20928); Chametla, 8 km W La Paz (24.098°N, –110.383°W; CIB 21408); 1.2 km S, 6.6 km E El Sargento (24.0827°N, –110.0621; CIB 27499, CIB 27501); 1 km S, 6.6 km E El Sargento (24.0823°N, –110.0622°W; CIB 27500); 4 km S, 7 km W El Sargento (24.0488°N, –110.0687°W; CIB 31572); 3 km N, 2.6 km W Los Planes (23.9966°N, –109.9622°W; CIB 23075); San Bartolo (23.6982°N, –109.7991°W; CIB 27503); La Calambrina, Sierra de La Laguna (23.5472°N, –110.0163°W; CIB 20867); Palo extraño (23.5171°N, –109.9352°W; CIB 22675); El Edén, 4 km N, 21 km W Santiago (23.5165°N, –109.9294°W; CIB 22676 to 22677); Agua del Tulito, Cañón de la Zorra, Sierra de la Laguna (23.4871°N, –109.5153°W; CIB 3471), 6.2 km S, 2 km E Todos Santos (23.3894°N, –110.2102°W; CIB 30813).

Notiosorex villai (*n* = 4): Nuevo León: 23.7 km N, 19 km E Sabinas Hidalgo (26.7447°N, –100.0308°W; UANL LP-6). Tamaulipas: 5.6 km W Primavera (23.4320°N, –98.8000°W; CIB 31459); Palmillas (23.3020°N, –99.5520°W; KU 54933 Paratype); 0.3 mi SW Rancho Carricitos, San Carlos Mt (25.9934°N, –100.8014°W; TCWC 30492 Paratype).