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A new species and three subspecies of the desert shrew (*Notiosorex*) from the Baja California peninsula and California

Issac Camargo and Sergio Ticul Álvarez-Castañeda*

Centro de Investigaciones Biológicas del Noroeste, Instituto Politécnico Nacional 195, La Paz 23096, Baja California Sur, México

**Correspondent: sticul@cibnor.mx*

Desert shrews of the genus *Notiosorex* comprise four species with morphological characteristics that are difficult to distinguish among the species. Indeed, *N. cockrumi* was described using only genetic markers. Based on molecular divergence documented in *N. crawfordi*, we hypothesize that a fifth species is present in the Baja California peninsula. Genetic variation at the species level was analyzed using individuals from locations west of the Colorado River in the Baja California peninsula, Mexico, and California, United States. Molecular markers of mitochondrial origin (cytochrome *b*, 1,140 bp; cytochrome *c* oxidase subunit I, 542 bp; and cytochrome *c* oxidase subunit III, 672 bp), as well as the nuclear intron 7 of the beta fibrinogen gene (385 bp) were used to construct a phylogeny for species of the genus *Notiosorex*. Genetic distances of 12.46–15.58% between west and east of the Colorado River were obtained using *p*-distance models. Our phylogenetic analyses showed almost identical topologies, placing populations from west of the Colorado River in three monophyletic clades with high bootstrap support values. Results of molecular phylogenetic identity among shrews of the genus *Notiosorex* support the existence of an undescribed, polytypic species of *Notiosorex* west of the Colorado River.

Key words: California desert, genetic cryptic diversity, molecular evolution, shrews, Soricidae

Las musarañas desérticas del género *Notiosorex* son un grupo de cuatro especies con caracteres morfológicos indistintos. De hecho, una de las especies, *N. cockrumi* fue descrita usando exclusivamente marcadores genéticos. Con base en la variación molecular detectada en *N. crawfordi*, postulamos que pudiera estar presente una quinta especie, en la península de Baja California. Analizamos la variación genética en individuos del género de diferentes localidades al oeste del Río Colorado, en la península de Baja California, México y California, EE. UU. Utilizamos marcadores moleculares de origen mitocondrial (*Cytb*; 1,140 pb, *Co1*; 542 pb, y *Co3*; 672 pb) y un intrón del beta fibrinógeno (*Fgb*; 385 pb). Construimos una filogenia de las especies del género *Notiosorex*, dentro de los marcos de Máxima Verosimilitud (MV) e Inferencia Bayesiana (IB) para así confirmar la identidad molecular de las poblaciones analizadas. Obtuvimos distancias genéticas entre 12.46–15.58% usando los modelos de distancia *p* entre poblaciones del oeste y este del Río Colorado. Los análisis filogenéticos muestran topologías prácticamente idénticas, ubicando a las poblaciones al oeste del río Colorado en tres clados monofiléticos con valores altos de soporte de bootstrap. Los resultados de identidad filogenética molecular entre las musarañas del género *Notiosorex* soportan la existencia de una especie politípica no descrita al oeste del Río Colorado.

Palabras clave: Desiertos de California, diversidad genética críptica, evolución molecular, musarañas, Soricidae

Nomenclatural statement.—The life science identifier (LSID) number was obtained for this work: urn:lsid:zoobank.org:pub: 7B2384D1-3789-4428-ADAA-ADE095BEA6E9.

Shrews of the genus *Notiosorex* are the only members of the family Soricidae that have adaptations allowing them to thrive in arid and semiarid areas of North America. *Notiosorex* has four recognized species: *N. cockrumi* Baker et al. 2003, *N. crawfordi* (Coues, 1877), *N. evotis* (Coues, 1877), and *N. villai* Carraway and Timm, 2000, all distributed in arid areas of northern Mexico and the southwestern United States (Carraway and Timm 2000; Carraway 2007). Three of these species can be differentiated based on morphological characteristics: *N. crawfordi*, *N. evotis*, and *N. villai* (Carraway and Timm 2000).

In contrast, *N. cockrumi*, which co-occurs with *N. crawfordi* (McAiley et al. 2007), only can be distinguished using molecular markers (Baker et al. 2003). *Notiosorex* also includes four fossil taxa: *N. dalquesti* Carraway 2010, *N. harrisi* Carraway 2010, *N. jacksoni* Hibbard, 1950, and *N. repenningi* Lindsay and Jacobs, 1985. The fossil record shows that *Notiosorex* was widely distributed across deserts of North America for at least 6.7 million years (Carraway 2010).

Molecular analyses have indicated the possibility of a fifth extant species in the Baja California peninsula (Odhachi et al. 2006; McAiley et al. 2007; Manning et al. 2014). However, morphological variation in populations of *Notiosorex* from Baja California was not detected easily because differences either are minimal or difficult to evaluate (Carraway and Timm 2000). The Baja California peninsula is a region with a complex geological history and a climate characterized by environmental heterogeneity. Several taxa that either are endemic, morphologically cryptic, widely distributed, geographically restricted, or vulnerable from a conservation perspective have been the subject of phylogeographic studies addressing the distribution of their genetic variation (Zink 1996; Riddle et al. 2000a, 2000b; Álvarez-Castañeda and Murphy 2014).

We examined individuals of *Notiosorex* from the Baja California peninsula, Mexico, and California, United States, to determine phylogenetic relationships within the genus. Our working hypothesis was that the Colorado River acted as a geographic barrier that fostered speciation in desert shrews, and that these changes would be reflected in the molecular genetics, morphology, and variation in the color pattern of the pelage of the individuals we examined.

Materials and Methods

Sample collection.—We collected individuals of *Notiosorex* using pitfall traps. Pitfall traps were one gallon buckets, and were set in clusters of five traps with one central pitfall trap and four linear drift fences of 5 m with a pitfall trap at the end of each drift fence. Each pitfall was baited with live scorpions, such that captured shrews had food available and would survive until the pitfalls were examined (Camargo and Álvarez-Castañeda 2019b). Traps were examined twice daily: early in the morning and late in the afternoon. All animals were handled and euthanized following the recommendations of the American Society of Mammalogists (Sikes et al. 2016). Voucher specimens were deposited in the Centro de Investigaciones Biológicas del Noroeste (CIB).

DNA sequence data.—Analyses included 17 geographical samples collected from California and the Baja California peninsula, and one insular population (western group). We also examined specimens deposited at Texas Tech University (TTU), Angelo State University (ASK), and the Museum of Vertebrate Zoology, University of California (MVZ; Appendix I). We sequenced the complete cytochrome *b* gene (*Cytb*; n = 23), and portions of two other functional mitochondrial genes: cytochrome *c* oxidase subunit I (*Co1*; n = 24) and cytochrome *c* oxidase subunit III (*Co3*; n = 35). In addition, we sequenced intron 7 of the beta fibrinogen gene (*Fgb*; n = 28) for specimens representing *N. crawfordi*, *N. cockrumi*, and individuals from California and the Baja California peninsula (Appendix I).

Genomic DNA was extracted from muscle tissue preserved in 95% ethanol (stored at −20°C) or frozen (stored at −80°C) using the DNeasy Kit (Qiagen Inc., Valencia, California) protocols. For the proximal 5′–3′ ~800 bp of *Cytb*, we used primer pairs MVZ05 and MVZ16; the distal ~800 bp were obtained using MVZ45 and MVZ14 (Smith and Patton 1993; Smith 1998). Overlapping concatenation of both fragments resulted in the complete sequence (1,140 bp) of *Cytb*. A 717-bp fragment of the *Co3* gene was obtained using primer pairs L8618 and H9323 (Riddle 1995); a 658-bp fragment of the *Co1* gene was obtained using primers LCO1490 and HCO2198 (Ivanova et al. 2007); and a 385-bp fragment of the *Fgb* gene was sequenced using primers β-fib I7L and β-fib I7U (Wickliffe et al. 2003).

The following conditions were used for the initial double-strand amplification: 12.5 µl of (10 ng) template; 4.4 µl ddH_2O; 2.5 µl of each primer pair (10 nM); 0.474 µl (0.4 nM) dNTPs; 0.5 µl (3 mM) $MgCl_2$; 0.125 µl *Taq* polymerase (Platinum *Taq* DNA Polymerase High Fidelity, Invitrogen, Carlsbad, California); and 1× *Taq* buffer, to a final volume of 25 µl. Amplification conditions consisted of a 3-min initial denaturation at 94°C followed by 37 denaturation cycles at 94°C for 45 s each; 60 s annealing at 50°C (*Cytb*), 51°C (*Co1*), 55°C (*Co3*), or 58.5°C (*Fgb*); and a 60-s extension at 72°C for the mitochondrial genes and 90 s for *Fgb*. PCR amplicons were cleaned using the QIAquick PCR Purification Kit (Qiagen), and templates were cycle-sequenced in both directions using Big Dye terminator chemistry (Applied Biosystems Inc., Foster City, California). All products were sequenced on an ABI 3730 sequencer (Applied Biosystems) at the Museum of Vertebrate Zoology, and deposited in GenBank (Appendix I).

