Journal of Mammalogy, 100(6):1847–1864, 2019
DOI:10.1093/jmammal/gyz130

Version of Record, first published online 20 September 2019, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

Phylogeography and taxonomic revision of Nelson's pocket mouse (*Chaetodipus nelsoni*)

Sean A. Neiswenter,* David J. Hafner, Jessica E. Light, Gabriella D. Cepeda, Kathleen C. Kinzer, Lois F. Alexander, and Brett R. Riddle

School of Life Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, MS4004, Las Vegas, NV 89154, USA (SAN, GDC, BRR)
Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131, USA (DJH)
Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA (JEL)
Biology Department, Normandale Community College, 9700 France Ave. S, Bloomington, MN 55431, USA (KK)
Department of Biological Sciences, College of Southern Nevada, Henderson, NV 89002, USA (LFA)

* *Correspondent:* sean.neiswenter@unlv.edu

Chaetodipus nelsoni occurs on rocky substrates across the Mexican Altiplano. We investigated phylogeographic diversity within the species using morphologic, karyotypic, and molecular data. Data from nuclear (AFLP) and mitochondrial DNA support three distinct genetic groups with minimal substructuring coincident with biogeographic barriers previously identified in the Chihuahuan Desert and drainage basins of the Altiplano. We examined the morphological and karyotypic data in light of the molecular data. The results support recognition of three species within the currently accepted widespread *C. nelsoni*: 1) *C. nelsoni* restricted to a distribution centered on the El Salado River Basin; 2) elevation of *C. n. collis* to species, with two subspecies: one centered on Trans-Pecos Texas, the other on the Mapimí Basin (new subspecies); and 3) recognition of a new species, *C. durangae*, centered on the Nazas Basin and upper Río Mezquital drainage.

Chaetodipus nelsoni tal como actualmente reconocido está distribuido en sustratos rocosos a lo largo de Altiplano Mexicano. Investigamos la diversidad filogeográfica enrecognition la especie usando datos morfológicos, cromosómicos, y moleculares. Los datos de ADN nuclear (AFLP) y mitocondrial apoyan el reconocimiento de tres grupos genéticos distintos con subestructuración interna mínima, grupos que coinciden con la presencia de barreras biogeográficas previamente identificadas en el desierto Chihuahuense y en las cuencas del Altiplano. Examinamos los datos morfológicos y cromosómicos a la luz de los datos moleculares. Nuestros resultados se adhieren al reconocimiento de tres especies dentro de la actualmente reconocida y generalmente distribuida *C. nelsoni*: 1) *C. nelsoni*, con una distribución restringida a la cuenca del Río El Salado; 2) elevamos *C. n. collis* a especie, con dos subespecies distribuidas por una parte en el Bolsón de Mapimí y por otra en el Texas Trans-Pecos; 3) por último, reconocemos una nueva especie, *C. durangae*, cuya distribución se centra en la Cuenca del Río Nazas y la Cuenca alta del Río Mezquital.

Key words: amplified fragment length polymorphisms, chromosomes, Heteromyidae, Mexican Altiplano, mitochondrial DNA, morphometrics

Nomenclatural statement: A Life Science Identifier (LSID) number was obtained for this publication: urn:lsid:zoobank.org:pub:6AD9D26B-4C12-4941-BF8E-21BF09227D67

Nelson's pocket mouse (Rodentia: Heteromyidae: *Chaetodipus nelsoni*) has a widespread distribution and broad elevational range across the Altiplano (Altiplanicie Mexicana) of northern Mexico, where it commonly is found in association with rocks or rocky soils. It is a member of a clade of coarse-haired, saxicolous species of the Mexican mainland (apart from the Baja California Peninsula) along with *C. intermedius*, *C. artus*, and *C. goldmani* (Alexander and Riddle 2005). It morphologically resembles *C. intermedius*, with which it is contiguously distributed in Trans-Pecos Texas (Wilkins and Schmidly 1979) and on alternate sides of the Río Conchos in neighboring Chihuahua (Anderson 1972; Fig. 1a). The center of distribution of *C. nelsoni* coincides with the principal endorheic or closed basins (bolsones) of the arid Altiplano (Fig. 1a): 1) the El Salado Basin; 2) the Nazas-Aguanaval Basin (drained by those two rivers, both emptying into the former Laguna, now Desierto, Mayrán, of the Bolsón Mayrán); and 3) the Mapimí Basin. As depicted by Hall (1981; Fig. 1a), the southern subspecies (*C. n. nelsoni*) occupies the El Salado and Nazas-Aguanaval basins, spilling over into the upper edges of adjoining river drainages, while the northern subspecies (*C. n. canescens*) descends from the northern rim of the Mapimí Basin across the Río Grande into Trans-Pecos Texas. Rediscovery of a long-unreported population in New Mexico (Geluso and Geluso 2004), records found in museum collections, and the first record from Guanajuato (reported herein) expand the known distribution of the species (Fig. 1b; Supplementary Data SD1).

The most common and widely distributed chaetodipine pocket mouse across the Altiplano, *C. nelsoni* generally avoids sandy soils but occurs in an otherwise broad array of arid habitats from 400 to 2,450 m in elevation. It has the largest distribution in the subgenus *Chaetodipus* (which excludes *C. hispidus*, subgenus *Burtognathus*). While the extensive distribution, variety of occupied habitats, and elevational range of the species likely result in extensive geographic variation, only slight and subtle morphological differences between the two recognized subspecies have been reported. Where the two are contiguously distributed in southern Coahuila, *C. n. nelsoni* has a somewhat darker pelage, larger rostrum, and smaller mastoids than *C. n. canescens* (Baker 1956). Different diploid numbers (2n) have been reported for the two subspecies: 2n = 46 in *C. n. nelsoni*, and 2n = 48 in *C. n. canescens* (Patton 1970; Modi 2003).

The geographic transition between the two subspecies of *C. nelsoni* corresponds roughly to the Southern Coahuila filter-barrier (SCFB; filter-barrier "3" in Fig. 1b) as originally defined by Baker (1956) and in more detail by Hafner et al. (2008). Composed of the Río Nazas on the west, the Bolsón Mayrán in the center, and a western extension of the Sierra Madre Oriental on the east, the SCFB marks the division between two major subregions of the Chihuahuan Desert: the Altiplano Norte and Altiplano Sur of Arriaga et al. (1997), or the Coahuilan and Zacatecan of Hafner and Riddle (2011). As currently recognized, *C. n. canescens* spans the Río Grande filter-barrier (filter-barrier "1" in Fig. 1b; Baker 1956), which marks the division between the Chihuahuan, Coahuilan, and

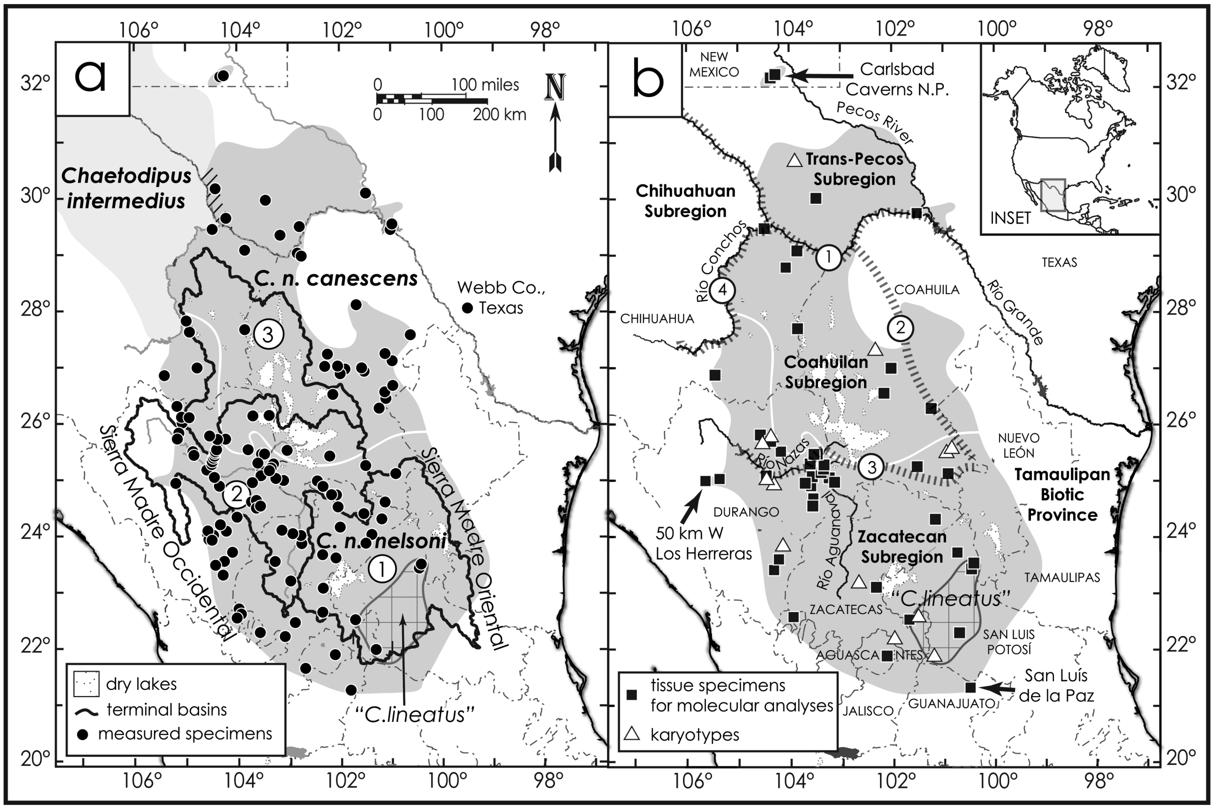

Fig. 1.—(a) Distribution of *Chaetodipus nelsoni* ssp. (darker shading), *C. intermedius* (lighter shading), and *C. lineatus* (cross-hatched area) in northern Mexico and adjacent Texas and New Mexico, indicating localities of measured specimens and additional museum records. Major endorheic basins of the Mexican Altiplano: 1) El Salado; 2) Nazas-Aguanaval; and 3) Mapimí. The record in Webb Co., Texas, is of questionable provenance (see text). (b) Localities of tissue specimens used in molecular analyses and of karyotypes; new marginal records (arrows); and major biogeographic regions and filter-barriers: 1) Río Grande; 2) Sierra del Carmen – Sierra Madre Oriental; 3) Southern Coahuila; and 4) Río Conchos. Inset: location of study area.

Trans-Pecos subregions of the Chihuahuan regional desert (Hafner and Riddle 2011), and the subspecies extends from the Chihuahuan subregion across the Sierra del Carmen-Sierra Madre Oriental filter-barrier (filter-barrier "2" in Fig. 1b; Baker 1956) into the Tamaulipan biotic province (Morrone 2005). Similarly, *C. n. nelsoni* extends well north across the Río Nazas into south-central Chihuahua. Baker and Greer (1962:97) concluded that "The canyon of the Río Nazas does not seem to be a barrier to [*C.*] *nelsoni*." Subtle morphological variation across such a broad area that is divided by multiple filter-barriers, coupled with karyotypic variation, suggests that morphological homoplasy may mask cryptic genetic structure within this widespread species such that additional subspecies, or even species, may be present.

We evaluated mitochondrial and nuclear DNA complements, non-preferentially stained karyotypes, and cranial morphometric variation within the species to determine the impacts (if any) of filter-barriers between major biogeographic regions on the phylogeographic history, and hence genetic composition of *C. nelsoni*. Considering the wide variety of species and subspecies concepts employed by different researchers, it is important to define our concepts. We define "species" as monophyletic, diagnosable, and genetically isolated clades, following Hafner et al. (2005, 2011) and Mathis et al. (2013). We define subspecies as monophyletic infraspecific lineages that exhibit "opportunities for sustained evolutionary divergence," following Mathis et al. (2014:762). For delineating and diagnosing both species and subspecies, we use as our primary tools a combination of nuclear and mitochondrial sequence data, and then evaluate non-preferentially stained karyotypes and cranial morphology in light of our defined clades. Our subspecies concept explicitly disregards body size and pelage coloration, because these characters often show plastic responses to environmental factors. We examine cranial morphometrics to determine whether morphology tracks phylogeny, to assign museum specimens lacking molecular data to genetic groups, and to evaluate variation over geographical environments. Overall, this multidisciplinary approach using molecular, karyotypic, and morphological data allows a rigorous assessment of *C. nelsoni* taxonomy and phylogeography.

MATERIALS AND METHODS

Specimens examined.—We examined a total of 470 specimens of *C. nelsoni* from 142 localities (Appendix I; Supplementary Data SD2). Localities included a rediscovered peripheral population and several extensions of the known range as depicted in Hall (1981; peripheral records noted in Fig. 1). Geluso and Geluso (2004) rediscovered a population of *C. nelsoni* within Carlsbad Caverns National Park in the Guadalupe Mountains of southeastern New Mexico that had not been detected since 1953 (Webb 1954). A specimen housed in the Museum of Texas Tech University (TTU 76121 collected in 1995) documents *C. nelsoni* at Arroyo El Triguero, 50 km W of Las Herreras [= Los Herreras], Durango, extending the species' distribution to 2,450 m elevation and to the western ridge of the Nazas Basin in the Sierra Madre Occidental. A specimen of *C. nelsoni* from San Luís de la Paz, Mineral de Pozos, Guanajuato (J. A. Fernández, Universidad Autónoma de Chihuahua, pers. comm., December 2015) extends the known distribution south into Guanajuato. Finally, Davis and Schmidly (1994) reported the species from Webb Co., Texas, based on a single specimen collected in 1969 (Texas A&M University, Kingsville, TAIU 233; now located at Texas A&M University, College Station, in the Biodiversity Research and Teaching Collections, TCWC 66810). Specimens collected for this study were captured in the wild under authority of Mexican Scientific Collecting Permit FAUT-0002 issued to F. A. Cervantes, National Park Service Collecting Permit CAVE-2003-SCI-0013 issued to DJH, and scientific collecting permits from the New Mexico Department of Game and Fish and the Texas Parks and Wildlife Department issued to DJH, using standard trapping methods approved by the American Society of Mammalogists (Sikes et al. 2016) and the Institutional Animal Care and Use Committees at the University of New Mexico and the University of Nevada, Las Vegas.