Resulting nucleotide sequences were edited in Bioedit (Hall 1999), followed by alignment of sequences and matrix manipulations. Sequences were verified manually and translated into amino acids to check for spurious stop codons and for alignment confirmation.

Phylogenetic analyses.—The most appropriate substitution model for the data set for each of the four gene regions as well as for the concatenated series was determined using the Akaike information criterion (AIC) as implemented in MrAIC (Nylander 2004). All analyses were carried out separately on each gene, as well as on the concatenated genes data set. Four separate Bayesian inference (BI) and maximum likelihood (ML) analyses were undertaken on the four genes; the concatenated series was carried out with four partitions, one for each gene (*Cytb*, *Co1*, *Co3*, *Fgb*). Bayesian analyses were undertaken in MrBayes ver. 3.0b4 (Huelsenbeck and Ronquist 2001), using four separate runs with Markov-chain Monte Carlo simulations starting from a random tree. Each run was allowed to go for 20 million generations, sampling at intervals of 1,000 generations. The first 25% of samples were discarded as burn-in; remaining sampled trees were analyzed to obtain the posterior probability of the resulting nodes. Reliability was assessed using each

of the three codon positions separately while applying equal weights and nodal support using nonparametric bootstrapping.

ML analyses (Felsenstein 1981) were executed in PAUP ver. 4.0b10 (Swofford 2002) using a heuristic search with 1,000 replicates and swapping with the Tree Bisection Reconnection (TBR) algorithm. Reliability was assessed using each of the three codon positions separately while applying equal weights and nodal support using nonparametric bootstrapping. Species representing the genera *Blarina*, *Cryptotis*, and *Sorex* were used because the phylogenetic relationship among the shrews of North American is uncertain (Appendix I).

Morphometric analysis.—Specimens examined are listed in Appendix I and are deposited in research collections at Centro de Investigaciones Biológicas del Noroeste (CIB) and the Museum of Natural History at the University of Kansas (KU). Skull and mandibular morphologies were evaluated for shrews of the genus *Notiosorex* following Carraway (2010). Morphometric measurements recorded from digital images of the specimens were captured using a Canon EOS 50D (15.1 megapixels) with a macro lens that was fixed on a tripod stand directly above the skulls and jaws and the lens was adjusted so the margins of viewfinder aligned with margins of the graph paper in X-Y directions, each image included a scale to standardize the individual sizes, and further scaling was applied in TPSDig, ver. 2.16 (Rohlf 2010) using the millimeter grid in graph paper. Twenty-two cranial measurements, following Carraway (2010) were obtained by one of us (IC), as follows: 1) rostral breadth (RB); 2) least interorbital breadth (LIB); 3) condylobasal length (CL); 4) breadth across M2–M2 (BM2); 5) length of P4–M3 (LPM); 6) palatilar length (PL); 7) length of unicuspid toothrow (LUT); 8) length of U1–M3 (LUM); 9) length of coronoid process–posterior point of upper condylar facet (LPC); 10) height of coronoid process (HCP); 11) height of coronoid valley (HCV); 12) height of articular condyle (HAC); 13) length of mandible (LM); 14) length of coronoid process–ventral point of lower condylar facet (LPVC); 15) length of c1–m3 (LCM); 16) length of c1 (LC1); 17) length of p4 (LP4); 18) length of m1 (LM1); 19) length of m2 (LM2); 20) length of m3 (LM3); 21) length from upper articular condyle to posterior edge of m3 (LUA); and 22) depth of dentary at m1 (DDM; Fig. 1).

For descriptive and comparative purposes, standard statistics (mean, *SE*, and range in mm) were calculated for each variable and species. Morphometric assignment of individuals to each lineage was determined with Principal Component Analysis (PCA). Statistical significance of the PCs was evaluated following the broken stick method (Frontier 1976; Jackson 1993). Canonical variates (CVA) derived from multigroup discriminant function classification were computed using the 22 craniodental variables. To explain the variance in the data, a PCA using only skulls that were complete and not broken (southern part of the Baja California peninsula [n = 21], northern part of the Baja California peninsula and California [n = 10], and San Martin Island [n = 11]) was performed. PCs were extracted from the variance–covariance matrix and variable loadings are expressed as correlation coefficients of the extracted components or CVs

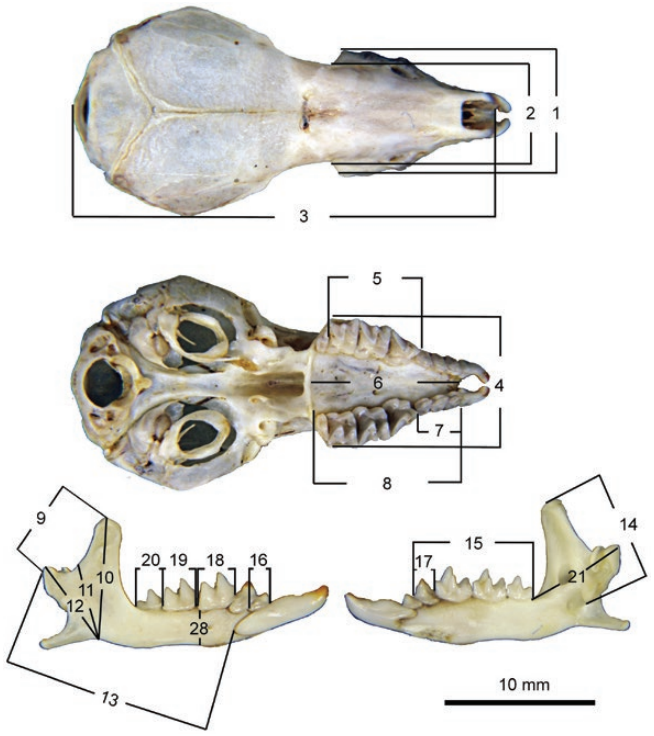

Fig. 1.—Dorsal and ventral view of the skull and mandible of *Notiosorex*. The morphological measurements analyzed were: 1) rostral breadth (RB); 2) least interorbital breadth (LIB); 3) condylobasal length (CL); 4) breadth across M2–M2 (BM2); 5) length of P4–M3 (LPM); 6) palatilar length (PL); 7) length of unicuspid toothrow (LUT); 8) length of U1–M3 (LUM); 9) length of coronoid process–posterior point of upper condylar facet (LPC); 10) height of coronoid process (HCP); 11) height of coronoid valley (HCV); 12) height of articular condyle (HAC); 13) length of mandible (LM); 14) length of coronoid process–ventral point of lower condylar facet (LVC); 15) length of c1–m3 (LCM); 16) length of c1 (LC1); 17) length of p4 (LP4);18) length of m1 (LM1); 19) length of m2 (LM2); 20) length of m3 (LM3); 21) length from upper articular condyle to posterior edge of m3 (LUA); and 22) depth of dentary at m1 (DDM). Modified from Carraway (2010).

with the original cranial measurements. Differences among the geographic groups in *Notiosorex* were examined using one-way analyses of variance (ANOVAs) for each of the 22 morphometric variables. Analyses were undertaken using the software PAST version 2.17b (Hammer et al. 2001).

Variation in pelage coloration.—The pelage color of 63 shrews (Appendix I) was determined with an X-Rite Digital Swatchbook spectrophotometer (X-Rite, Inc., Grandville, Michigan) and through direct visual comparison with Munsell Soil Color Charts (Munsell Color Co. 1975). Spectrophotometric measurements were taken indoors. The instrument provides its own source of light and returns the reflectance spectrum (390–700 nm) of the object measured, as well as tri-stimuli color scores (CIE X, Y, and Z). Pelage coloration was measured in four areas: dorsal, midventral, anterior dorsal, and lateral (Supplementary Data SD1). Color was measured on individual specimens using a 3-mm-diameter port. Five measurements of pelage coloration of each shrew were recorded and averaged

for statistical analyses. Each measured character was transformed logarithmically to reduce the variation in the magnitude of the variances between *Notiosorex* populations. Uniform light conditions were used to record colors from Munsell Soil Color Charts. For each color, the key, chart hue, chroma, and color name were recorded (i.e., 10YR 8/4, chart hue/chroma).

The variation in CIE X, Y, and Z of the pelage coloration of each specimen was analyzed with a PCA. Differences among the residuals from the analysis of main components among the three subclades we identified (see "Results") were tested using an ANOVA. A Kruskal–Wallis test (multiple comparisons with Dunn's method) was used to test for differences in pelage color among groups.

Results

DNA sequence data.—The best-fit model of sequence evolution using the AIC was HKY + I + G for each of the individual genes *Cytb*, *Co1*, *Co3*, and *Fgb*, as well as for the concatenated data set (Nylander 2004). BI and ML trees for *Cytb*, *Co1*, *Co3*, and *Fgb*, and the concatenated data with four partitions converged on a virtually identical topology (Fig. 2). Three haplogroups were resolved within *Notiosorex*. Haplogroup A included all specimens of *N. crawfordi*; haplogroup B, individuals of *N. cockrumi*; and haplogroup C, desert shrews west of the Colorado River, from California and the Baja California peninsula. Haplogroup C consisted of two subgroups. Group C1 included specimens from California and Baja California, whereas group C2 represented desert shrews from Baja California Sur (Fig. 2).