Molecular analyses.—We included 71 specimens from 32 localities ($\bar{n} = 2.2$) in the AFLP analyses and 129 specimens from 42 localities ($\bar{n} = 3.1$) in the mtDNA analyses (Fig. 1b; Appendix I). DNA was extracted using DNeasy Kits (Qiagen Inc., Germantown, Maryland) following manufacturer's instructions. Polymerase chain reaction (PCR) conditions for the mtDNA cytochrome oxidase subunit 3 gene (*COIII*) were 95°C for 1 min, 55°C for 1 min, and 72°C for 1 min, for 30 cycles. Genes were amplified and sequenced using PCR primers *COIII*, H8618, and L9232 (Riddle 1995). Sequences were run on an ABI 3730 automated sequencer (Applied Biosystems, Foster City, California), checked for ambiguous base calls in Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, Michigan), and aligned in MEGA7 (Kumar et al. 2016) with final corrections by eye for alignment integrity. Because *COIII* is a protein-coding gene, it was converted to amino acids to ensure no stop codons were present, an indication of a possible nuclear copy of the mitochondrial gene. Pair-wise distances and *SE* were calculated using MEGA7 (Kumar et al. 2016). *C. artus* (AY009260) and *C. goldmani* (AY009261) sequences were downloaded from GenBank and used as outgroup taxa for the mitochondrial phylogenies. All newly generated sequences were deposited in GenBank under accession numbers: MN163136–MN163261.

Amplified fragment length polymorphisms were generated using the ABI plant genotyping kit (Applied Biosystems) following manufacturer's protocol. Briefly, genomic DNA was digested with EcoRI and MSEI and oligonucleotides were ligated to the sticky ends of the fragments. An initial preamplification using proprietary ABI preamplification primers was followed by a selective amplification with two combinations of primers from the genotyping kit: EcoRI + AGC and MSEI + CAC; EcoRI + ACA, and MSEI + CTT. The selective amplifications were then sequenced on an ABI 3730 in the genomics facility at the University of Nevada, Reno. We performed the entire process twice, starting with the genomic DNA for approximately 9% of the samples to ensure reproducibility of amplicons. The replicated samples were chosen from different populations across the geographic range of *C. nelsoni* to represent the breadth of genetic diversity in the species. Fragment lengths were called by eye for the replicated samples using GENEMAP ver3.7 (Applied Biosystems). Only fragment lengths that could be reliably called between repeated samples were used to create bins to automatically call peaks in the other samples. All automatic peak calls were then confirmed by eye. This resulted in calling 38 loci for selective amplification primers AGC + CAC and 16 loci for ACA + CTT.

We estimated the number of populations (K) from the AFLP data using STRUCTURE 2.3 (Pritchard et al. 2000). We ran three replicate analyses from $K = 2$ to $K = 8$ for 2,000,000 generations following a 500,000 generation burn-in. We determined the optimum K using the method of Evanno et al. (2005) using Structure Harvester (Earl and von Holdt 2012; http://taylor0.biology.ucla.edu/structureHarvester/).

Prior to phylogenetic analysis of the *COIII* gene, PartitionFinder (Lanfear et al. 2012) was used to identify the best partitioning scheme and model of molecular evolution for each partition (with *COIII* codon positions designated as potential partitions). Three optimal partitions were identified with TrN + G, K81 + G, and HKY + I models of evolution selected for the *COIII* first, second, and third codon positions, respectively. Bayesian phylogenetic analysis was performed using MrBayes v.3.2.6 (Ronquist and Huelsenbeck 2003) in the CIPRES Science Gateway (Miller et al. 2010). This Bayesian analysis was run with random starting trees, 10 million generation runs with four incrementally heated chains (Metropolis-coupled Markov chain Monte Carlo—Ronquist and Huelsenbeck 2003), and sampled at intervals of 1,000 generations. Four runs were conducted simultaneously and independently, and 25% of the sampled trees were disregarded as burn-in. Resulting log files were examined in Tracer version 1.6.0 (Rambaut et al. 2014) to ensure that effective sample sizes for all parameters were sufficient and that all four chains reached convergence. Likelihood phylogenetic analysis was performed using RaxML (Stamatakis 2014), also in CIPRES (specifically, RAxML-HPC BlackBox), with three data partitions corresponding to each codon position and the GTRGAMMA model of evolution. Bootstrap (bs) analyses also were performed, allowing RAxML to stop bootstrapping automatically. All Bayesian and Likelihood trees were examined in FigTree 1.4.2. Clade support was assessed using Bayesian posterior probabilities (pp) and bs values.

Karyotypic analysis.—We examined 25 non-preferentially stained chromosomal preparations representing two localities of *C. n. canescens* (north and south of the Río Grande) and 11 localities within *C. n. nelsoni* (Fig. 1b). These included published karyotypes, our own preparations (prepared in the field using the procedure described by Hafner and Sandquist 1989; Appendix I), and photographs of chromosomal spreads (James L. Patton, University of California, Berkeley, pers. comm., September 2013). We determined 2n and fundamental number (FN) for all karyotypes. For two specimens of *C. n. canescens* (Texas—Patton 1970 and central Coahuila—Modi 2003), and 14 specimens of *C. n. nelsoni*, we determined the sex chromosomes (X- and Y-chromosomes) and measured autosomal chromosomes to determine the relative arm lengths and total lengths of metacentric, subtelocentric, and acrocentric chromosome pairs. The 14 *C. n. nelsoni* included seven specimens from north of the Río Nazas in Durango, six specimens from south of the Río Nazas in Durango, and the karyotype from southern Coahuila figured in Patton (1970).

Morphometric analyses.—Seven mensural cranial characters were recorded from 411 adult specimens (based on wear of permanent dentition) from 131 localities (Fig. 1a): greatest skull length (GL), maxillary breadth (MB), rostral breadth (RB), least nasal breadth (LNB), least interorbital breadth (IOB), interparietal breadth (IPB), and interparietal length (IPL). Multiple analysis of variance of four grouped populations with $n > 30$ ($\bar{n} = 43.3$) revealed no consistent secondary sexual dimorphism in any of the characters, therefore sexes were grouped for subsequent analyses. We grouped localities that were geographically close into 38 groups ($\bar{n} = 10.8$; Fig. 2a), ensuring that these group localities did not cross obvious geographic discontinuities and did not include multiple clades identified in the molecular or karyotypic analyses. The 38 group localities were secondarily grouped within drainage basin (within molecularly defined clades; $\bar{n} = 47.4$). All statistical analyses were conducted using SYSTAT 7.0 (Wilkinson 1997). Principal component analyses (PCA) and box plots of the first principal component (PC1) were employed to allow visual inspection of qualitative differences among cranial dimensions of grouped localities, and *t*-tests were used to compare adjacent grouped localities. Discriminant function analyses (DFAs) were employed to determine which characters were important in distinguishing among grouped localities and if pocket mice could be separated based on an a priori hypothesis of group membership in clades identified by molecular analyses.

RESULTS

Molecular analyses.—Analysis of AFLP data revealed that $K = 3$ was the best number of populations. Three groups were clearly delineated (Fig. 3b): group I south of the SCFB in the Nazas Basin; group II north of the SCFB and west of the Sierra del Carmen-Sierra Occidental Oriental filter-barrier; and group III containing remaining populations south of the SCFB. Nineteen of the 23 localities examined had a single dominant allele with a frequency > 0.93 (Fig 3a; Supplementary Data SD2). Exceptions were locality 3, with a frequency of 0.15 of the AFLP group I allele, and localities 9 (two populations) and 26, which have frequencies > 0.13 of the alternative (group II or group III) dominant allele (Fig. 3b).

MrBayes and RAxML phylogenetic analysis of 678 bp of the mtDNA *COIII* produced similar topologies (Bayesian phylogram shown; RAxML tree available upon request). After collapsing branches that were not supported with bs > 80% or pp > 0.95, three major clades were evident that correspond with the three groups identified in the AFLP analysis (compare Fig. 4 with Fig. 3). Additional localities (versus AFLP analysis)

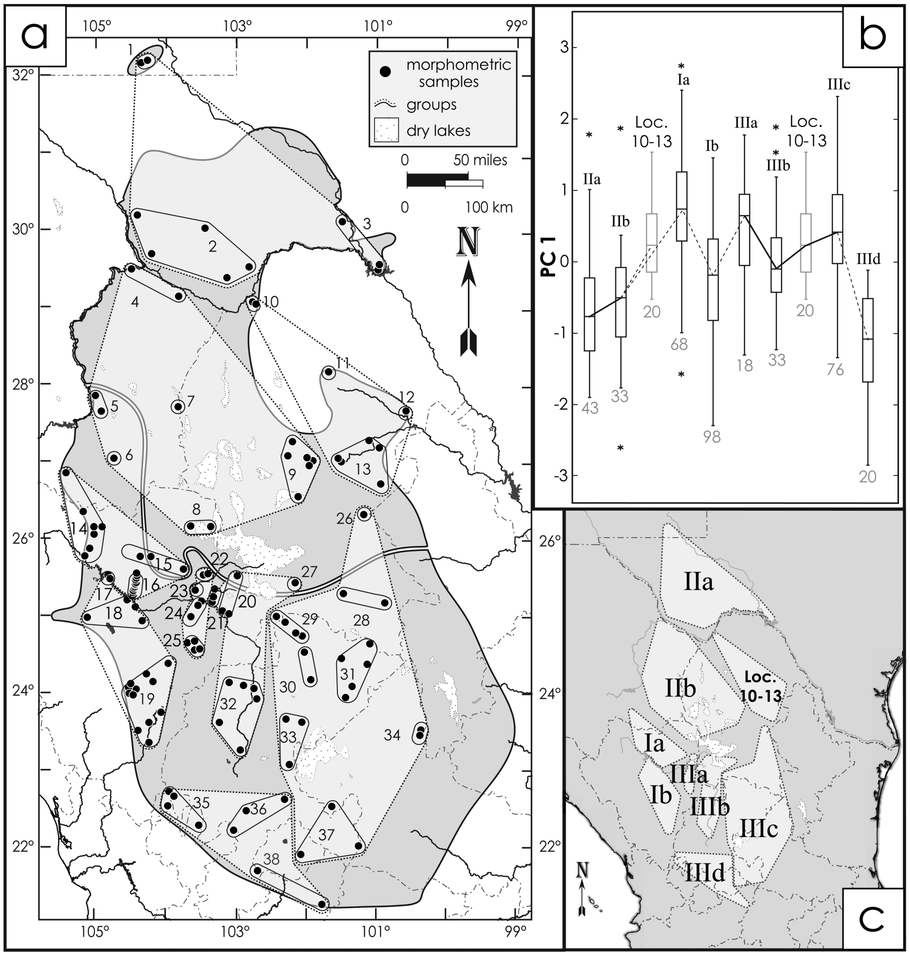

Fig. 2.—Grouping of localities for morphometric analyses: (a) initial grouping (solid lines) and secondary grouping within drainage basins (dotted lines) of localities within the distribution of *Chaetodipus nelsoni* (shaded region); group localities numbered as in Appendix I. (b) Box plots of PC1 values for drainage-basin groups; Loc. 10–13 group (light gray) lacks molecular or karyotypic data. Solid lines between medians indicate non-significant differences (> 0.05); dotted lines indicate significant differences between adjacent groups. (c) Distribution of drainage-basin groups shown in (a) and labeled as in (b).

extend clade I south into the headwaters of the Río Mezquital and clade III south into Guanajuato (Fig. 4b; Supplementary Data SD2). In contrast to the AFLP analysis, there was no mixture of mtDNA alleles in any population, including localities 9 (clade II) and 26 (clade III). Clade II was divided into two subclades, one north of the Río Grande in the Brazos-Conchos drainage of Trans-Pecos Texas (three localities), and the other south of the Río Grande in the Mapimí Basin (three localities) or in the Brazos-Conchos drainage (three localities). A subclade within clade I included all four localities north of the Río Nazas, but the localities south of the Río Nazas formed a polytomy. There was little geographic structure within clade III, although most (but not all) of the individuals and populations from within the El Salado Basin clustered together (Figs. 4a and 4b).

Karyotypic analyses.—All *C. nelsoni* karyotypes possessed a FN = 58 (58 autosomal arms), four or five pairs of medium-to-large metacentric autosomes, 14 or 16 pairs of acrocentric autosomes, two pairs of submetacentric or subtelocentric autosomes, one pair of microchromosomes, a metacentric X-chromosome, and a small acrocentric Y-chromosome (Fig. 5). Referring to the clades identified in the molecular analyses, clade III (δ form) had 2n = 46 with five pairs of metacentric and 14 pairs of acrocentric autosomes, whereas clades I and II had four pairs of metacentric and 16 pairs of acrocentric autosomes (variable chromosomes shown in Fig. 5b). Clades IIa and IIb appeared to possess identical karyotypes (α form), with three of the four pairs of medium-to-large metacentric autosomes larger than the fourth pair (as in the δ form), whereas in the karyotypes of clade I, two of the four pairs of medium-to-large metacentric autosomes were larger than the other two pairs (Fig. 5b). Finally, the X-chromosome in karyotypes of clade I from the population south of the Río Nazas (γ form) was noticeably larger than that of the population north of the Río Nazas (β form).