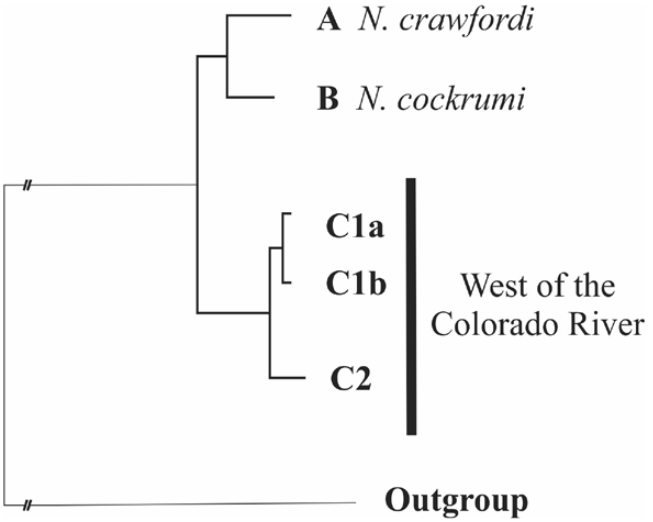

Fig. 2.—Bayesian tree using three mitochondrial DNA genes (cytochrome *b*, cytochrome oxidase subunit I, and cytochrome oxidase subunit III) and one nuclear gene (intron 7 of the beta fibrinogen gene) of *Notiosorex* shrews. The tree includes all specimens of *N. crawfordi* (haplogroup A), *N. cockrumi* (haplogroup B), and specimens living west of the Colorado River from California and the Baja California peninsula (haplogroup C). Haplogroup C has two clades: Clade C1 includes specimens from the northern Baja California peninsula and California; clade C2, those from the southern Baja California peninsula. Black circles at nodes indicate support ≥ 90.

Genetic variation from west of the Colorado River.—Haplogroup C individuals exhibit *p*-distances of 12.46–15.58% to *N. crawfordi*, and 13.88–14.16% to *N. cockrumi* (Table 1). The percent difference between the two subclades within lineage C is 1.42% for *mt*DNA and 0.52–0.68% for *Fgb* (Table 1).

Morphometric analyses.—The craniodental measurements of *N. crawfordi* are smaller than those of *Notiosorex* from the Baja California peninsula (Table 2). Measurements with the largest differences are: length of the coronoid process–ventral point of lower condylar facet, length of the lower canine, and length of the fourth lower premolar. Based on one-way ANOVAs, all craniodental characters are highly significant in allowing differentiation of *Notiosorex* populations ($P < 0.001$; Supplementary Data SD2).

Morphometric variation within the lineage west of the Colorado River.—At the intraspecific level, no sexual dimorphism was observed in terms of size (*t*-test, $P > 0.05$). Accordingly, males and females of each species were pooled in subsequent analyses. Twenty-one of the 22 craniodental characters showed significant differences in the ANOVA ($P \leq 0.05$); the only exception was least interorbital breadth (LIB; Supplementary Data SD2). The greatest differences were found between specimens from San Martín Island and those from the southern part of Baja California, with 20 of 22 variables being different ($P \leq 0.05$; Supplementary Data SD2). There is an overall increase in size from southern to northern localities in the continental populations, but specimens from San Martín Island are the smallest, while those from the southern part of the peninsula are the largest.

Table 1.—Genetic distances (patristic distance, *p*) among samples of *Notiosorex crawfordi*, *Notiosorex cockrumi*, and a phylogroup found in Baja California peninsula, Mexico and California for the mitocondrial cytochrome *b*, cytochrome oxidase subunit I, cytochrome oxidase subunit III, and intron 7 of the beta fibrogen gene.

Species	*N. cockrumi*	*N. crawfordi*	*Notiosorex* west of Colorado River
N. cockrumi			
Cytb	0–0.11	13.25–13.87	13.88–14.16
Co1	0–0.16	6.87–6.89	6.87–7.64
Co3	0–0.18	11.81–12.1	10.94–10.97
Fgb	0–0.13	4.27–4.55	3.42–5.34
Concat	0–0.19	9.35–11.01	9.1–11.22
N. crawfordi			
Cytb	13.25–13.87	0.72–1.27	12.46–15.58
Co1	6.87–6.89	0.33–1.19	12.78–13.13
Co3	11.81–12.1	0–1.22	11.11–11.26
Fgb	4.27–4.55	0–0.57	4.11–5.27
Concat	9.35–11.01	0.24–1.06	10.41–10.71
Notiosorex west of Colorado River			
Cytb	13.88–14.16	12.46–15.58	0.85–1.13
Co1	6.87–7.64	12.78–13.13	0.86–1.27
Co3	10.94–10.97	11.11–11.26	0.58–1.44
Fgb	3.42–5.34	4.11–5.27	0.52–0.68
Concat	9.1–11.22	10.41–10.71	1.06–1.81

Table 2.—Craniodental measurements *Notiosorex cockrumi*, *Notiosorex crawfordi*, *Notiosorex evotis*, *Notiosorex tataticuli*, and *Notiosorex villai*. Mean and *SE* are given in mm; *n* is the sample size. Measurements are defined in "Materials and Methods."

Character	*N. cockrumi*[a] *n* = 18	*N. crawfordi*[a] *n* = 224	*N. evotis* *n* = 17	*N. tataticuli*[b] *n* = 42	*N. villai*[a] *n* = 3
RB	4.88 ± 0.03	4.84 ± 0.01	5.67 ± 0.29	4.68 ± 0.25	5.19
	14.6–5.1	4.4–5.2	5.28–5.97	4.18–5.03	5.0–5.3
LIB	3.74 ± 0.02	3.76 ± 0.01	4.14 ± 0.47	3.70 ± 0.26	3.83
	3.5–3.9	3.4–4.1	3.74–4.81	3.08–4.27	3.6–4.0
CL	16.14 ± 0.07	16.08 ± 0.04	16.95 ± 0.83	16.78 ± 0.73	17.11
	15.71–16.78	14.95–17.25	16.18–17.96	15.50–17.96	16.9–17.2
BM2	4.77 ± 0.02	4.83 ± 0.01	5.11 ± 0.23	4.68 ± 0.29	5
	4.6–5	4.4–5.1	4.89–5.41	3.76–5.49	4.9–5.1
LPM	4.37 ± 0.02	4.31 ± 0.01	4.47 ± 0.27	4.10 ± 0.3	4.60
	4.1–4.6	4.1–4.6	4.08–4.68	3.68–4.72	4.4–4.7
PL	7 ± 0.05	6.79 ± 0.02	7.44 ± 0.14	6.76 ± 0.41	7.20
	6.5–7.3	6.2–7.3	7.29–7.62	6.27–8.18	7.0–7.4
LUT	1.96 ± 0.02	1.88 ± 0.01	2.02 ± 0.15	1.66 ± 0.26	2.20
	1.7–2.1	1.5–2.2	1.84–2.19	1.18–2.12	2.0–2.3
LUM	6.18 ± 0.03	6.03 ± 0.05	6.69 ± 0.25	6.11 ± 0.24	6.40
	6–6.5	5.1–6.8	6.39–6.97	5.66–6.72	6.1–6.8
LPC	3.53 ± 0.05	3.3 ± 0.02	3.52 ± 0.03	3.20 ± 0.36	3.35
	3–3.9	2.7–3.9	3.48–3.54	2.45–3.66	3.3–3.4
HCP	4.1 ± 0.04	4.02 ± 0.01	4.09 ± 0.12	3.86 ± 0.30	4.05
	3.7–4.4	3.4–4.6	3.92–4.16	3.29–4.36	4.0–4.1
HCV	2.43 ± 0.02	2.25 ± 0.02	2.38 ± 0.06	2.24 ± 0.31	2.35
	2.3–2.6	1.8–2.7	2.29–2.42	1.63–2.69	2.3–2.4
HAC	2.9 ± 0.03	2.79 ± 0.03	2.69 ± 0.16	2.67 ± 0.30	2.95
	2.7–3	2.5–3.5	2.52–2.90	2.11–3.02	2.9–3.0
LM	7.08 ± 0.05	7.04 ± 0.02	7.07 ± 0.04	7.06 ± 0.41	7.40
	6.7–7.4	6.4–7.7	7.01–7.09	6.45–8.18	7.3–7.5
LVC	3.77 ± 0.05	3.74 ± 0.02	3.61 ± 0.09	3.25 ± 0.38	3.75
	3.3–4.1	3.2–4.3	3.49–3.70	1.82–3.70	3.7–3.8
LCM	4.72 ± 0.03	4.71 ± 0.01	4.59 ± 0.01	4.55 ± 0.41	5.05
	4.3–4.9	4.4–5.1	4.58–4.60	3.87–5.23	5.0–5.1
LC1	0.76 ± 0.01	0.76 ± 0.29	0.47 ± 0.01	0.40 ± 0.16	0.90
	0.7–0.9	0.6–0.9	0.45–0.47	0.50–0.68	0.9–0.9
LP4	1.05 ± 0.02	1.01 ± 0.01	0.73 ± 0.02	0.62 ± 0.16	1.05
	0.9–1.2	0.9–1.2	0.71–0.75	0.23–0.85	1.0–1.1
LM1	1.48 ± 0.02	1.44 ± 0.01	1.68 ± 0.10	1.26 ± 0.23	1.45
	1.4–1.7	1.1–1.6	1.53–1.75	0.90–1.63	1.1–1.5
LM2	1.38 ± 0.02	1.36 ± 0.01	1.28 ± 0.08	1.31 ± 0.26	1.40
	1.3–1.6	1.2–1.5	1.24–1.39	0.71–1.98	1.4–1.4
LM3	0.97 ± 0.01	0.98 ± 0.01	0.99 ± 0.02	0.77 ± 0.22	1
	0.9–1	0.9–1.0	0.97–1.0	0.83–0.97	0.9–1.1
LUA	3.56 ± 0.03	3.46 ± 0.02	4.6 ± 0.11	3.43 ± 0.26	3.45
	3.4–3.7	3.1–3.9	4.49–4.7	2.98–3.94	3.4–3.5
DDM	1.12 ± 0.01	1.12 ± 0.01	1.07 ± 0.02	0.90 ± 0.20	1.20
	1–1.2	0.9–1.4	1.05–1.09	0.55–1.21	1.2–1.2