Morphometric analyses.—A one-way MANOVA performed on the untransformed morphometric data for the three molecularly defined clades was significant for all three groups (Wilks' $\lambda = 0.58$, $F_{14,754} = 16.81$; Pillai's Trace = 0.47, $F_{14,756} = 16.70$; Hotelling's Trace = 0.63, $F_{14,752} = 16.92$; $P = 0.0001$ for all three tests). Exploring Tukey's honestly significant difference

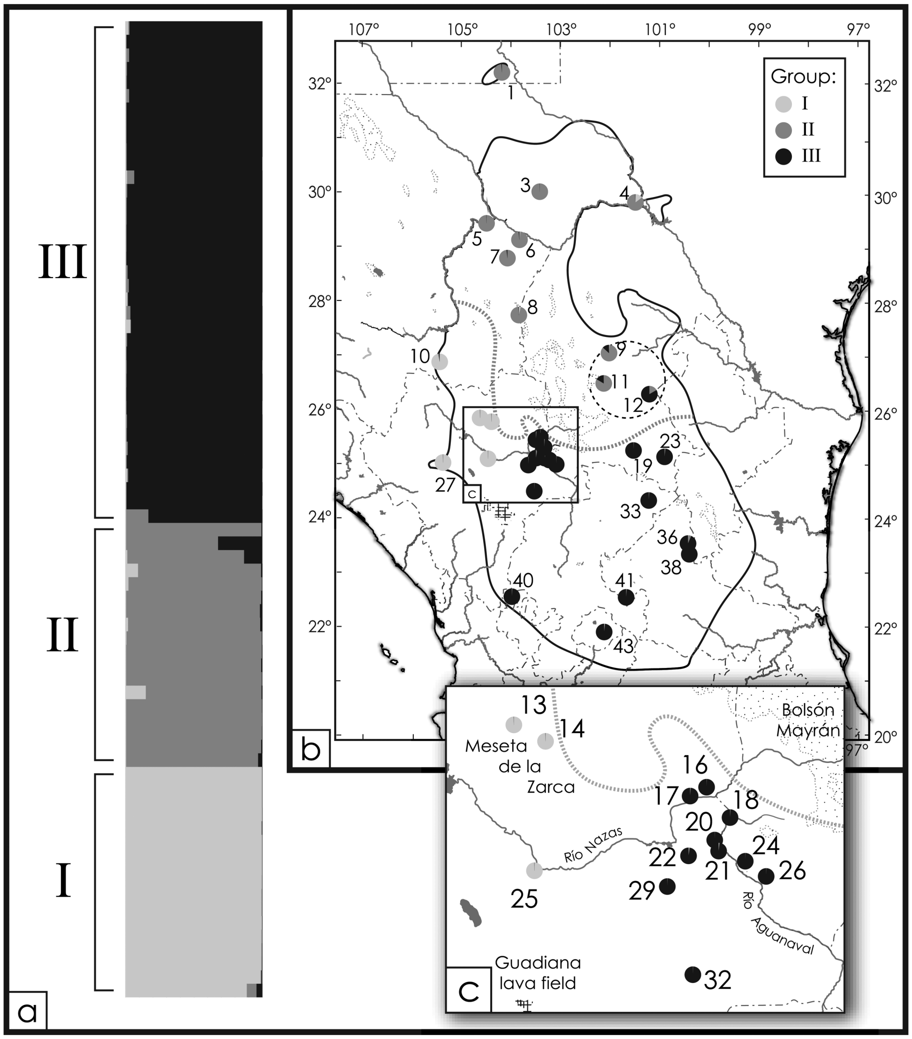

Fig. 3.—(a) Bar graph of the results of the exploratory AFLP analysis in STRUCTURE version 2.2.3 (Pritchard et al. 2000) for $K = 3$. Each bar represents the probability of a single individual belonging to one of the three groups. (b) Distribution of populations assayed in the AFLP analysis. Pie-diagrams for each population are based on the bar graph in (a), with corresponding shading for each of the clades. The dotted circle indicates a region of contact between clades II and III in which alternate alleles are shared between three localities. Solid line outlines the distribution of *Chaetodipus nelsoni*; hatched line is division between recognized subspecies. (c) Enlarged view of area in (b) showing localities relative to the Meseta de la Zarca, Guadiana (= Durango) lava field, Bolsón Mayrán, Río Nazas, and Río Aguanaval.

post hoc tests on the MANOVA revealed several differences between members of the three clades. On average, members of clade I were larger than those of clade II for five of the seven variables ($P = 0.000$–0.005), but smaller for RB ($P = 0.01$). Members of clade III were larger than those of clade II for five of the seven variables ($P = 0.000$–0.009), but smallest for IPL ($P = 0.000$); members of clades I and III differed only in IPL (clade I > clade III; $P = 0.000$). Members of clade II were smallest for five of seven variables ($P = 0.000$–0.009), but larger than clade III for IPL ($P = 0.000$) and larger than clade I for RB ($P = 0.001$). Raw measurements for all specimens are given in Supplementary Data SD2.

No DFA either between or among the clades resulted in any eigenvalues ≥ 1.0. A DFA including all three clades correctly identified only 63% of the individuals to clade (63% of clade I, 55% of clade II, and 66% of clade III). DFA between clades I and II correctly identified 76% of the individuals to clade; loading was high and positive on LNB (3.63) and IOB (1.95), and negative on RB (−1.25). DFA between clades II and III correctly identified 82% of the individuals to clade; loading was high and positive on LNB (2.21), and IOB (1.69), and low and negative on IPL (−2.09). DFA between clades I and III correctly identified 77% of the individuals to clade; loading was high and positive on IPL (3.19), and low and negative for all other variables except GL. IPL alone could identify correctly 75% of the individuals to clade. PC1 of a PCA of the 38 grouped localities explained 32.8% of the total variance. All seven cranial characters had positive loadings on this component ($\overline{X} = 0.511$), indicating an overall influence of size on PC1. RB had a strong and negative loading on PC2, which explained another 15% of the total variance.

Secondary grouping of the initial 38 group localities resulted in nine drainage-basin groups (Fig. 2a). Differentiation along PC1 among group localities within these drainage-basin groups was low ($P > 0.4$). Each of these drainage-basin groups

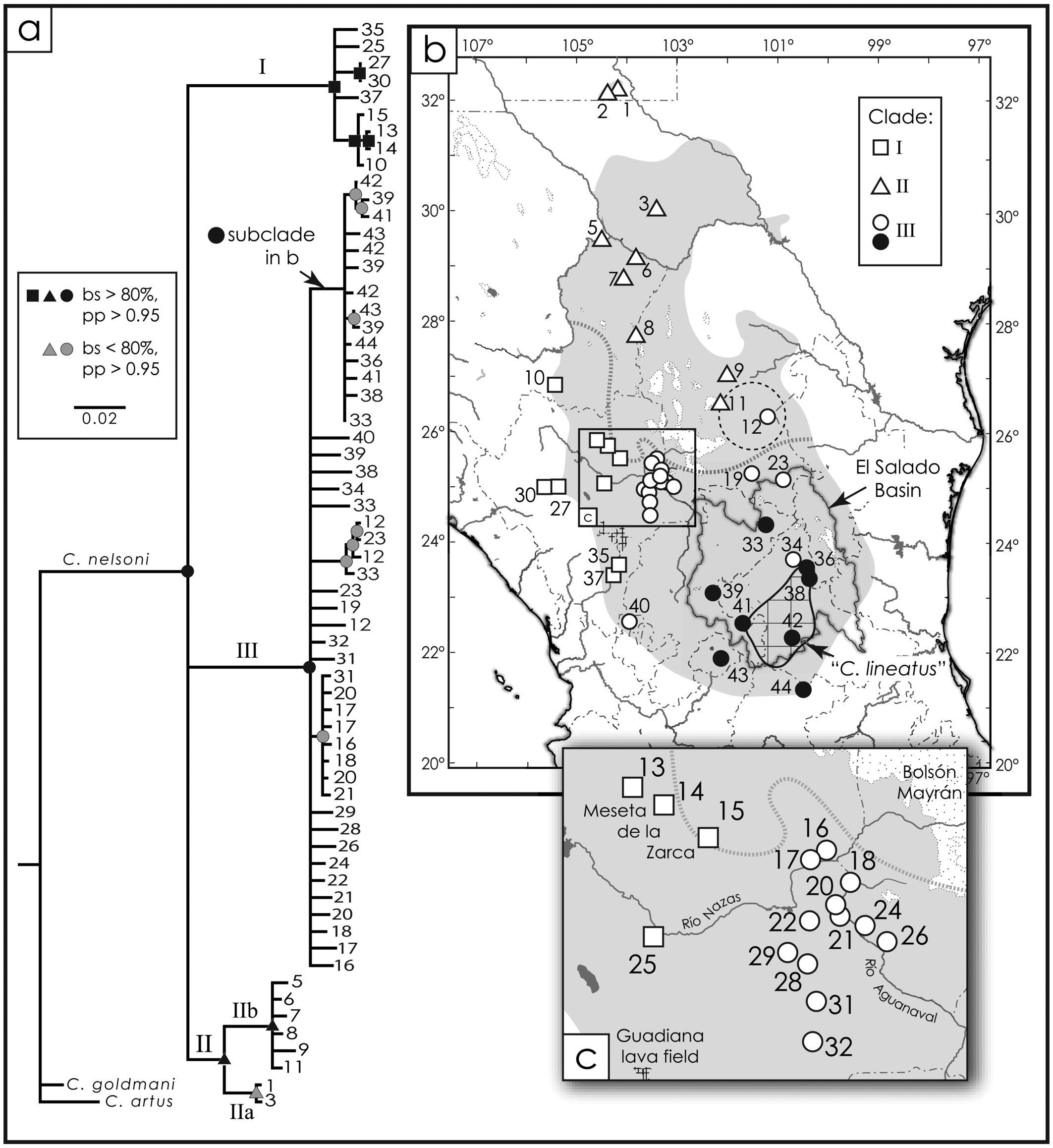

Fig. 4.—Genetic relationships among populations of *Chaetodipus nelsoni*. (a) Bayesian phylogram of localities (numbered as in Appendix I), after collapsing branches with multiple individuals from the same locality. Black symbols indicate well-supported nodes, gray symbols indicate nodes with high posterior probabilities but weaker bootstrap support, and nodes with weak support (posterior probability < 0.95 and bootstrap support < 80%) are collapsed. Branch lengths are substitutions per site. (b) Geographic distribution of localities and clades identified in (a) within the range of *C. nelsoni* (shaded). (c) Enlarged view of area in (b) showing localities relative to the Meseta de la Zarca, Guadiana (= Durango) lava field, Bolsón Mayrán, Río Nazas, and Río Aguanaval.

included at least one locality assigned in the molecular analyses, except for group localities 10–13 (Fig. 2a), which are east of the Sierra del Carmen – Sierra Madre Oriental filter-barrier (SCSMO; filter-barrier "2" in Fig. 1b).

When grouped by clade (leaving out localities 10–13, which lack molecular or karyotypic information), there were significant differences on PC1 between clades I and II ($t_{242} = 5.60$, $P < 0.0001$) and between clades II and III ($t_{216} = 6.26$, $P < 0.0001$), but clades I and III were similar ($t_{308} = 0.59$, $P = 0.557$). Drainage-basin groups Ia and Ib (clade I populations north and south of the Río Nazas, respectively) were morphologically distinct ($t_{166} = 7.81$, $P < 0.0001$). In contrast, there was no significant morphological difference between drainage-basin group IIa (clade IIa, north of the Río Grande) and drainage-basin group IIb (clade IIb, south of the Río Grande and west of the SCSMO; $t_{74} = 0.58$, $P = 0.567$). Within clade III, only populations from the Lerma-Santiago drainage (group IIId) were morphologically differentiated ($t_{140} = 7.07$, $P < 0.000$).

Based on PC1, localities 10–13 (*incertae sedis* from east of the SCSMO) were significantly different from neighboring drainage-basin groups IIa ($t_{66} = 3.81$, $P < 0.0001$) and IIb ($t_{56} = 3.09$, $P = 0.003$), but were not significantly different from groups IIIa, IIIb, and IIIc ($t_{148} = 1.51$, $P = 0.122$). Conversely, based on IPL alone, localities 10–13 were significantly different from groups IIIa, IIIb, and IIIc ($t_{140} = 3.60$, $P < 0.0001$), but not

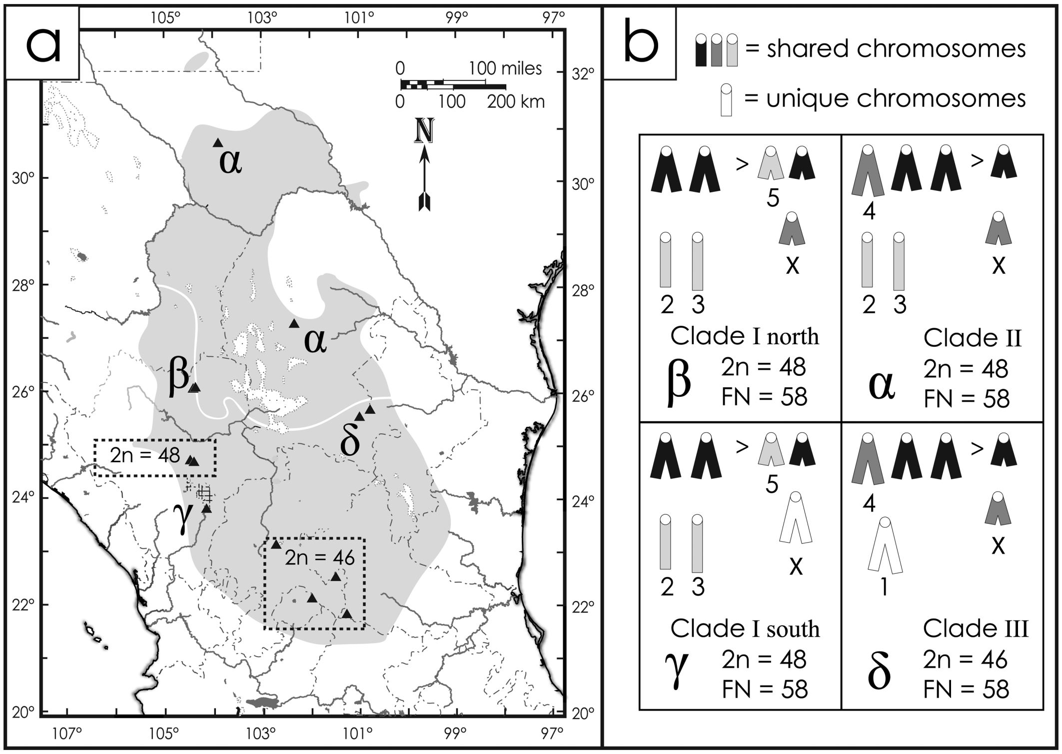

Fig. 5.—(a) Karyotypic forms found within *Chaetodipus nelsoni* (shading). Localities in which only diploid numbers have been determined cannot be assigned to a specific form. (b) Variable chromosomes among the four karyotypic forms of *C. nelsoni*. Diploid number (2n) and fundamental number (FN) are indicated; the X-chromosome is indicated with an X. Chromosomes 4 and 5 differ by an addition or deletion; chromosome 1 versus chromosomes 2 and 3 indicate a fission or fusion event.

significantly different from groups IIa ($t_{61} = 1.47$, $P = 0.141$) or IIb ($t_{51} = 1.89$, $P = 0.064$). When compared relative to overall size (IPL/GL), localities 10–13 were significantly different from IIa ($t_{61} = 2.84$, $P = 0.006$) as well as IIIa, IIIb, and IIIc ($t_{140} = 3.46$, $P = 0.001$), but not significantly different from IIb ($t_{51} = 0.988$, $P = 0.331$).