[a] Measurements listed are from Carraway (2010).
[b] Measurement of the nominal subspecies, southern distribution.

Loadings on PC1 all were positive and of similar magnitude, suggesting that this axis represents overall size. Consequently, the data were log-transformed. The first three principal components explained 76.4% of the total variation, with PC1 accounting for 58.0% of the variation; PC2, 9.7%; and PC3, 8.6% (Fig. 3; Supplementary Data SD3). The PCs showed that the first two principal components were significant using the broken stick method, comprising 64.56% of the total variance. The highest loading for variables on PC1 was length of coronoid process–posterior point of upper condylar facet (LPC); on PC2, palatilar length (PL); and on PC3, length of P4–M3 (LPM). The canonical analysis carried out on the three sample groups separated the three groups on axis 1 (CV1; Supplementary Data SD4), and the northern-group samples from the remainder others on CV2. Depth of dentary at m1 (DDM) and length of unicuspids toothrow (LUT) had the largest and smallest loadings on CV1 (Supplementary Data SD4). The differences across geographic groups all are related variables associated with the rostral region of the skull.

Variation in coloration of the lineage west of the Colorado River.—Differences in pelage coloration were observed among specimens from California and northern Baja California, San Martín Island, and the southern part of the Baja California peninsula (Table 4). Pelage color, in terms of the four characters, exhibited significant differences when the three geographic groups were compared (ANOVA, $P < 0.0001$). Each

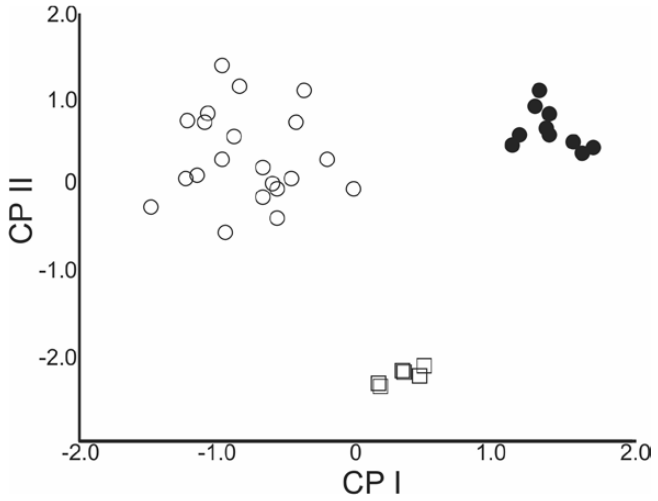

Fig. 3.—Graph of PC1 and PC2 extracted from the analysis of morphometric data comprising 22 craniodental measurements of *Notiosorex* shrews west of the Colorado River. Southern population (white circles), northern population (black circles), and San Martin Island (white squares).

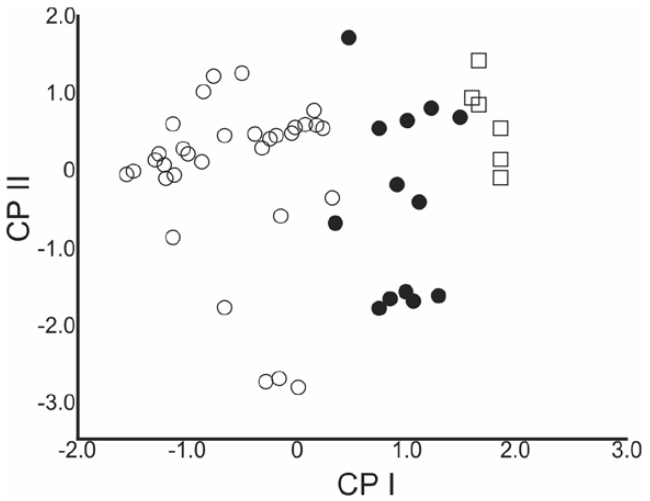

Fig. 4.—Graph of PC1 and PC2 extracted from the analysis of log-transformed morphometric data on the dorsal, lateral, and ventral coloration variables for *Notiosorex* shrews west of the Colorado River. Southern population (white circles), northern population (black circles), and San Martín Island (white squares).

group displayed a geographic pattern similar to that obtained with the Munsell charts.

Loadings on PC1 were all positive and of similar magnitude; consequently, the data set was log-transformed. PC1 = 79.6% and PC2 = 13.4%. Variables CIE X, Y, and Z obtained from spectrophotometric data discriminated the shrews examined into three distinct groups (Fig. 4; Supplementary Data SD5).

Discussion

The Colorado River is a geographic barrier that likely contributes to the speciation process in desert shrews. The genetic divergence of *Notiosorex* shrew populations separated by the river is evident, as the genetic distances between populations east and west of the Colorado River range from 11.11% to 15.58% for *mt*DNA and 4.11% to 5.27% for nuclear DNA. The Colorado River has been documented as a barrier in scorpions (*Centruroides*—Gantenbein et al. 2001) and cacti (*Lophocereus*—Nason et al. 2002). The role of the Colorado River as a species-level barrier has also been suggested between *Chaetodipus baileyi* and *C. rudinoris*, *Neotoma lepida* and *N. devia*, *N. bryanti* and *N. devia*, and *Peromyscus fraterculus* and *P. eremicus* (Riddle et al. 2000a; Patton et al. 2008; Cornejo-Latorre et al. 2017). These speciation events are hypothesized to have occurred approximately 3.4 Mya (Upton and Murpy 1997; Cornejo-Latorre et al. 2017).

The percent genetic distances obtained between lineage C relative to *N. crawfordi* (15.58%) and *N. cockrumi* (14.16%) are similar to those between *N. crawfordi* and *N. cockrumi* (13.87%—McAliley et al. 2007). The distances within *Notiosorex* species are greater than those previously obtained for sister species of mammals that occur on both sides of the Colorado River (> 15.58% for Cytb), such as *Neotoma varia–N. bryanti* (2.7%—Patton et al. 2008), *C. baileyi–C. rudinoris* (8.7%), and *Peromyscus eremicus–P. fraterculus* (8.7% for *Co3*—Riddle et al. 2000b). The magnitude of genetic distance between *Notiosorex* west of the Colorado River is over 10%, higher than the values proposed by Bradley and Baker (2001) for interspecific differences both in rodents and bats, albeit using Kimura 2-parameter distances, rather than patristic distances, as we employed.

We also found morphological and morphometric differences between the specimens collected west of the Colorado River and those living to the east (*N. crawfordi*). Morphological differences between these lineages were evident and differed from those reported in the description of *N. cockrumi*, implying that external morphology is highly conservative within the genus *Notiosorex*, allowing for cryptic species (Baker et al. 2003).

Likewise, individuals of *N. evotis*, *N. crawfordi*, and *N. cockrumi,* do not have clear morphological characters that could be used to differentiate among them; as such, we consider them to be morphologically cryptic species. Analyses within the western lineage show two monophyletic haplogroups with genetic distances between 0.58% and 1.44% in *mt*DNA. Haplogroup C includes two subgroups exhibiting a 1.81% difference. C1 includes specimens from the southern part of the peninsula (Baja California Sur), while C2 includes populations on San Martín Island, Baja California, and mainland populations from the northern Baja California peninsula and California.

Specimens of each subgroup within haplogroup C and the population inhabiting San Martín Island can be differentiated by morphometrics and color pattern. Each has unique characteristics and is geographically isolated. We found more marked morphometric and color variations in the clade living west of the Colorado River than in remaining species of *Notiosorex*.

Overall, our data support the hypothesis that the *Notiosorex* population west of the Colorado River should be considered a

species distinct from those currently described. Moreover, this new taxon is comprised of three distinct populations with no geographic overlap, that differ in morphology and coloration.

The clade structure, high level genetic differences, and nodal support obtained from the analyses reported herein are consistent with the Phylogenetic Species Concept (Cracraft 1997). Within the species each clade being morphologically distinct in multivariate ordination of craniodental variables (Figs. 3 and 4). Based on the combined morphological and molecular distinctness of these groups, it appears that three subspecies should be recognized. We used the subspecies concept advocated by Lidicker (1962).

Taxonomy

Family Soricidae Fischer, 1814

Subfamily Soricinae Fischer, 1814

Tribe Notiosoricini Reumer, 1984

Genus *Notiosorex* Coues, 1877

Notiosorex tataticuli, new species

Ticul's desert shrew; musaraña desértica de Ticul

Holotype.—CIB 23981, an adult male collected by Evelyn Ríos (collector number 2335) on 3 November 2013, from Mexico: Baja California Sur; 4 km N, 6.6 km W El Sargento, 24.1189°N, −110.0670°W, 675 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, plus liver tissue preserved in 95% ethanol; all body parts are in good condition (Fig. 5).

Paratypes.—Nine individuals from the locality type CIB 23980, 23982, 23983, 25225, 25226, 27873, 27886, 29343, and 29344 (see Appendix I for localities).

Diagnosis.—The teeth are proportionally smaller than in the other species of *Notiosorex*, in particular the lower molars; the dentary is shallow. *Notiosorex tataticuli* has the largest mean condylobasal length within the genus *Notiosorex*. Dorsal coloration is light gray (7.5YR 7/1), being slightly darker gray (7.5YR 5/1) in individuals collected in Sierra de La Laguna; ventral coloration ranges from pinkish gray (7.5YR 6/2) to pinkish white (7.5YR 8/2); tail is dark brown (10YR 2/1) to brown (7.5YR 4/2).

General characteristics.—Notiosorex tataticuli is small, gray coloration in different tones; scent gland on flanks; large ears; tail short, less than one-third of total length. Anterior teeth are slightly pigmented in labial view; there are three upper unicuspid teeth, and the socket of the first lower incisor extends below the paraconid first molar. From the lingual view, both upper molars are nonpigmented. Weight is 3.0–6.0 g.

Comparison.—Notiosorex tataticuli has a distribution that is allopatric with respect to all remaining species of *Notiosorex*. It can be differentiated from *N. crawfordi* only by DNA sequence data; the uncorrected patristic distances between the two taxa are: 15.58% in *Cytb*, 13.13% in *Co1*, 11.26% in *Co3*, and 5.27% in *Fgb*. We found no morphological characters that could be used to differentiate between these two species. Craniodental measurements of *N. tataticuli* in general are smaller (Table 2).

Notiosorex tataticuli can be distinguished from *N. cockrumi* by genetic characters. It differs from *N. cockrumi* by: 14.16% in *Cytb*; 7.64% in *Co1*, 10.97% in *Co3*, and 5.34% in *Fgb*. We found no morphological characters that could be used to differentiate between these two species. The craniodental measurements of *N. tataticuli* in general are smaller (Table 2).

Notiosorex tataticuli can be differentiated from *N. villai* based on skull morphology. The roof of the glenoid fossa does not extend laterally from the cranium when the skull is viewed from the dorsal aspect in *N. villai* but does so in *N. tataticuli*

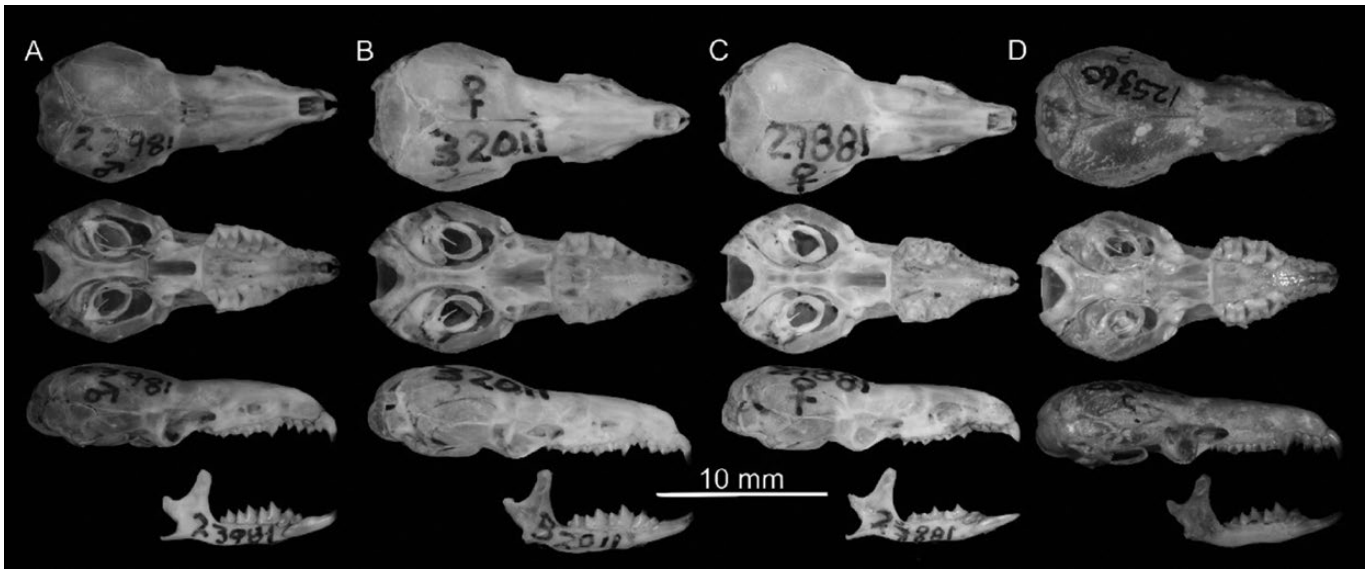

Fig. 5.—Comparison of mandible and skull of holotypes of the *Notiosorex tataticuli tataticuli* from Baja California Sur (CIB 23981), *N. t. ocanai* (CIB 27881) from Baja California, *N. t. arroyoi* (CIB 32011) from San Martin Island, and *N. crawfordi* from Colorado (KU 125360).

Table 3.—Holotype and paratype mean and *SE* (in mm) for cranial measurements of *Notiosorex tataticuli arroyoi*, *N. t. ocanai*, and *N. t. tataticuli*. Subspecies not listed with same letter from the Tukey test are significantly different ($P < 0.05$). Measurements are defined in "Materials and Methods."

Character	*N. t. arroyoi* Holotype CIB 32011	*N. t. arroyoi* Paratypes *n* = 10	*N. t. ocanai* Holotype CIB 27881	*N. t. ocanai* Paratypes *n* = 5	*N. t. tataticuli* Holotype CIB 23981	*N. t. tataticuli* Paratypes *n* = 9	Tukey
RB	4.54	4.48 ± 0.16 4.18–4.67	4.98	4.96 ± 0.05 4.55–5.03	4.9	4.76 ± 0.18 4.26–5.03	a b b
LIB	3.51	3.51 ± 0.10 3.33–3.71	3.73	3.84 ± 0.11 3.38–3.90	3.98	3.77 ± 0.30 3.08–4.27	a a a
CL	16.42	16.01 ± 0.44 15.69–16.96	16.04	15.85 ± 0.35 15.50–16.49	17.3	17.33 ± 0.31 17.00–17.96	a a b
BM2	4.55	4.41 ± 0.30 3.76–5.10	4.72	4.72 ± 0.11 4.60–4.90	4.84	4.80 ± 0.26 4.44–5.49	a ab b
LPM	3.86	3.91 ± 0.24 3.78–4.55	3.92	3.85 ± 0.10 3.71–3.94	4.65	4.24 ± 0.30 3.68–4.72	a a b
PL	6.81	6.70 ± 0.39 6.40–7.64	6.88	6.97 ± 0.07 6.87–7.03	6.75	6.76 ± 0.48 6.27–8.18	a ab b
LUT	1.44	1.37 ± 0.17 1.29–1.88	1.53	1.51 ± 0.02 1.50–1.57	1.79	1.85 ± 0.19 1.38–2.12	a a b
LUM	6.15	6.11 ± 0.12 6.07–6.32	5.66	5.78 ± 0.08 5.66–5.84	6.15	6.18 ± 0.24 5.82–6.72	a b a
LPC	2.49	2.77 ± 0.27 2.45–3.10	3.11	2.99 ± 0.17 2.91–3.33	3.2	3.46 ± 0.13 3.12–3.66	a b c
HCP	3.79	3.66 ± 0.16 3.29–3.79	3.77	3.69 ± 0.06 3.64–3.78	3.29	4.00 ± 0.31 3.29–4.36	a ab b
HCV	1.76	1.87 ± 0.18 1.63–2.07	2.22	2.08 ± 0.09 2.00–2.22	2.59	2.48 ± 0.15 2.25–2.69	a a b
HAC	2.22	2.28 ± 0.11 2.11–2.41	2.73	2.65 ± 0.06 2.60–2.73	2.84	2.89 ± 0.15 2.29–3.02	a b c
LM	6.58	6.61 ± 0.10 6.45–6.72	7.18	7.00 ± 0.14 6.92–7.21	6.88	7.30 ± 0.35 6.77–8.18	a a b
LVC	2.87	2.83 ± 0.38 1.82–3.28	3.06	3.14 ± 0.08 3.06–3.28	3.47	3.52 ± 0.10 3.31–3.70	a b b
LCM	3.92	4.04 ± 0.13 3.87–4.20	4.89	4.49 ± 0.36 4.04–4.90	4.63	4.81 ± 0.24 4.50–5.23	a b b
LC1	0.52	0.31 ± 0.24 0.05–0.68	0.53	0.52 ± 0.04 0.50–0.61	0.54	0.51 ± 0.06 0.43–0.61	a b b
LP4	0.66	0.46 ± 0.17 0.23–0.75	0.79	0.74 ± 0.03 0.69–0.79	0.69	0.71 ± 0.06 0.60–0.85	a b b
LM1	0.96	0.94 ± 0.04 0.90–0.97	1.35	1.27 ± 0.06 1.24–1.37	1.32	1.43 ± 0.12 1.14–1.63	a b b
LM2	0.82	0.79 ± 0.06 0.71–0.87	1.26	1.25 ± 0.02 1.20–1.26	1.3	1.31 ± 0.15 1.19–1.98	a b b
LM3	0.41	0.47 ± 0.11 0.33–0.63	0.91	0.93 ± 0.01 0.91–0.95	0.92	0.93 ± 0.03 0.84–0.97	a b b
LUA	3.09	3.10 ± 0.11 2.98–3.33	3.56	3.44 ± 0.11 3.40–3.63	3.5	3.58 ± 0.17 3.19–3.94	a b b
DDM	0.72	0.64 ± 0.08 0.55–0.84	0.90	0.96 ± 0.04 0.90–1.01	0.95	1.04 ± 0.10 0.92–1.21	a b b