DISCUSSION

Molecular patterns.—Molecular analyses of both mtDNA and nuclear DNA (nuDNA; AFLP) were concordant in indicating three major lineages within *C. nelsoni*: a clade closely similar to the distribution of *C. n. canescens* (clade II); a clade that includes eastern populations of *C. n. nelsoni* and extends slightly farther north into Coahuila (clade III); and a formerly unrecognized yet equally divergent clade that includes western populations of *C. nelsoni* (clade I). The clades are reciprocally monophyletic based on sequence analysis of mtDNA. Although three populations (localities 9 and 26) indicate some mixing of nuDNA (AFLP) between clades II and III where they meet in southern Coahuila, there is no mixing of alleles in mtDNA data from the same populations. Based on the lack of any mtDNA evidence of past gene flow, we interpret the AFLP pattern among these populations as evidence for past, limited hybridization that has been retained by incomplete sorting rather than ongoing introgression.

Compared to other *Chaetodipus* species, the average percent sequence divergences (% sd) based on uncorrected *p*-distances among these three clades for *COIII* (8.1–11.3%) are similar to those among the *C. penicillatus* species group (7.3–10.1%; Jezkova et al. 2009) and between the sister species *C. baileyi* and *C. rudinoris* (10.5%; Riddle et al. 2000). The average % sd within *C. hispidus* is less than 4% (Andersen and Light 2012). Spradling et al. (2001) reported a high rate of mtDNA *Cytb* evolution in *Chaetodipus* relative to other rodents, and this high rate may also be true for *COIII*. The border between reciprocally monophyletic subclades within clade II (% sd = 3.9%) coincides with the Río Grande filter-barrier; the subclades are undifferentiated morphologically and karyotypically.

Genetic distinction between clades I and III is supported by allozymic data (Patton et al. 1981). The two lowest intraspecific levels of genetic similarity (Rogers' *S*-value) reported by Patton et al. (1981) within chaetodipine pocket mice were a mean $S = 0.777$ between chromosomal races of *C. penicillatus* that are now recognized as distinct species (*C. penicillatus* versus *C. eremicus*—Lee et al. 1996) and $S = 0.869$ between populations representing clade I (Durango: Rodeo) and clade III (Zacatecas: Zacatecas) of *C. nelsoni*. Patton et al. (1981) did not include a sample representing clade II.

Karyotypic pattern.—The genus *Chaetodipus* exhibits extensive variation in chromosomal complements, with most of the 16 species possessing a unique 2n and FN and several species (*C. pernix*, *C. penicillatus*, and particularly *C. goldmani*) with intraspecific variation (Patton and Rogers 1993). While all *C. nelsoni* examined have a FN = 58 (Fig. 5b), there are two diploid numbers within *C. nelsoni*: 2n = 48 in both clade I (β and γ forms) and clade II (α form), and 2n = 46 in clade III (δ form); in Fig. 5b, chromosome 1 = chromosomes 2 + 3, via fusion or fission. Distinction between the 2n = 48 karyotypes (α, β, and γ forms) is less definitive, as it is based on relative arm length and relative overall size of chromosomes; chromosome 4 = 5 and large X = small X via addition or deletion (Fig. 5b). Assignment of chromosomes based on relative arm length (metacentric, submetacentric, subtelocentric, acrocentric) and relative overall size is rather subjective, being based on nonpreferentially stained karyotypes; homologous chromosomes cannot be identified confidently without preferential staining. Further, arm and chromosomal lengths were measured from only one site for each of the five geographic groups (clade I north and south of the Río Nazas; clades IIa and IIb; and clade III), and these may not be representative of karyotypes throughout each geographic region.

Geographic variation in morphology.—It is evident from DFA and PCA of cranial measurements that geographic variation is subtle, not always concordant with molecular patterns, and is heavily influenced by size. The ecological diversity of arid habitats (requiring only a rocky, gravelly substrate) and wide range of elevations (400–2,450 m) occupied by *C. nelsoni* present multiple opportunities for homoplasious variation that may obscure phyletic relationships. For these reasons, we place little confidence that geographic patterns in morphology will reflect phylogeographic patterns. For example, Baker (1956:239) set the boundary between *C. n. nelsoni* and *C. n. canescens* north of Saltillo (Hall 1981) based on slight pelage and cranial characters, and our morphometric analysis supports this shift ($P = 0.028$ between localities 26 and 28), yet locality 26 is not significantly different from the drainage-basin group IIIc, and clade III now extends north to at least La Muralla based on molecular data. While there is a significant difference between clade I morphological groups north and south of the Río Nazas (Ia and Ib, respectively; Figs. 2b and 2c), and there are slight karyotypic differences between the two localities sampled (β form and γ form, respectively), there is no concordant molecular shift. Finally, clades IIa and IIb, defined on molecular data and without karyotypic differences, are not significantly different in morphology.

Localities from eastern Coahuila, east of the SCSMO filter-barrier (localities 10–13; Fig. 2) are morphologically similar to each other and to most of clade III groups but distinct from all clade II based on PC1, which reflects overall size. However, they are more similar to clade II and distinct from clade III based on IPL, which best discriminates between these two clades. When the effect of size is removed (using the ratio IPL/GL), localities 10–13 are similar to clade IIB but distinct from both clade IIa and clade III. We lacked tissue samples for molecular analysis and have no representative karyotypes from this region with which to provide definitive assignment of these localities and are reluctant to assign them to clade III based only on subtle and potentially homoplasious differences in morphology that might have resulted from environmental influences in common with eastern populations of clade III (e.g., increased size due to higher precipitation along the edge of the Tamaulipan biotic province). Accordingly, we retain them provisionally along with most other populations of *C. n. canescens* south of the Río Grande in clade IIb, but regard them as *incertae sedis* pending molecular or karyotypic evidence. Patterns of variation in cranial morphology, AFLP, mtDNA, and karyotypes among drainage-basin groups of *C. nelsoni* are summarized and compared in Table 1.

The specimen of *C. nelsoni* from Webb Co., Texas (Davis and Schmidly 1994) could not be assigned unambiguously to neighboring localities in either Texas or Coahuila based on DFA. This locality is 200 km south of the nearest Texas record near the junction of the Pecos River and Río Grande and > 100 km east and across the Río Grande from the nearest record in Coahuila. Efforts to obtain additional specimens of *C. nelsoni* from around the locality in Webb Co. have been unsuccessful (J. E. Light, pers. obs.). The record may have resulted from confusion of a specimen of *Peromyscus pectoralis* collected 2 days later from near the mouth of the Pecos River (J. Baskin, Texas A&M University – Kingsville, pers. comm., October 2016). Because of doubts about the provenance of this specimen, it was not included in morphological analyses.

Historical biogeography.—Chaetodipus nelsoni is a species of the Mexican Altiplano, and it is likely that the northern extension of the species into Trans-Pecos Texas occurred only after the latest glacial maximum, as warming and drying climate allowed the species to move north. Perhaps the population at Carlsbad Caverns National Park was established during the warmer, drier Xerithermal, and then isolated with subsequent cooling. The fossil record is not informative: although there are six Wisconsinan-to-Holocene records of *Chaetodipus* from southeastern New Mexico and Trans-Pecos Texas, one is identified only as "not *C. hispidus*," two as "*C. penicillatus* type," two only as "*Chaetodipus* sp.," and a record from Guadalupe National Park was identified as *C. intermedius*, a species that is currently found within that park (see references in Harris 2008–2016).

Each of the three major clades identified in this study are associated with one of the three closed basins of the Altiplano (Fig. 6): 1) 74% of clade I occurs in either the Nazas portion of the Nazas-Aguanaval Basin (46%) or the Presidio-Mezquital drainage (28%); 2) 99% of clade II occurs in either the Mapimí Basin (31%) or the Bravo-Conchos drainage (68%); and 3) 88% of clade III occurs either in the El Salado Basin (48%), the Aguanaval portion of the Nazas-Aguanaval Basin (22%), or the Lerma-Santiago drainage (18%). Similarly, while all of clade IIa occurs within the Bravo-Conchos drainage, 62% of clade IIb occurs within the Mapimí Basin. It initially may seem contradictory that the distribution of a saxicolous species coincides with basins that are defined by their sandy dry lake beds, which the saxicolous species avoids. The arid, rocky habitat of *C. nelsoni* is found at intermediate elevations above the more mesic (e.g., grassland) habitats surrounding the pluvial lakes or their eventual dry lake beds and below the piñon-juniper and pine-oak woodland (Fig. 7). During full-pluvial times (Fig. 7a), this intermediate-elevation habitat would have been squeezed between pluvial lakes and descending woodland (e.g., Van

Table 1.—Comparison of geographic patterns in cranial morphology, AFLP, mtDNA, and karyotype forms of *Chaetodipus nelsoni* across drainage basins (Fig. 6) within biogeographic subregions (Fig. 1b). Morphological groups are mapped in Fig. 2; groups indicated in bold are not significantly different from one-another ($P < 0.05$). AFLP groups are mapped in Fig. 3, mtDNA clades in Fig. 4, and karyotype forms in Fig. 5.

Subregion:	Coahuilan	Coahuilan	Trans-Pecos	Coahuilan	Zacatecan	Zacatecan	Zacatecan	Coahuilan	Zacatecan
Drainage basin:	Nazas	Nazas, Presidio-Mezquital	Bravo-Conchos	Mapimí	Nazas	Aguanaval	El Salado	Bravo-Conchos	Lerma-Santiago
Morphology:	Ia	Ib	**IIa**	**IIb**	**IIIa**	**IIIb**	**IIIc**	**Loc. 10–13**	IIId
AFLP:	I	I	II	II	III	III	III	?	III
mtDNA:	I	I	IIa	IIb	III	III	III	?	III
Karyotype:	β	Λ	α	α	?	?[a]	δ	?	?[a]

[a] 2n = 46 as in karyotype form δ.

Devender and Burgess 1985). Paleolake Irritila (Czaja et al. 2014) and its overflow spillway may have excluded *C. nelsoni* from two regions of potential secondary contact between clades (Areas 1 and 2 in Fig. 7a) during these pluvial periods. Baker (1956) identified the eastern region around 26°N in southeastern Coahuila as the junction of routes by which montane mammals may have reached Coahuila (i.e., habitat likely excluding *C. nelsoni*). In the western region, near Gómez Palacio-Torreón on the Durango-Coahuila border, the Nazas and Aguanaval rivers spilled from steep mountains into Paleolake Irritila. With warmer and drier conditions of the interpluvial, *C. nelsoni* would have followed retreating woodland and lakes, expanding from isolated refugia and spreading around basin margins and over lower divides (Fig. 7b). This would have brought clades II and III into secondary contact and clades I and III into close proximity.

Our finding of multiple clades within *C. nelsoni* adds to a growing body of literature that highlights the cryptic diversity of mammals of the Altiplano (e.g., Neiswenter and Riddle 2010; Fernández 2012; Fernández et al. 2012; Castañeda-Rico et al. 2014), and may sharpen focus on the role of drainage basins in effecting that diversity. In contrast to the general congruence between clades and drainage basins, the clades show less correspondence with filter-barriers within the Altiplano, and there appears to be no impact of the SCFB. The species is restricted by the Río Conchos, and the subclades within clade II are divided by the Río Grande. Populations of *C. nelsoni* in eastern Coahuila, on the eastern side of the SCSMO filter-barrier, may be members of clade IIb that have moved east across the montane filter-barrier (as they have traditionally been recognized). Alternatively, they may be members of clade III that have moved north across the SCFB and continued north to the Río Grande, as might be indicated by morphological similarities (Fig. 2). The locality at the base of the Sierra del Carmen along the Río Grande (locality 10; Fig. 2) may represent a crossing of the Río Grande by clade IIa, such that these four localities might represent a combination of clade IIa, IIb, and III that have converged on the region, and simply resemble each other morphologically due to selection in a common environment. Comparison of molecular sequences from museum specimens from these localities with representatives of each of the three surrounding clades should readily resolve this question.

Modern environmental changes.—Baker and Greer (1962:982) suspected that *C. nelsoni* had "become more abundant or even extended its range in the grassland habitat as a result of severe grazing by livestock." The environmental consequences of overgrazing that began with the arrival of the Spanish to Mexico in 1519 have been well documented (e.g., Melville 1967), and continue to be obvious along fence-lines between overgrazed and ungrazed areas. We have repeatedly travelled to documented localities of the desert grassland species *C. hispidus* in Coahuila only to find extensive farms or ranches from which all grassland has been eradicated and have found only *C. nelsoni* in rocky soil and *C. eremicus* in sandy soil surrounding the disturbed area.