(Supplementary Data SD6). The craniodental measurements of *N. tataticuli* in general are smaller (Table 2).

The coloration of the guard dorsal coat in *N. tataticuli* is homogeneous. Unlike *N. tataticuli*, the dorsal guard hairs in *N. evotis* are about 4–6 mm, showing multibanded hairs with a narrow distal band about 1 mm that is very dark grayish brown (10YR 3/2), a narrow pinkish white band about 1 mm (7.5YR 8/2) medially, and a wide dark gray band about 3 mm (7.5YR 3/0) proximally. *Notiosorex evotis* is distributed in the coastal plain of the Mexican states of Sinaloa, Nayarit, Jalisco, and Michoacán.

Measurements.—Table 3 provides external and craniodental values for the holotype as well as the mean and range for nine paratypes.

Distribution.—*Notiosorex tataticuli* ranges from west of the Colorado River into the Mojave Desert to the Transverse Range of California and Nevada in the United States and through all the Baja California peninsula in Mexico. Can be found from sea level up to 2,200 m a.s.l. in Sierra La Laguna (Fig. 6).

Ecology.—We consider *N. tataticuli* uncommon and difficult to collect. We found that individuals are abundant across most of their range; however, they appear to only occur in restricted

habitats. The largest number of specimens were collected in the cooler months, in areas with strong moist winds from the sea. They are most abundant in areas near bodies of water or with vegetation cover. Specimens that we kept alive for various months showed a preference for consuming Arachnida, mainly scorpions, and avoid beetles. We found that *Notiosorex* killed all the scorpions introduced in a terrarium and ate them later if the body size of the scorpion was no greater than twice that of the shrew (Camargo and Álvarez-Castañeda 2019b). One lactating female was collected in July 2015 (CIB 27565) and a second in January 2016 from the same locality (CIB 27501).

Notiosorex tataticuli is associated with heterogeneous types of vegetation. In the Sierra de la Laguna it occurs in pine (*Pinus cembroides*), madrone (*Arbutus xalapensis*), brandegee oak (*Quercus brandegeei*), and agaves (*Agave promontorii*). In aridlands it was taken in sarcocaule scrub (Garcillán et al. 2012); Limberbush (*Jatropha cuneata*), Arizona Nettlespurge (*J. cinerea*), cardon (*Pachycereus pringlei*), pitaya (*Stenocereus gummosus*), peninsular holdback (*Caesalpinia peninsualris*), and gobernadora (*Larrea divaricata*). On the coast it was found in association with red mangroves (*Rhizophora mangle*) and black mangroves (*Avicennia germinans*). In the oasis of Comondú, Todos Santos, they were found in riparian vegetation and tropical deciduous forest. *Notiosorex tataticuli* is syntopic with *Chaetodipus ammophilus*, *C. arenarius*, *C. rudinoris*, *C. spinatus*, *Dipodomys merriami*, *Neotoma bryanti*, *Peromyscus maniculatus*, and *P. eva*.

Shrews were collected with pitfall traps under a shrub-dominant vegetation of sarco crasicaule (Garcillan et al. 2012); palo Adan (*Fouquieria diguetii*), peninsular palo verde (*Parkinsonia florida*), cardón (*P. pringlei*), and choya (*Cylindropuntia cholla*).

Etymology.—The species name *tataticuli* means "father Ticul," and is composed by *tata*, a Tarasco word meaning father, and *Ticul*, in honor of José Ticul Álvarez Solórzano. José Ticul Álvarez Solórzano had an outstanding career in mammalogy in Mexico; his research contributed to the understanding of the systematics and taxonomy of recent and Pleistocene mammals and reptiles of México.

Notiosorex tataticuli ocanai new subspecies

Holotype.—CIB 27881, an adult female collected by Issac Camargo (original number 614) on 21 November 2015 at Mexico: Baja California; 22.5 km S San Quintin (30°22′17″N, −115°51′52″W). The specimen consists of a museum study skin with accompanying cranium and mandibles deposited at Centro de Investigaciones Biológicas del Noroeste, plus liver tissue preserved in 95% ethanol; all body parts are in good condition (Fig. 5).

Paratypes.—Five individuals from the type locality: CIB 27880, 27882, 32017–32019 (see Appendix I for localities).

Diagnosis.—Notiosorex t. ocanai is dorsally dark gray (7.5YR 4/1), underparts gray (7.5YR 5/1), and tail dark brown (10YR 2/1). Skull and body characteristics of *N. t. ocanai* are similar to those of *N. t. tataticuli* (Fig. 5; Table 3). The differences relate to the shorter size, condylobasal length in average less than 17.0 mm, length of unicuspid toothrow on average less than 1.5 mm, and darker coloration of *N. t. ocanai* (Fig. 4).

Comparison.—Notiosorex t. ocanai can be distinguished from *N. t. tataticuli* by a darker pelage color than *N. t. tataticuli*: the dorsal pelage coloration is dark gray (7.5YR 4/1) compared to light gray (7.5YR 7/1), underparts gray (7.5YR 5/1) versus pinkish gray (7.5YR 6/2) to pinkish white (7.5YR 8/2), and tail from brown (7.5YR 4/2) to dark brown (10YR 2/1) compared to dark brown (10YR 2/1; Table 4). *Notiosorex t. ocanai* in average is smaller (Table 3).

Measurements.—Table 3 provides external and craniodental values for the holotype as well as the mean and range for five paratypes.

Distribution.—Notiosorex t. ocanai is distributed in the northern part of the Baja California peninsula, California, and likely western Nevada; its eastern limit could be the Colorado River (Fig. 6). Habitat includes chaparral and pine forests of northern Baja California peninsula in México and California, United States. In California, it is widespread within the coastal sage scrub, but it was relatively abundant in only a few localities, associated with desert scrub, riparian desert, mixed chaparral, and piñon-juniper habitats (Armstrong and Jones 1972). The San Quintín plain of Baja California includes flat areas with deep soil and shrubs, and El Rosario is associated with marshy shrubland. In Cataviña and Punta Prieta, this species lives in a transition zone from the coastal deserts of the Gulf of California to the center of the peninsula.

Ecology.—Notiosorex t. ocanai is associated with heterogeneous types of chaparral vegetation dominated by *Larrea tridentata*. This subspecies was found associated with the mammal species *Sorex ornatus*, *N. bryanti*, *P. maniculatus*, *P. fraterculus*, and *Reithrodontomys megalotis* (Camargo and Álvarez-Castañeda 2019a).

Etymology.—This name honors Aurelio Ocaña for his exemplary career in mammalogy. Aurelio Ocaña was a close collaborator of José Ticul Álvarez Solórzano for more than 30 years. He is a Mexican collector who has made significant

Table 4.—Description of coloration of three subspecies of *Notiosorex tataticuli* west of the Colorado River. Keys and color were taken with Munsell Soil Color Charts (Munsell Color Co. 1975), dorsal head, dorsal back, ventral back, lateral medial region of the body.