It is likely that human-mitigated changes of the flow regimes of both the Río Grande and Río Nazas have impacted

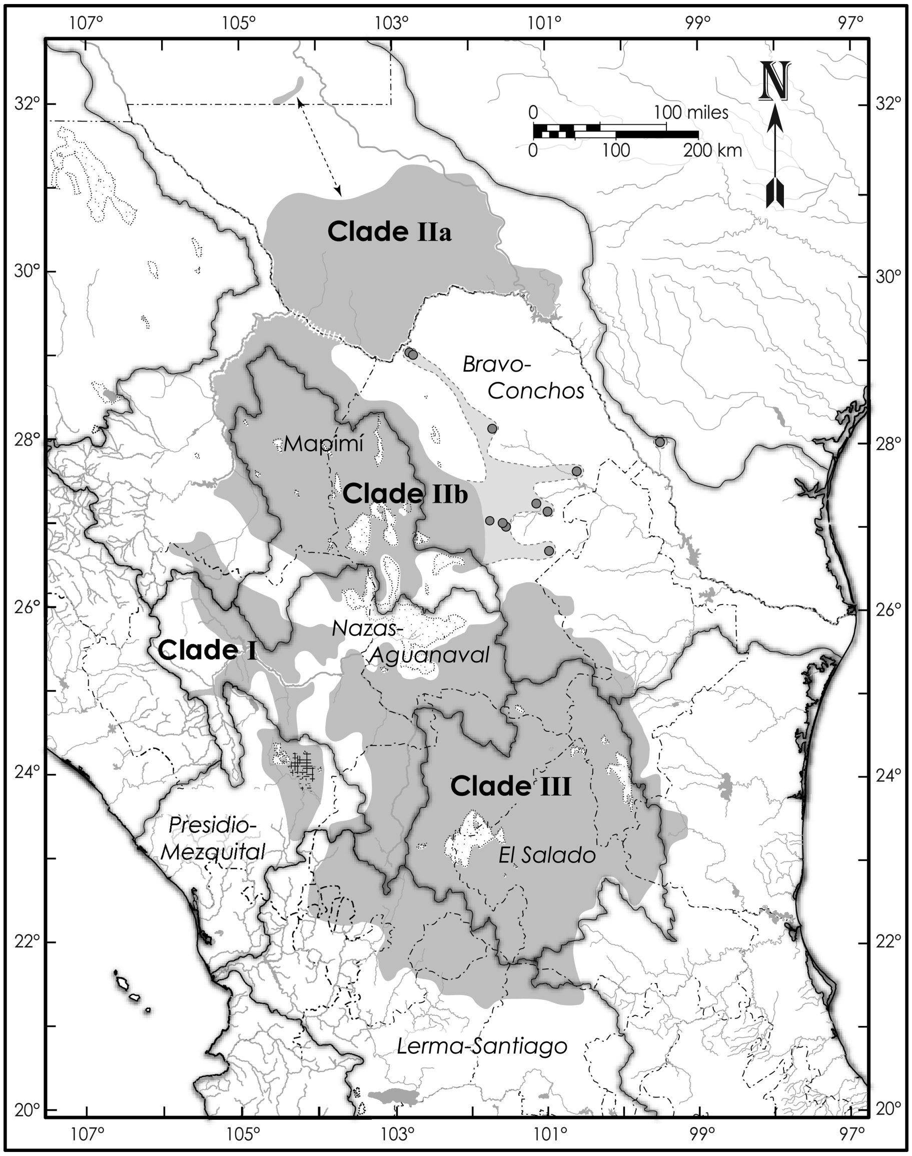

Fig. 6.—Distribution of clades within *Chaetodipus nelsoni* relative to drainage basins (outlined in shaded lines). The localities indicated by gray-filled circles are considered incertae sedis, as they lack molecular or karyotypic data; the locality in southern Texas is of questionable provenance.

dispersal and gene flow among genetic units. Historically, the Río Grande was a perennial river with a reliable flow. By 1907, due to irrigation and increased sedimentation resulting from destruction of vegetation in watersheds and increased erosion in New Mexico, the river was described by Lee (1907) as "mainly a floodwater stream subject to great fluctuations in volume." Construction of dams and agricultural irrigation has moderated and reduced the flow such that the river is now seasonally dry between El Paso, Texas, and the confluence with the Río Conchos. In contrast, the Río Nazas, formed by the joining of the Río Sextín and the Río Ramos, was historically a floodwater stream. It collected seasonal floodwaters from an extensive area, and torrential seasonal floods scoured out the canyon of the Río Nazas and emptied into Laguna Mayrán. The Laguna Mayrán was at least a seasonal lake that was important to migratory birds and supported extensive cotton production in the Lake District (Comarca Lagunera) since the early 19th Century (Wolfe 2011). Damming and irrigation now regulate the flow of the Río Nazas, with little water reaching the Desierto Mayrán. El Palmito Dam (Presa Lázaro Cardenas) was completed in 1946, and Las Tórtolas Dam (Presa Francisco Zarco) was completed in 1965. In summary, the Río Nazas, previously intermittently dry, now flows continuously between El Palmito and Torreón, whereas the Río Grande, previously perennial, is now intermittently dry between El Paso and confluence with the Río Conchos.

Taxonomic validity of Chaetodipus lineatus.—Dalquest (1951) described *C. lineatus* from central and western San Luis Potosí (see Fig. 1a) as resembling *C. nelsoni* in size, proportions, cranial characters, and habitat preference, but differing in having a somewhat darker pelage coloration and, like *C. eremicus*, lacking rump spines. Caire (1976) found *C. lineatus* to be distinct from both *C. nelsoni* and *C. eremicus* in a numerical taxonomic analysis of the subgenus *Chaetodipus*.

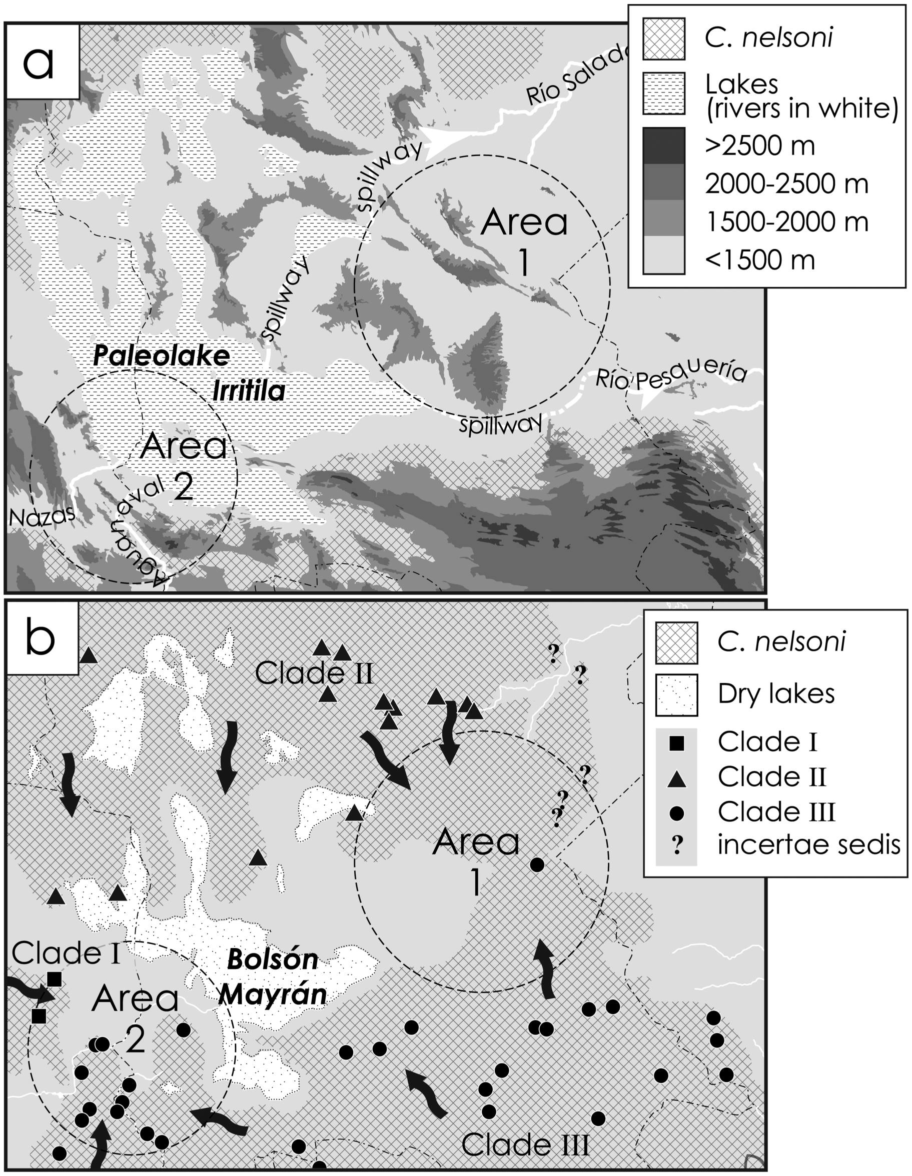

Fig. 7.—(a) The distribution of *Chaetodipus nelsoni* was likely fragmented and reduced during pluvial maxima, compressed between lower-elevation mesic habitats associated with pluvial lakes and spillways and higher-elevation piñon-juniper and pine-oak woodlands. (b) With the return of drier conditions in the Xerithermal, *C. nelsoni* was spread along with spreading xeric habitat (arrows). Clades II and III came into secondary contact in Area 1, while clades I and III reinvaded the lower Río Nazas and Río Aguanaval, coming into near contact in Area 2.

Matson and Baker (1986) later assigned two specimens from east-central Zacatecas to *C. lineatus* (and 54 other specimens in the region to *C. nelsoni*).

Trapping at or near localities in San Luis Potosí from which *C. lineatus* were reported by Dalquest (1951), neither we (25 specimens from three localities) nor J. L. Patton (University of California, Berkeley, pers. comm., September 2014; 23 specimens from two localities) have encountered any smooth-haired *Chaetodipus* from rocky habitat, or anything that resembled the description of *C. lineatus*. All of our specimens of *Chaetodipus* from these localities have been assigned on the basis of mtDNA analysis to either *C. nelsoni* (*n* = 22) or *C. eremicus* (*n* = 3, collected in sandy soils). Similarly, specimens that were karyotyped by J. L Patton (University of California, Berkeley, pers. comm., September 2014) from two localities within the purported range of *C. lineatus* share the identical karyotype (δ form) with clade III of *C. nelsoni.* In his original description of *C. nelsoni*, Merriam (1894:266) noted that "… the spines are absent in the young and in certain conditions of the molt." Williams et al. (1993:146) concluded that "Variability in presence or absence of rump spines has been noted for a number of species of *Chaetodipus* …Three species of similar sized *Chaetodipus* sharing the same area would be unusual. Specimens of *C. lineatus* may be spineless individuals of *C. nelsoni*. That they are also dull gray rather than the normal dark brownish suggests that a simple mutation or age is responsible for the differences." Further, broad sympatry between coarse-haired species of *Chaetodipus* is otherwise unknown: *C. californicus* and *C. fallax* are parapatrically distributed in the California chaparral and adjacent coastal scrub of California and Baja California (D. J. Hafner, pers. obs.); *C. artus* appears to exclude *C. goldmani* from riparian and mesic short-tree communities (Patton 1969); and the distributions of *C. intermedius* and *C. nelsoni* in Trans-Pecos Texas are essentially parapatric (Wilkins and Schmidly 1979). As with the genetic assignment of *C. nelsoni* from eastern Coahuila, comparison of molecular sequences from type specimens of *C. lineatus*, in this case with *C. nelsoni* and *C. eremicus*, should readily determine whether *C. lineatus* is a valid taxon.

TAXONOMIC CONCLUSIONS

Molecular (AFLP and mtDNA) analyses reveal clear and concordant phylogeographic structuring within *C. nelsoni* that is generally associated with drainage basins (Table 1). This structuring is supported by the available karyotypic data. The combination of subtle cranial differences that exhibit both geographic variation and homoplasy across an extensive and ecologically diverse area has obscured the existence of these three major phyletic lineages. While AFLP patterns retain evidence of past, geographically limited hybridization between clades II and III in southern Coahuila, there is no such evidence in mtDNA, and we regard all three clades as genetically isolated.

We recognize the three major clades within *C. nelsoni* as cryptic species within a species group, and further recognize geographically structured subsets within clade II as subspecies. The three clades are reciprocally monophyletic based on both mtDNA and nuDNA and possess variously distinguishing karyotypes, while revealing only subtle and variable morphological variation that is associated more with closed basins and river drainages of the Altiplano than with taxonomic groups. Although populations of clade I north and south of the Río Nazas may possess slightly different karyotypes (based on a single locality for each), and appear to differ morphologically, we are hesitant to recognize these as subspecies without molecular support.

Chaetodipus nelsoni (Merriam 1894)

Nelson's coarse-haired pocket mouse

Perognathus (*Chaetodipus*) *nelsoni* Merriam, 1894:266. Type locality: "Hacienda La Parada, about 25 mi. NW Ciudad San Luis Potosí, San Luis Potosí, México." Old adult female, skin and skull, United States National Museum number 50214, collected by Edward W. Nelson on 19 August 1892.

Perognathus (*Chaetodipus*) *intermedius canescens* Merriam, 1894:267. Type locality: "Jaral, Coahuila."

Perognathus nelsoni canescens: Osgood, 1900:54. Name combination.

Chaetodipus nelsoni: Hafner and Hafner, 1983:25. First use of current name combination.

Geographic range.—Restricted to the distribution of clade III (Fig. 6; Appendix I) centered in the El Salado Basin and extending west into the Aguanaval Basin, south into the upper reaches of the Lerma-Santiago drainage basin, and north to at least La Muralla in the Río Grande drainage basin of southern Coahuila. The species may extend farther north, perhaps to the base of the Sierra Carmen just south of the Río Grande (*incertae sedis* localities in Fig. 6). The revised distribution now includes the type locality for *C. n. canescens* (Jaral, Coahuila).

Description.—As noted by Baker (1956), most specimens of *C. nelsoni* are darker in pelage color than those of clade II to the north. They also average larger in most cranial dimensions (GL, MB, LNB, IOB, IPB), but are equivalent to clade II in RB and significantly smaller in IPL (although there is overlap). They are similar in cranial dimensions to clade I to the west, except that *C. nelsoni* averages significantly smaller in IPL. *Chaetodipus nelsoni* has a diploid number of 46 (versus all others in the *C. nelsoni* species group; δ form, Fig. 5) and exhibits an average of ~10–11% sequence differences in *COIII* from clades I and II, respectively.

Comments.—Hall and Kelson (1959) placed the boundary between *C. n. canescens* (our clade II) and *C. n. nelsoni* (our clade III) along the SCFB south of Saltillo, Coahuila, although Baker (1956:239) had already moved the boundary north of Saltillo (Hall 1981). We extend the distribution north to at least La Muralla, Coahuila, and restrict the distribution to exclude populations in the Nazas Basin, Presidio-Mezquital Basin, and points west.

Chaetodipus collis (Blair, 1938)

Highland coarse-haired pocket mouse

(Synonymy under subspecies)

Geographic range.—This species occurs in the Bolsón Mapimí of northern Mexico and along the Río Grande drainage into Trans-Pecos Texas, with an isolated population in the Guadalupe Mountains of New Mexico (clade II; Fig. 6; Appendix I).

Diagnosis and comparison.—"General effect of upper parts Tawny-Olive heavily washed with black. A distinct, Ochraceous-Buff lateral line present. Ears dusky. Underparts and feet white. Tail bicolor, blackish above, white below. … hairs on the hind legs coarser, flattened, and heavily grooved; rump spines coarser; annulations on the tail coarser." Skull "broader and heavier than in [clades I and III], rostrum more slender, mastoids larger, dorsal margin of mastoids with a distinct angle rather than evenly rounded as in [clades I and III]. Lower premolar slightly larger than last molar. … Interparietal distinctly pentagonal rather than rounded as in [clades I and III], larger; tubercle of the mandible formed by proximal end of lower incisor, weaker" (Blair 1938:1–2).

As noted by Baker (1956), most specimens of *C. collis* are lighter in pelage color than other populations of the former *C. nelsoni*. *Chaetodipus collis* averages smaller in most cranial dimensions (GL, LNB, IOB, IPB), but largest in IPL (with some overlap), is significantly larger than clade I and equivalent to *C. nelsoni* in RB, and is equivalent to clade I in MB. This species has a diploid number of 48 (which it shares with clade I), but has the α karyotype form (versus β and λ forms for clade

I), and exhibits an average of ~10–11% sequence differences in *COIII* from clades III and I, respectively.

Comments.—This species includes most of the populations formerly considered as *C. n. canescens*, except for those in southeastern Coahuila now included within *C. nelsoni*. The species may extend farther east across the SCSMO filter-barrier (*incertae sedis* localities in Fig. 6). The type locality for *C. n. canescens* (Jaral, Coahuila) is now included within *C. nelsoni*, making *canescens* a junior synonym. The species epithet *collis* refers to "the restriction of the species to high land [thus the common name], and is derived from the Latin word *collis* meaning hill or high land" (Blair 1938:2).

Chaetodipus collis collis (Blair 1938)

Perognathus collis Blair, 1938:1. Type locality: "Limpia Canyon, 4800 ft., about 1 mi. NW Fort Davis, Texas."

Perognathus collis popei Blair, 1938:3. Type locality: "Pinnacle Spring, Brewster Co., Texas."

Perognathus nelsoni canescens: Borell and Bryant, 1942:25. Part, not *Perognathus* (*Chaetodipus*) *intermedius canescens* Merriam, 1894.

Distribution.—Trans-Pecos Texas (north of the Río Grande; Wilkins and Schmidly 1979) and on the eastern escarpment of the Guadalupe Mountains within Carlsbad Caverns National Park, New Mexico (Geluso and Geluso 2004; clade IIa, Fig. 6; Appendix I).

Description.—Populations of *C. collis* from north and south of the Río Grande (clades IIa and IIb, Fig. 6) are not distinguishable based on pelage color, cranial morphology, or karyotype, but possess reciprocally monophyletic complements in both nuDNA (AFLP) and mtDNA (4.9% sd).

Comments.—Borell and Bryant (1942) regarded *C. collis* as a synonym of *C. n. canescens* and regarded *C. c. popei* as inseparable from *C. n. canescens*.

Chaetodipus collis mapimiensis, new subspecies

Holotype.—Adult female; skin, skull, skeleton, frozen tissue; MSB 274126; collected 25 August 2006, David J. Hafner; original number 5334; condition good.

Type locality.—35 km SW Hércules (Coahuila), Chihuahua, México; 27.768°N, 103.975°W, 1,420 m.

Distribution.—Bolsón Mapimí of northern Mexico and along the adjacent Río Grande drainage to the Río Grande and Río Conchos (clade IIb, Fig. 6; Appendix I).

Measurements of the holotype.—Morphometric data for the holotype including external measurements (transcribed from the specimen tag) and cranial characters are as follows (in mm): total length, 179; tail length, 97; hind foot, 21; ear, 9; GL, 25.72; MB, 13.39; RB, 4.49; LNB, 2.65; IOB, 6.51; IPB, 7.07; IPL, 4.14.

Description.—Not distinguishable from *C. c. collis* based on pelage color, cranial morphology, or karyotype, but the two subspecies possess reciprocally monophyletic complements in both nuDNA (AFLP) and mtDNA (4.9% sd).

Comments.—Based on relative size of IPL, the *incertae sedis* localities east of the SCSMO filter-barrier (10–13; Fig. 6) belong to this subspecies; based on PC1, these populations in the Tamaulipan biotic province are larger, similar in size to neighboring *C. nelsoni*.

Etymology.—The subspecific epithet *mapimiensis* refers to the Bolsón de Mapimí, the center of distribution of this subspecies.

Chaetodipus durangae, new species

Durango coarse-haired pocket mouse

Holotype.—Adult male; skin, skull, skeleton (appendicular elements complete on left side only), frozen tissue, karyotype; MSB 274021; collected 21 July 2008, David J. Hafner; original number 5470; condition good.

Type locality.—15 mi. E Crucero La Zarca, Durango, México; 25.804°N, 104.530°W, 1,920 m.

Distribution.—*Chaetodipus durangae* occurs in the Río Nazas portion of the Nazas-Aguanaval Basin, spilling over into the Río Grande drainage to Hidalgo de Parral, Chihuahua and into the upper Presidio-Mezquital drainage near Yerbanís, into the region surrounding Ciudad Durango (including the Guadiana lava field) to Mezquital, Durango (clade I, Fig. 6; Appendix I).

Measurements of the holotype.—Morphometric data for the holotype including external measurements (transcribed from the specimen tag) and cranial characters are as follows (in mm): total length, 203; tail length, 116; hind foot, 23; ear, 10; GL, 26.58; MB, 13.61; RB, 4.86; LNB, 2.85; IOB, 7.17; IPB, 8.17; IPL, 3.90.

Description.—Similar in pelage coloration and cranial dimensions to *C. nelsoni*, except that *C. durangae* averages larger in IPL. Populations north of the Río Nazas average larger in overall size than those south of the Río Nazas (GL = 26.29 ± 0.69, 24.69–28.54 versus 25.34 ± 0.68, 22.53–27.45) and are the largest in the species group. Four localities north of the river formed a well-supported subclade based on mtDNA (bs = 89%, pp = 1.00), but a subclade including all five localities south of the river is not well supported (bs = 44%, pp = 0.58) and was collapsed in Fig. 4. Single-site karyotypes from north and south of the river are slightly different (karyotype forms β and λ, respectively).

Comments.—More comprehensive sampling may reveal subspecies north and south of the Río Nazas within *C. durangae*.

Etymology.—The specific epithet *durangae* refers to the State of Durango, in which most of this species occurs.

ACKNOWLEDGMENTS

We gratefully thank the curators and collection managers from the museums that provided genetic and specimen loans for this project: Museum of Southwestern Biology (MSB), University of New Mexico (UNM); Michigan State University Museum Mammal Collection (MSU); Biodiversity Research and Teaching Collections, Texas A&M University

(BRTC); Collection of Recent Mammals, Museum of Texas Tech University (TTU); Museum of Natural History, University of Kansas; Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); and Texas A&M University Kingsville Collections (TAIU). J. McConachie assisted DJH in measuring specimens at MSU and MSB. L. Abraczinskas (MSU) and J. Cook (MSB) graciously assisted us as we examined specimens in their care. We thank C. Conroy (MVZ) and J. Baskin (TAIU) for measuring specimens in their care for our morphometric analysis. R. Bradley (TTU) and D. Schmidly (UNM) assisted DJH in locating the specimen at TAIU. We thank F. A. Cervantes and his graduate and undergraduate students at the Collección Nacional de Mamíferos, Instituto de Biología, Universidad Nacional Autónoma de México for their many years of support and assistance in the field; assisting us in the field for this project were J. Arcangeli, C. Ballesteros, J. Fernández, X. Isidro, M. Mancera, L. Mondragón, A. Montiel, and J. Ramírez. We also thank S. Mantooth and J. Williams (UNLV) and J. Redfern (UNM) for assistance in the field. J. Patton (MVZ) provided photographic negatives of chromosomal preparations from his fieldwork, and J. Fernández (Universidad Autónoma de Chihuahua) provided tissue from specimens he recently collected; both greatly augmented our samples. We thank A. Camargo for correcting the Spanish translation of the abstract. Financial support was provided through grants from the National Science Foundation to DJH (DEB-9629840 and DEB-0236957) and BRR (DEB-9629787 and DEB-0237166) and participation in the REU SITE: Mechanism of Evolution (DBI-1358896) by KK.

SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Distribution of measured specimens and additional museum records of *Chaetodipus nelsoni*. Museum records were downloaded from VertNet version 2016-09-29 (accessed November 2018).

Supplementary Data SD2.—Museum catalogue numbers, locality information, karyotypes, AFLP complements, mtDNA complements, and raw measurements for measured specimens of *Chaetodipus nelsoni*.

LITERATURE CITED

ALEXANDER, L. F., AND B. R. RIDDLE. 2005. Phylogenetics of the New World rodent family Heteromyidae. Journal of Mammalogy 86:366–379.

ANDERSON, S. 1972. Mammals of Chihuahua: taxonomy and distribution. Bulletin of the American Museum of Natural History 148:149–410.

ANDERSEN, J. J., AND J. E. LIGHT. 2012. Phylogeography and subspecies revision of the hispid pocket mouse, *Chaetodipus hispidus* (Rodentia: Heteromyidae). Journal of Mammalogy 93:1195–1215.

ARRIAGA, L., C. AGUILAR, D. ESPINOSA-ORGANISTA, AND R. JIMÉNEZ. 1997. Regionalización ecológica y biogeográfica de México. Taller de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Conabio), México, D.F.

BAKER, R. H. 1956. Mammals of Coahuia, México. University of Kansas Publications, Museum of Natural History 9:125–335.

BAKER, R. H., AND J. K. GREER. 1962. Mammals of the Mexican state of Durango. Publications of the Museum, Michigan State University: 25–154.

BLAIR, W. F. 1938. Two new pocket-mice from western Texas. Occasional Papers of the Museum of Zoology, University of Michigan 381:1–3.

BORELL, A. E., AND M. D. BRYANT. 1942. Mammals of the big bend area of Texas. University of California Publications in Zoology 48:1–62.

CAIRE, W. 1976. Phenetic relationships of pocket mice in the subgenus *Chaetodipus* (Rodentia: Heteromyidae). Journal of Mammalogy 57:375–378.

CASTAÑEDA-RICO, S., L. LEÓN-PANIAGUA, E. VÁZQUEZ-DOMÍNGUEZ, AND A. G. NAVARRO-SIGÜENZA. 2014. Evolutionary diversification and speciation in rodents of the Mexican lowlands: the *Peromyscus melanophrys* species group. Molecular Phylogenetics and Evolution 70:454–463.

CZAJA, A., M. R. PALACIOS-FEST, J. L. ESTRADA-RODRÍGUEZ, U. ROMERO-MÉNDEZ, AND J. A. ALBA-ÁVILA. 2014. Inland dunes fauna and flora from Paleolake Irritila in the Comarca Lagunera, Coahuila, northern Mexico. Boletín de la Sociedad Geológica Mexicana 66:541–551.

DALQUEST, W. W. 1951. Six new mammals from the state of San Luis Potosí, Mexico. Journal of the Washington Academy of Sciences 41:361–364.

DAVIS, W. B., AND D. J. SCHMIDLY. 1994. The mammals of Texas. Nongame and Urban Program, Texas Parks and Wildlife Department, Austin.

EARL, D. A., AND B. M. VONHOLDT. 2012. STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation Genetics Resources 4:359–361.

EVANNO, G., S. REGNAUT, AND J. GOUDET. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611–2620.

FERNÁNDEZ, J. A. 2012. Phylogenetics and biogeography of the microendemic rodent *Xerospermophilus perotensis* (Perote ground squirrel) in the Oriental Basin of Mexico. Journal of Mammalogy 93:1431–1439.

FERNÁNDEZ, J. A., F. A. CERVANTES, AND M. S. HAFNER. 2012. Molecular systematics and biogeography of the Mexican endemic kangaroo rat, *Dipodomys phillipsii* (Rodentia: Heteromyidae). Journal of Mammalogy 93:560–571.

GELUSO, K. N., AND K. GELUSO. 2004. Mammals of Carlsbad Caverns National Park, New Mexico. Bulletin of the University of Nebraska State Museum 17:1–180.

HAFNER, M. S., A. R. GATES, V. L. MATHIS, J. W. DEMASTES, AND D. J. HAFNER. 2011. Redescription of the pocket gopher *Thomomys atrovarius* from the Pacific coast of mainland Mexico. Journal of Mammalogy 92:1367–1382.

HAFNER, D. J., M. S. HAFNER, G. L. HASTY, T. A. SPRADLING, AND J. W. DEMASTES. 2008. Evolutionary relationships of pocket gophers (*Cratogeomys castanops* species group) of the Mexican Altiplano. Journal of Mammalogy 89:190–208.

Hafner, M. S., J. E. Light, D. J. Hafner, S. V. Brant, T. A. Spradling, and J. W. Demastes. 2005. Cryptic species in the Mexican pocket gopher *Cratogeomys merriami*. Journal of Mammalogy 86:1095–1108.

Hafner, D. J., and B. R. Riddle. 2011. Boundaries and barriers of North American warm deserts: an evolutionary perspective. Pp. 75–113 in Palaeogeography and palaeobiogeography: biodiversity in space and time (P. Upchurch, A. McGowan, and C. Slater, eds.). The Systematics Association Special Volume Series, CRC Press, Boca Raton, Florida.

Hafner, J. C., and D. R. Sandquist. 1989. Postmortem field preparation of bird and mammal chromosomes: an evaluation involving the pocket gopher, *Thomomys bottae*. The Southwestern Naturalist 34:330–337.