Subspecies	Dorsal head	Dorsal back	Dorsal back	Lateral medial
Baja California Sur	7.5YR 6/3	7.5YR 6/3	7.5YR 6/2 to 7.5YR 8/2	7.5YR 6/2 to 7.5YR 8/2
N. t. tataticuli	light gray	light gray	pinkish gray to pinkish white	pinkish gray to pinkish white
California and Baja California	7.5YR 4/1	7.5YR 4/1	7.5YR 5/1	7.5YR 4/1
N. t. ocanai	dark gray	dark gray	gray	dark gray
San Martin Island	7.5YR 2.5/3	7.5YR 2.5/3	7.5YR 7/8	10YR 2/2
N. t. arroyoi	very dark brown	very dark brown	reddish yellow	dark brown

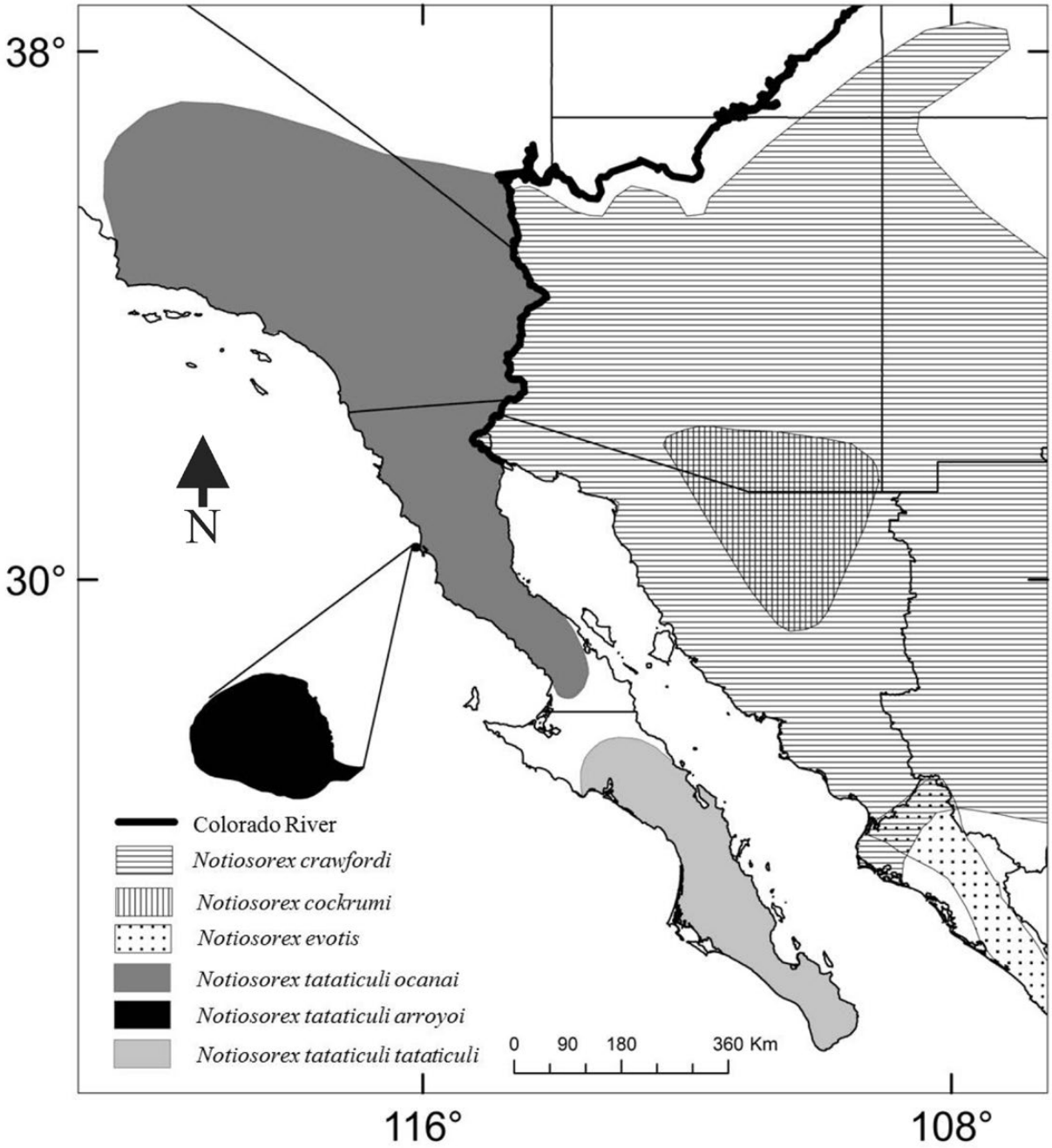

Fig. 6.—Distribution map of the species of *Notiosorex*. The area marked by horizontal lines represents *N. crawfordi*; vertical lines correspond to *N. cockrumi*; and the dotted area, to *N. evotis.* The proposed taxonomy of the populations west of the Colorado River, including the three subspecies of California and the Baja California peninsula, is shown as follows: dark gray for *N. t. ocanai*, black for the insular population of *N. t. arroyoi*, and light gray for *N. t. tataticuli*.

contributions to the knowledge of recent and Pleistocene mammals in Mexico.

Notiosorex tataticuli arroyoi new subspecies

Holotype.—CIB 32011, an adult female collected by Issac Camargo (original number 987) on 19 October 2017 at Mexico: Baja California; Isla San Martín (30.4900°N, −116.1100°W, 75 m a.s.l.). The specimen consists of a museum study skin with accompanying cranium and mandibles deposited at Centro de Investigaciones Biológicas del Noroeste, plus liver tissue preserved in 95% ethanol; all body parts are in good condition.

Paratypes.—Ten individuals from the type locality CIB 24050–24054, 32012–32016 (see Appendix I for localities).

Diagnosis.—Notiosorex t. arroyoi is smaller and darker than *N. t. tataticuli* and *N. t. ocanai*. Skull characteristics are similar to those of *N. t. tataticuli* (Fig. 5). In the lower jaw, height of articular condyle less than 2.5 mm. Teeth are significantly smaller compared to *N. t. tataticuli* and *N. t. ocanai* (Table 3). Length of U1–M3 less than 6.0 mm, and m2 (> 65%), m3 (> 50%), and

the depth of dentary at m1 (> 70%). It has a distinctive coloration, dorsally very dark brown (7.5YR 2.5/3), underparts reddish yellow (7.5YR 7/8), with a dark gray tail (5YR 3/1; Table 4).

Comparison.—Notiosorex t. arroyoi can be distinguished from *N. t. tataticuli* by its significantly smaller size (Table 3).

Notiosorex t. arroyoi is darker than *N. t. tataticuli.* Dorsal pelage coloration is light gray (7.5YR 7/1) versus very dark brown (7.5YR 2.5/3), underparts from pinkish gray (7.5YR 6/2) to pinkish white (7.5YR 8/2) compared to reddish yellow (7.5YR 7/8), and tail from dark brown (10YR 2/1) to brown (7.5YR 4/2) versus very dark gray (5YR 3/1; Table 4).

Notiosorex t. arroyoi can be distinguished from *N. t. ocanai* by its significantly smaller size (Table 3). *Notiosorex t. arroyoi* is darker than the specimens of *N. t. ocanai*, dorsal pelage dark gray (7.5YR 4/1) compared to very dark brown (7.5YR 2.5/3), underparts gray (7.5YR 5/1) versus reddish yellow (7.5YR 7/8), and tail dark brown (10YR 2/1) compared to very dark gray (5YR 3/1).

Measurements.—Table 3 lists external and craniodental values for the holotype as well as the mean and range for 10 paratypes.

Distribution.—Notiosorex t. arroyoi is known only from San Martín Island, off the western coast of the Baja California peninsula (Fig. 6).

Ecology.—San Marín island is approximately 1.5 km in diameter, with an area of 318 ha, and surrounded by cliffs up to 4.5 m, except on the southeastern side, where there is a small sandy beach and tidal lagoon. The island is part of a volcanic belt composed of Tertiary andesite and basalt, with little soil on most of the island (Camargo et al. 2016). The island is in the Upper Sonoran life zone and covered by dense Californian coastal scrub vegetation (Pase and Brown 1994), including the cacti *Myrtillocactus cochal* and *S. gummosus*, lichens, shrubs, and suffrutescent perennials (*Encelia californica* and *Euphorbia misera*), as well as the conspicuous succulents *Dudleya anthonyi* and *D. cultrata* (Junak and Philbrick 1994). Other mammal species found on the island are *Neotoma bryanti martinensis*, an island endemic subspecies (Patton et al. 2008) that is considered extinct (Cortés-Calva et al. 2001), and the endemic deer mouse *Peromyscus maniculatus exiguus* (Cortés-Calva et al. 2001).

Etymology.—We honor Joaquín Arroyo Cabrales for his outstanding career in the mammalogy of Mexico of current and Pleistocene mammals. Joaquín Arroyo Cabrales was one of the most prominent students of José Ticul Álvarez Solorzano.