Hall, E. R. 1981. The mammals of North America. Volume 1. John Wiley and Sons, New York.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Volume 1. The Ronald Press Co., New York.

Harris, A. H. 2008–2016. Pleistocene vertebrates of southwestern USA and northwestern Mexico. https://www.utep.edu/leb/pleistNM/default.htm. Accessed November 2018.

Jezkova, T., J. R. Jaeger, Z. L. Marshall, and B. R. Riddle. 2009. Pleistocene impacts on the phylogeography of the desert pocket mouse (*Chaetodipus penicillatus*). Journal of Mammalogy 90:306–320.

Kumar, S., G. Stecher, and K. Tamura. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33:1870–1874.

Lanfear, R., B. Calcott, S. Y. Ho, and S. Guindon. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29:1695–1701.

Lee, W. T. 1907. Water resources of the Rio Grande valley in New Mexico. Water Supply and Irrigation Papers of the United States Geological Survey 188:1–59.

Lee, T., E., B. R. Riddle, and P. L. Lee. 1996. Speciation in the desert pocket mouse (*Chaetodipus penicillatus* Woodhouse). Journal of Mammalogy 77:58–68.

Mathis, V. L., M. S. Hafner, and D. J. Hafner. 2014. Evolution and phylogeography of the *Thomomys umbrinus* species complex (Rodentia: Geomyidae). Journal of Mammalogy 95:754–771.

Mathis, V. L., M. S. Hafner, D. J. Hafner, and J. W. Demastes. 2013. Resurrection and redescription of the pocket gopher *Thomomys sheldoni* from the Sierra Madre Occidental of Mexico. Journal of Mammalogy 94:544–560.

Matson, J. O., and R. H. Baker. 1986. Mammals of Zacatecas. Special Publications, The Museum, Texas Tech University 24:1–88.

Melville, E. G. K. 1967. A plague of sheep: environmental consequences of the conquest of Mexico. Cambridge University Press, Cambridge and New York.

Merriam, C. H. 1894. Descriptions of eight new pocket mice (genus *Perognathus*). Proceedings of the Academy of Natural Sciences of Philadelphia 46:262–268.

Miller, M. A., W. Pfeiffer, and T. Schartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 November 2010, New Orleans, Louisiana.

Modi, W. S. 2003. Morphological, chromosomal, and molecular evolution are uncoupled in pocket mice. Cytogenetic and Genome Research 103:150–154.

Morrone, J. J. 2005. Hacia una síntesis biogeográfica de México. Revista Mexicana de Biodiversidad 76:207–252.

Neiswenter, S. A., and B. R. Riddle. 2010. Diversification of the *Perognathus flavus* species group in emerging arid grasslands of western North America. Journal of Mammalogy 91:348–362.

Patton, J. L. 1969. Chromosome evolution in the pocket mouse, *Perognathus goldmani* Osgood. Evolution 23:645–662.

Patton, J. L. 1970. Karyotypes of five species of pocket mice, genus *Perognathus* (Rodentia: Heteromyidae), and a summary of chromosome data for the genus. Mammalian Chromosomes Newsletter 11:3–8.

Patton, J. L., and D. S. Rogers. 1993. Cytogenetics. Pp. 236–258 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publications, American Society of Mammalogists 10:1–719.

Patton, J. L., S. W. Sherwood, and S. Y. Yang. 1981. Biochemical systematics of chaetodipine pocket mice, genus *Perognathus*. Journal of Mammalogy 62:477–492.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945–959.

Rambaut, A., A. J. Drummond, and M. Suchard. 2014. Tracer v1.6 http://beast.bio.ed.ac.uk. Accessed May 2015.

Riddle, B. R. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the late Cenozoic development of a North American aridlands rodent guild. Journal of Mammalogy 76:283–301.

Riddle, B. R., D. J. Hafner, and L. F. Alexander. 2000. Comparative phylogeography of Baileys' pocket mouse (*Chaetodipus baileyi*) and the *Peromyscus eremicus* species group: historical vicariance of the Baja California Peninsular Desert. Molecular Phylogenetics and Evolution 17:161–172.

Ronquist, F., and J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics (Oxford, England) 19:1572–1574.

Sikes, R. S. and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Spradling, T. A., M. S. Hafner, and J. W. Demastes. 2001. Differences in rate of cytochrome-*b* evolution among species of rodents. Journal of Mammalogy 82:65–80.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England) 30:1312–1313.

Van Devender, T. R., and T. L. Burgess. 1985. Late Pleistocene woodlands in the Bolson de Mapimi: a refugium for the Chihuahuan Desert Biota? Quaternary Research 24:346–353.

Webb, O. L. 1954. *Perognathus nelsoni canescens* in New Mexico. Journal of Mammalogy 35:453.

Wilkins, K. T., and D. J. Schmidly. 1979. Identification and distribution of three species of pocket mice (genus *Perognathus*) in Trans-Pecos Texas. The Southwestern Naturalist 24:17–31.

Wilkinson, L. 1997. Systat 7.0 for Windows. SPSS, Inc., Chicago, Illinois.

Williams, D. F., H. H. Genoways, and J. K. Braun. 1993. Taxonomy. Pp. 38–196 in Biology of the Heteromyidae (H. H. Genoways and J. H. Brown, eds.). Special Publications, American Society of Mammalogists 10:1–719.

Wolfe, M. 2011. Bringing the revolution to the dam site: how technology, labor, and nature converged in the microcosm of a northern Mexican company town, 1936–1946. Journal of the Southwest 53:1–32.

Submitted 3 April 2019. Accepted 5 August 2019.

Associate Editor was Tereza Jezkova.

APPENDIX I

Specimens Examined.—Specimens used in this study are housed in the Museum of Southwestern Biology, University of New Mexico (MSB); the Michigan State University Museum (MSU); the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the University of Kansas Natural History Museum (KU); the Museo de Zoología "Alfonso L. Herrera," Universidad Nacional Autónoma de México (MZFC); the Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango, Instituto Politécnico Nacional (CIIDIR); Universidad Autónoma de Chihuahua, Facultad de Zootecnia y Ecología, Colección de Vertebrados (UACH-CV-M); Texas A&M University Biodiversity and Research Teaching Collections (BRTC; all specimens have a "TCWC" acronym); the Museum of Texas Tech University (TTU); or the University of Arizona Collection of Mammals (UA). Localities are arranged north to south within morphological grouped localities. Specimens used in the morphometric analyses are designated "m," those used in the AFLP analyses "a," those in the mtDNA analysis as "mt," and those used in the karyotypic analyses "k." Sample sizes for each type of analysis are indicated following the taxon names. Numbers in boldface and parentheses refer to morphometric localities mapped in Fig. 2a and molecular localities mapped in Figs. 3 and 4. GenBank numbers for *COIII* sequences are listed for specimens in the mtDNA analysis.

Chaetodipus collis collis (m = 43, a = 6, mt = 6, k = 2).—**(1)** New Mexico: Eddy Co.; Slaughter Canyon, 5.5 mi. W Rattlesnake Spring, 1,300 m, 32.108°N, 104.566°W (m4 [MSB], a3 [MSB 271161, 271163, 271164], mt1 [MSB 271161]); Yucca Canyon, 1 mi. S, 6.5 mi. W Rattlesnake Spring, 1,425 m, 32.099°N, 104.586°W (m1 [MSB], a1 [MSB 271165]); **(2)** Texas: Jeff Davis Co.; 1 mi. E McDonald Observatory, Davis Mtns. 30.671° N, 104.004° W (k2 [Patton 1970); Presidio Co.; 8 mi. NE Candelaria, 1,025 m, 30.220°N, 104.590°W (m5 [TCWC]); Pinto Canyon, 45 mi. SW Marfa, Chinati Mts.; 1,056 m, 29.720°N, 104.350°W (m4 [TCWC]); Brewster Co.; Elephant Mountain Wildlife Management Area, 1,328 m, 30.030°N, 103.555°W (m5 [MSB], a1[MSB 285903], mt5 [MSB 285903–285904, 285917–285919]); Black Gap WMA, 50 mi. SSE Marathon, Black Gap, 762 m, 29.540°N, 102.920°W (m17 [TCWC]); Black Gap Wildlife Mgt. Area, 712 m, 29.363°N, 103.244°W (m4 [MSU]); **(3)** Val Verde Co.; Thomas Everett Ranch, 1.6 mi. E Pandale Crossing, 505 m, 30.130°N, 101.550°W (m1 [TCWC]); Eagle Nest, Langtry, 358 m, 29.809°N, 101.540°W (a1 [MSB 285921]); Amistad Reservoir, 5 mi. SE Jct. Hwy. 90 & 406, 346 m, 29.550°N, 101.010°W (m1 [TCWC]); Evans Creek, 12.8 mi. NW Del Rio on US 90, 342 m, 29.480°N, 101.030°W (m1 [TCWC]).

Chaetodipus collis coahuilensis (m = 58, a = 14, mt = 15, k = 3).—**(4)** Chihuahua; 1 mi. E El Mezquite, 880 m, 29.530°N, 104.634°W (m4 [MSB], a4 [MSB 28580–285851, 285853–285854], mt3 [MSB 285850–285851, 285854]); 6 km NW Manuel Benavides, 1,130 m, 29.151°N, 103.948°W (m3 [MSB], mt2 [MSB 274069–274070]); 6 km NW Escobillas, 1,525 m, 28.858°N, 104.166°W (m2 [MSB]); 8 km SW Escobillas, 1,500 m, 28.813°N, 104.182°W (a1 [MSB 274099], mt1 [MSB 274099]); **(5)** Chihuahua; 15 mi. N of Camargo, 1,235 m, 27.883°N, 105.167°W (m2 [MSU]); 2 mi. N, 6 mi. E Camargo, 1,264 m, 27.710°N, 105.080°W (m1 [KU]); **(6)** Chihuahua; 5 km S Jimenez, 27.080°N, 104.910°W (m2 [KU]); **(7)** 35 km SW Hércules (Coahuila), 1,420 m, 27.768°N, 103.975°W (m5 [MSB], a3 [MSB 274125, 274155, 274242], mt5 [MSB 274103, 274125–274126, 274155, 274242]); **(8)** Durango; 7 mi. N Campana, 1,144 m, 26.234°N, 103.523°W (m4 [MSU]); 3 mi. E Conejos, 1,220 m, 26.233°N, 103.835°W (m1 [MSU]); **(9)** Coahuila; 3.5 mi. W Ocampo, 27.313°N, 102.457°W (k3 [Modi 2003]); 2.5 mi. SE Ocampo, 1,005 m, 27.280°N, 102.360°W (m1 [KU]); 8 mi. N, 25 mi. W Cuatro Cienegas, 1,219 m, 27.100, 102.430°W (m1 [KU]); 6 mi. NW Cuatro Ciénegas, 850 m, 27.042°N, 102.142°W (m1 [MSB], a1 [MSB 273575], mt1 [MSB 273575]); 3 mi. NW Cuatro Cienegas, 746 m, 27.010°N, 102.090°W (m1 [KU]); 4.2 mi. W Cuatro Cienegas, 824 m, 26.986°N, 102.128°W (m1 [MSU]); 1 mi. SE Hundido, 853 m, 26.596°N, 102.296°W (m4 [MSB], a2 [MSB 272640, 272642], mt3 [MSB 272642–272643, 272721]); **(10)** Coahuila; 7 mi. S, 2 mi. E Boquillas, 548 m, 29.080°N, 102.900°W (m2 [KU]); 10 mi. S, 5 mi. E Boquillas, 457 m, 29.040°N, 102.850°W (m4 [KU]); **(11)** Coahuila; 4 mi. W Hda. La Mariposa, 701 m, 28.150°N, 101.810°W (m1 [KU]); **(12)** Coahuila; 9 mi. NW Don Martín, 27.610°N, 100.700°W (m2 [KU]); **(13)** Coahuila; 8 mi. N Hermanas, 457 m, 27.330°N, 101.220°W (m3 [KU]); 9 mi. E Hermanas, 609 m, 27.220°N, 101.080°W (m3 [KU]); 8 mi. W Nadadores, 641 m, 27.029°N, 101.708°W (m2 [MSU]); 4 mi. S, 9 mi. W San Buenaventura, 548 m, 26.990°N, 101.690°W (m1 [KU]); Pánuco, 372 m, 26.750°N, 101.060°W (m2 [KU]); 4 mi. N Acatita, 1,021 m, 26.591°N, 101.241°W (m4 [KU]); Acatita, 1,150, 26.533°N, 101.240°W (m1 [KU]).

Chaetodipus durangae (m = 166, a = 17, mt = 17, k = 9).—**(14)** Chihuahua; 3 mi. NE Parral, 1,753 m, 26.941°N, 105.598°W (m4 [MSB], a4 [MSB 272579–272580, 272602, 272895]; mt1 [MSB 272602]); Durango; 3 mi. E Las Nieves, 1,647 m, 26.401°N, 105.345°W (m5 [MSU]); 7 mi. NNE of Boquilla, 1,891 m, 26.217°N, 105.164°W (m2 [MSU]); 9 mi. NE of Boquilla, 2,501 m, 26.216°N, 105.088°W (m1 [MSU]); 2 mi. NE of Boquilla, 1,952 m, 26.139°N, 105.162°W (m2 [MSU]); 7 mi. NNE La Zarca, 1,737 m, 25.906°N, 104.695°W (m4 [MSB, 3; MSU, 1], a2 [MSB 272630, 272949], mt1 [MSB 272608]); 3 mi. SW of [Santa Cruz de] Tepehuanes, 1,781 m, 25.826°N, 105.315°W (m1 [MSU]); **(15)** Durango; 15 mi. E Crucero La Zarca, 1,920 m, 25.804°N, 104.530°W (m2, a1 [MSB 274020], mt1 [MSB 274020], k2 [MSB]); 14 mi. E La Zarca (on Hwy. 30), 25.801°N, 104.556°W (k2 [MVZ]); San Pedro Del Gallo, 5 de Mayo, 1,665 m, 25.776°N, 104.287°W (mt1 [UACH-CV-M 426]); 12 mi. SSW Mapimí, 1,525 m, 25.672°N, 103.915°W (m1 [MSU]); **(16)** Durango; 9.7 mi. N Alamillo, 1,891 m, 25.546°N, 104.590°W (m3 [MSU]); 8.5 mi. N Alamillo, 1,800 m, 25.502°N, 104.590°W (m1 [MSU]); 4.6 mi. N Alamillo, 1,769 m, 25.446°N, 104.598°W (m2 [MSU]); 3.9 mi. N Alamillo, 1,739 m, 25.437°N, 104.603W (m4 [MSU]); 3.7 mi. N Alamillo, 1,708 m, 25.434°N, 104.602°W (m7 [MSU]); 3.1 mi. N Alamillo, 1,678 m, 25.425°N, 104.604°W (m1 [MSU]); 2.5 mi. N Alamillo, 1,647 m, 25.416°N, 104.601°W (m1 [MSU]); 1.4 mi. N Alamillo, 1,617 m, 25.401°N, 104.609°W (m4 [MSU]); 0.7 mi. N Alamillo, 1,586 m, 25.391°N, 104.610°W (m11 [MSU]); 2 mi. S Alamillo, 1,525 m, 25.372°N, 104.612°W (m5 [MSU]); 2.6 mi. S Alamillo, 1,495 m, 25.346°N, 104.627°W°W (m6 [MSU]); 3.5 mi. S Alamillo, 1,464 m, 25.333°N, 104.631°W (m1 [MSU; **(17)** Durango; Río Nazas, 0.75 mi. E Lazaro Cardenas Dam, 1,485 m, 25.595°N, 105.003°W (m1 [KU]); 2 mi. S El Palmito, 1,479 m, 25.574°N, 104.983°W (m5 [MSU]); **(18)** Durango; Río Nazas, 10 mi. NNW Rodeo, 25.300°N, 104.630°W (m1 [KU]); 6.1 mi. S Alamillo, 1,403 m, 25.298°N, 104.643°W (m5 [MSU]); 1.7 mi. S (by road) Rodeo, 1,354 m, 25.145°N, 104.547°W (m5, a5 [MVZ 150615–150619], mt4 [MVZ 150616–150619], k2 [MVZ]); 1.8 mi. SE Rodeo 25.145°N, 104.547°W (m15, k2 [MVZ]); 6 mi. WNW of Chinacates, 2,166 m, 25.017°N, 105.217°W (m2 [MSU]); 15 mi. SSE of Rodeo, 1,693 m, 24.989°N, 104.478°W (m7 [MSU]); **(39)** 1.5 mi. SE Los Herreras, 1,760 m, 25.107°N, 105.466°W (a5 [TTU 48507, 48511, 48514, 48524, 48555], mt4 [TTU 48507, 48511, 48514, 48555]); 50 km W Los Herreras, 2,486 m, 25.027°N, 105.728°W (mt1 [TTU 48536]); **(19)** Durango; 26 mi. SW Yerbanis, 2,051 m, 24.474°N, 104.138°W (m2 [MSU]); 1 mi. N Chorro, 1,965 m, 24.300°N, 104.150°W (m8 [KU]); 6 mi. NW La Pila, 1,876 m, 24.180°N, 104.350°W (m18 [MSU]); 6 mi. NW Hda. La Pila, 1,876 m, 24.180°N, 104.350°W (m2 [MSU]); 9 mi. N Durango, 1,889 m, 24.150°N, 104.660°W (m1 [KU]); 8 mi. N Durango, 1,889 m, 24.140°N, 104.660°W (m1 [KU]); 8 mi. NE Durango, 1,889 m, 24.100°N, 104.580°W (m2 [KU]); 5 mi. N Durango, 1,952 m, 24.096°N, 104.670°W (m1 [MSU]); 4 mi. E Durango, 1,891 m, 24.024°N, 104.612°W (m1 [MSU]); 4 mi. W Durango, 1,889 m, 24.020°N, 104.610°W (m10 [KU]); 3 mi. NW Nombre de Dios on road to La Constancia, 23.877°N, 104.258°W (k1 [MVZ]); 15 mi. S, 29 mi. E Durango, 1,737 m, 23.800°N, 104.240°W (m10 [KU]); 2.7 km N, 2.2 km W Chachacuaxtle, 1,780 m, 23.706°N, 104.321°W (mt2 [CIIDIR CRD 6927–6928]); 11 mi. N Mezquital, 1,739 m, 23.633°N, 104.396°W (m2 [MSU]); 0.7 km N, 1.5 km W Agua Zarca, 1,767 m, 23.524°N, 104.435°W (mt2 [CIIDIR CRD 8220–8221]); 2 km SW Mezquital, 1,450 m, 23.460°N, 104.408°W (m1 [MSU]).

Chaetodipus nelsoni (m = 144, a = 37, mt = 88, k = 9).—**(20)** Coahuila; 11 km NNE of Matamoros, 1,250 m, 25.620°N, 103.190°W (m1 [MSU]); 4.7 mi. N Flor de Jimulco, 1,274 m, 25.158°N, 103.382°W (m1, mt2 [MSB285855, 285859]); 2 mi. E Flor de Jimulco, 1,344, 25.117°N, 103.308°W (m3, a3 [MSB 285856–285857, 285861], mt4 [MSB 285856–285858, 285861]); **(21)** Durango; 7 mi. SW Nazareño, 1,203 m, 25.349°N, 103.492°W (m3, a2 [MSB 273922–283923]; mt3 [MSB 273900–273901, 273922]); 5 km NW La Unión, 1,245 m, 25.316°N, 103.532°W (m6, a3 [MSB 274193, 274215–274216]; mt5 [MSB 274193, 274215–274216, 274218–274219]); 2 km SW La Unión, 1,170 m, 25.283°N, 103.515°W (m3, a3 [MSB 273917–273918, 274210], mt3 [MSB 273917–273918, 274210]); **(22)** Durango; 5 km SW Lerdo, 1,158 m, 25.535°N, 103.694°W (m1, a1 [MSB 272554]; mt3 [MSB 272554, 272664–272665]); 7 km SW Lerdo, 1,158 m, 25.534°N, 103.589°W (m8, a2 [MSB 272583, 272585]; mt8 [MSB 272582–272587, 272609–272610]); **(23)** Durango; 7 mi SW León Guzmán, 1,464 m, 25.429°N, 103.730°W (m1 [MSU]); **(24)** Durango; 3 mi. SW of Chocolate, 1,388 m, 25.263°N, 103.662°W (m1 [MSU]); 5 km SE Graseros, 1,235 m, 25.223°N, 103.713°W (m2, a2 [MSB 273946, 274240]; mt2 [MSB 273946, 274240]); 8 km S Pedriceña, 1,395 m, 25.060°N, 103.833°W (m1, a1 [MSB 274063]; mt1 [MSB 274063]); **(25)** Durango; La Velardeña, 1,331 m, 25.088°N, 103.758°W (mt2 [UACH-CV-M 427–8]); 1 km S Cuencamé, 1,612 m, 24.857°N, 103.698°W (mt3 [UACH-CV-M 436–8]); Capasuya, 5 km E of Yerbanis, 1,938 m, 24.740°N, 103.790°W (m1 [MSU]); 6.4 km W of Atotonilco, 2,196 m, 24.665°N, 103.752°W (m1 [MSU]); Hacienda Atotonilco, 1,976 m, 24.645°N, 103.705°W (m4, a1 [MSB 285885]; mt5 [MSB 285881–285885]); Hacienda de Atotonilco, 2,040 m, 24.645°N, 103.705°W (m1 [MSU]); **(26)** Coahuila; La Muralla, 2,017 m, 26.357°N, 101.352°W (m3, a1 [MSB 285872]; mt4 [MSB 285872–285874, 285892]); **(27)** 20 mi. W, 8 mi. N Parras, 1,098 m, 25.513°N, 102.363°W (m3 [MSU]); **(28)** Coahuila; ca. 14 mi. N Saltillo, 25.670°N, 100.977°W (k1 [Patton 1970]); 0.7 mi. S San Miguel on Hwy. 57, 25.606°N, 101.101°W (k1 [MVZ]); 5 km S, 16 km W General Cepeda, 1,650 m, 25.331°N, 101.642°W (m4, a3 [MSB 285867, 285869, 285880]; mt4 [MSB 285860, 285866–285867, 285880]); 2 mi. E Agua Nueva, 2,017 m, 25.184°N, 101.059°W (m3, a2 [MSB 285865, 285871]; mt5 [MSB 285863–285865, 285870–285871]); **(29)** Zacatecas; 4 km N of San Juan de los Charcos, 1,350 m, 25.078°N, 102.609°W (m2 [MSU]); 10 km ESE of Charcos, 1,500 m, 24.999°N, 102.508°W (m3 [MSU]); 6 km W of Apizolaya, 1,800 m, 24.815°N, 102.329°W (m3 [MSU]); 3 km SE of Apizolaya, 1,920 m, 24.796°N, 102.256°W (m2 [MSU]); **(30)** Zacatecas; 25 km NE of Camacho, 1,975 m, 24.613°N, 102.217°W (m4 [MSU]); 3 km NW San Felipe de Nuevo Mercurio, 1,770 m, 24.248°N, 102.173°W (m6, MSU]); **(31)** Zacatecas; 12 km ENE Concepción del Oro, 1,854 m, 24.656°N, 101.321°W (m5 [MSU]); 2 km SE Sabana Grande, 1,945 m, 24.479°N, 101.699°W (m3 [MSU]); 26 km S Concepción del Oro, 1,859 m, 24.402°N, 101.392°W (m3, a1 [MSB 273609]; mt4 [MSB 273609, 273631, 273719, 273851]); 15 km WSW of San Tiburcio, 1,980 m, 24.142°N, 101.571°W (m3 [MSU]); 25 km SW of San Tiburcio, 2,030 m, 23.986°N, 101.645°W (m1 [MSU]); **(32)** Zacatecas; 10 mi SE Juan Aldama, 2,211 m, 24.187°N, 103.292°W (m1 [MSU]); 15 km NNW of Nieves, 1,910 m, 24.119°N, 103.071°W (m3 [MSU]); 9 mi. NE of Nieves, 2,013 m, 24.086°N, 102.927°W (m1 [MSU]); 23 km NE of Río Grande, 1,800 m, 23.970°N, 102.889°W (m1 [MSU]); 3 km E El Arenal, 2,460 m, 23.645°N, 103.418°W (m1 [MSU]); 2 km S of Monte Mariana, 2,110 m, 23.309°N, 103.112°W (m2 [MSU]); 1.8 mi. N Fresnillo on Hwy. 45, 23.194°N, 102.887°W (k1 [MVZ]); **(33)** Zacatecas; 6.5 km S of La Colorada, 1,970 m, 23.747°N, 102.472°W (m5 [MSU]); 13 km WNW of Capriote, 2,100 m, 23.691°N, 102.244°W (m5 [MSU]); 1 mi. SE Bañon, 2,138 m, 23.164°N, 102.466°W (m4, mt5 [MSB 285998–285902]); **(34)** San Luis Potosí; 11 km W Cedral, 1,745 m, 23.845°N, 100.826°W (mt1 [UACH-CV-M 435]); 3 mi. S, 0.5 mi. W Matehuala, 1,494 m, 23.590°N, 100.644°W (m1, a1 [MSB 272775], mt3 [MSB 272775–272776, 272809]); 10 mi. S, 1 mi. W Matehuala, 1,463 m, 23.483°N, 100.627°W (m4, a2 [MSB 272669, 272746]; mt5 [MSB 272667, 272669, 272746–272748]); **(35)** Zacatecas; 18 km N of San Juan Capistrano (nr. Las Tablas), 1,100 m, 22.804°N, 104.099°W (m2 [MSU]); Jalisco; 30 km W Huejuquilla El Alto, 1,166 m, 22.683°N, 104.061°W (a4 [TTU 75569–75572]; mt1 [TTU 75571]); Zacatecas; 5 km NE of San Juan Capistrano, 1,330 m, 22.673°N, 104.067°W (m1 [MSU]); 3 km N of San Juan Capistrano, 1,500 m, 22.668°N, 104.099°W (m1 [MSU]); Jalisco; 1 mi. NW Mezquitic, 1,523 m, 22.390°N, 103.730°W (m3 [KU]); **(36)** Zacatecas; 2 mi. S and 5 mi. E Zacatecas, 2,349 m, 22.743°N, 102.503°W (m1 [MSU]); 8 km SW of Jerez (Nr. Susticacan), 2,030 m, 22.586°N, 103.027°W (m4 [MSU]); Jalisco; 3 mi. S Huejucar, 1,798 m, 22.310°N, 103.210°W (m2 [KU]); **(37)** San Luis Potosi; 10 mi. W Salinas, 2,134 m, 22.640°N, 101.857°W (m2, a3 [MSB 273744, 273878–273879]; mt4 [MSB 273658, 273744, 273878–273879]); 5.7 mi. E, 1.0 mi. N (by road) Peñon Blanca, 22.592°N, 101.680°W (k2 [MVZ]); San Luis Potosi; La Tinaja, 1,760 m, 22.353°N, 100.803°W (mt5 [UACH-CV-M 432–4, UACH-CV-M 429–30]); Aguascalientes; 3.1 mi. (by road) E Tepezala, 22.226°N, 102.117°W (k2 [MVZ]); Zacatecas; 25 km SSE of Pinos, 2,425 m, 22.089°N, 101.488°W (m5 [MSU]); Aguascalientes; 2 km NE Chicalote, 1,924 m, 22.018°N, 102.246°W (m5, a2 [MSB 274016, 274035]; mt5 [MSB 274016–274019, 274035]); San Luis Potosí; 0.25 mi. W Villa de Arriaga (on Hwy. 80), 21.910°N, 101.386°W (k2 [MVZ]); **(38)** Zacatecas; 30 km NE of Jalpa (La Palma), 1,740 m, 21.751°N, 102.816°W (m5 [MSU]); Jalisco; 2 mi. WNW Lagos de Moreno, 1,943 m, 21.367°N, 101.960°W (m1 [MSU]); **(40)** Guanajuato; 9 km W, 3 km N San Luís de la Paz, 2,014 m, 21.315°N, 100.610°W (mt1 [UACH-CV-M 431]).