Key to the subspecies of *Notiosorex tataticuli*

1. Dorsal coloration light gray. Condylobasal length on average greater than 17.0 mm; length of unicuspid toothrow on average greater than 1.5 mm. Range in the southern part of the Baja California peninsula (from latitude 28ºN south) ..... *N. t. tataticuli*
   1a. Dorsal coloration darker, brownish gray or dark gray. Condylobasal length in average less than 17.0 mm; length of unicuspid toothrow on average less than 1.5 mm 2
2. Dorsal coloration dark brownish gray. Length of U1–M3 greater than 6.0 mm; height of articular condyle less than 2.5 mm. Range restricted to San Martín Island ..... *N. t. arroyoi*
   2a. Dorsal coloration dark gray. Length of U1–M3 less than 6.0 mm; height of articular condyle greater than 2.5 mm. Range in the northern part of the Baja California peninsula (from latitude 29ºN north), California and probably southern Nevada and northwestern Arizona ..... *N. t. ocanai*

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Supplementary Data

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

Supplementary Data SD1.—Sketch of the four anatomical regions used for the colorimetry analysis of *Notiosorex*. Dorsal head (DH). Dorsal back (DB). Ventral back (VB). Lateral medial region of the body (LM).

Supplementary Data SD2.—One-way ANOVAs from all craniodental characters of *Notiosorex* species and three morphotypes from west of the Colorado River. The post hoc Holm–Sidak test was used to access the statistical significance of the comparisons in skull and jaw of desert shrews. The asterisk highlights the existence of significant differences.

Supplementary Data SD3.—Eigenvalues and variance from principal component analysis for 22 log-transformed craniodental variables within *Notiosorex* shrews living west of Colorado River.

Supplementary Data SD4.—Graph of CV1 and CV2 extracted from the analysis of morphometric variation data of skull and jaw of 22 variables for *Notiosorex* shrews living west of the Colorado River. Southern population (white), northern population (light gray), and San Martin Island (dark gray).

Supplementary Data SD5.—Factor coefficients for trichromatic color variables X, Y, and Z for each *Notiosorex* western to the Colorado River of the study skin for the first two PC axes. Eigenvalues and the proportion of variance explained are also given; dorsal head (DH), dorsal back (DB), ventral back (VB), lateral medial region of the body (LM).

Supplementary Data SD6.—Comparasion of lateral view and ventral in *Notiosorex* species, in lateral view solid

arrows show the small paraoccipital process lying against the exoccipitals, and in ventral view the solid arrows show the glenoid gossa. (A) Skull of *N. crawfordi* (KU 125360). (B) *N. tataticuli* (CIB 23981). (C) *N. evotis* (KU 100319). (D) *N. villai* (KU 54933).

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Appendix I

Specimens examined. Specimens included in the molecular analysis are in parentheses with their associated GenBank accession numbers listed. Specimens included in the morphometric analysis are indicated in bold. Specimens examined in the color variation analysis are underlined. Museum acronyms (Dunnum et al. 2018) are as follows: Angelo State Natural History Collection (ASNHCK), Centro de Investigaciones Biológicas del Noroeste (CIB), University of Kansas, Natural History Museum and Biodiversity Research Center (KU), University of California, Berkeley, Museum of Vertebrate Zoology (MVZ), and the Museum of Texas Tech University (TTU).

Taxon	State	Locality	Specimens	GenBank accession number
Blarina brevicauda	Maryland	Patuxent Wildlife Research Center	(MVZ161314)	AF534123, MN061456
Cryptotis mexicanus	Veracruz	3.1 km S Puerto del Aire	(MVZ163012)	AB175143, MN061457
Notiosorex cockrumi	Arizona	Leslie Canyon National Wildlife Reserve	(TTU49928, TTU49909, TTU49922, TTU49924, TTU49930, ASK10653, TTU49918, TTU49917)	TK49909, TK9910, TK49912, TK49917, TK49918, TK49922, TK49924, TK49926, TK49928–TK49931, MN061466, MN061467, MK965949, MK965955
		SE Tucson, Exit 275	(TTU90852)	MN061475, MN061476, MK965956, MK89549506
	Sonora	14.6 mi E Mazocahui	(MVZ148830)	MN061469, MK965947
		4.1 mi NW Nácori Chico	(MVZ148831)	MK965948
Notiosorex crawfordi	Arizona	Guadalupe Canyon, 30 mi E Douglas	**KU145261**	
		Leslie Canyon National Wildlife Reserve	(TTU82991, TTU82993)	TK49919, TK49921
	Chihuahua	2 mi W Miñaca	**KU109475**	
	Colorado	Mesa Verde National Park	**KU105109**	
		Phantom Cayon, Eightmile Creek	**KU125350**, **KU125360**	
		9.9 mi NW Aguilar, Las Animas	(MVZ122087)	MN061478
	New Mexico	Vicinity of Antelope Pass	(MVZ191470, MVZ191472)	AY611573, MK965957
		9, 7 mi E Hwy	(MVZ176473, MVZ176474)	MN061479, MN061480
	Texas	Chaparral Wildlife Management Area	(TTU80965)	MN061468, MK965950, TK84584, TK84585
		Devils River State Natural Area	(ASK4277)	MN061477, MK965951
		4.5 mi W San Angelo	(ASK4530)	ASK4350, MK965954, TK22986
		5 mi N, 9.8 mi W Mertzon	(ASK4571)	MN061474, MK965952, MN061471
Notiosorex evotis	Jalisco	21 mi SW Guadalajara	**KU42583**, **KU42584**	
		6.41 km NW Soyatlán del Oro	**CIB29625**	
	Sinaloa	1 mi S El Cajón	**KU100319**	
		10 km S, 38 km E Sinaloa	**KU125477**	
		19 km W Choix	**CIB27876, CIB27877, CIB27878, CIB28196, CIB29201**	
		20 km N, 5 km Badiraguato	**KU96419**	
		44 km NE Sinaloa	**KU89998**	
		5 mi NW El Carrizo	**KU105409**	
		5.6 km N, 3 km W Villa Unión	**CIB27875**	
		Rosario	**KU90581**	
		El Fuerte	**KU75184**	
		Isla Palmito del Verde, 6 mi NW Teacapan	**KU98880**	

Appendix I Continued

Taxon	State	Locality	Specimens	GenBank accession number
Notiosorex tataticuli arroyoi	Baja California	Isla San Martín	**(CIB24050, CIB24051, CIB24052, CIB24053, CIB24054), CIB32011, CIB32012, CIB32013, CIB32014, CIB32015, CIB32016**	MK955168–MK955170, MN061462–MN061464, MN061465, MK965940–MK965944
Notiosorex tataticuli ocanai	Baja California	1 km SE Cataviña	**CIB27883**	
		10 mi SE El Rosario	(MVZ154748)	MK955167
		14 mi S San Quintín, Playa El Socorro	(LACM91027, LACM91029)	AB91027, AB91029
		2.6 km S Punta Prieta	**CIB27884**	
		22.5 km S San Quintín	**CIB27880, CIB27881, CIB27882, CIB32017, (CIB32018, CIB32019)**	MK895444, MN061488, MN06489
		9 mi S Rosarito	(MVZ154747)	MVZFC4830, MN061459, MK965931, MK895495
	California	Camp Pendleton	(MVZ221962)	MK965945
		14 mi S Kelso	(MVZ175997)	MN061488
		14805 Sierra Highway	**KU160254**	
		Lakeside, head of Wildcat Canyon	**KU92627**	
Notiosorex tataticuli tataticuli	Baja California Sur	1.2 km S, 6.6 km E El Sargento	(CIB27500, CIB27499), CIB27501	MK895492, MK895493
		1.5 km NW Misión Santa Gertrudis	**CIB27885**	
		12.2 km S km 15.2 W Santa Rita	(CIB24056)	MK965958
		28 km N, 52 km W Las Pocitas	(CIB18893)	MK955166, MK965938
		3 km N, 2.6 km W Los Planes	CIB23075	
		3 km S, 8.7 km W La Paz	(CIB20928)	MK955172
		3.9 km N, 6.5 km W El Sargento	(CIB23270) CIB23984, CIB27567, CIB29341, CIB29342	MN061460
		4 km N, 6.6 km W El Sargento	**CIB23980, (CIB23981) CIB23982, CIB23983, CIB25225, CIB25226, CIB27873, CIB27886, CIB29343, CIB29344, CIB31573**	MK955165, MN061461, MK965935, MK965935
		4 km S, 7 km W El Sargento	CIB31572	
		5 km N, 30 km W Santa Rita	(CIB24055)	MN6147782
		6 km S, 16 km E San Juanico	CIB27498, CIB27872	
		6 km SE Los Planes	CIB32169, CIB32492, CIB32493	
		7 km N, 4.5 km W El Sargento	**CIB27563**, CIB27564, **CIB2765, CIB29345, CIB27566, CIB23979**	
		9 km N, 28 km E Santo Domingo	CIB28685	
		9 km S Todos Santos	(CIB23392)	MK955162, MK965932
		Chametla, 8 km W La Paz	(CIB21408)	MK955171
		El Comitán, 17.5 km W La Paz	CIB27502, CIB27874	
		El Edén, 4 km N, 21 km W Santiago	**(CIB22676, CIB22677)**	MK955163, MK955164, MK965933
		La Calambrina, Sierra de La Laguna	CIB20867	
		Palo extraño	**(CIB22675)**	MK965934
		San Bartolo	**CIB27503**	
Notiosorex villai	Tamaulipas	Palmillas	**KU54933**	
Sorex trowbridgii	California	3 km SE Mud Lake	(MVZ223020)	MVC223020, MN061458