TEXAS TECH UNIVERSITY
Natural Science Research Laboratory

SPECIAL PUBLICATIONS
Museum of Texas Tech University
Number 78 1 November 2023

GENETIC IDENTIFICATION OF POCKET GOPHERS (GENERA *CRATOGEOMYS*, *GEOMYS*, AND *THOMOMYS*) IN TEXAS AND SURROUNDING AREAS

ROBERT D. BRADLEY, ANNIE T. PHAM, KINSEY A. RICH, EMMA K. ROBERTS, TAYLOR J. SONIAT, CASSIE M. POEHLEIN, MARIAH N. MILLS, MORGAN BALLARD, RICHARD M. PITTS, LARAMIE L. LINDSEY, MICHAELA K. HALSEY, DAVID A. RAY, RICHARD D. STEVENS, DAVID J. SCHMIDLY, AND EMILY A. WRIGHT

Front cover: Top left, *Cratogeomys castanops angusticeps*, photograph by Brandon A. Gross; bottom left, *Geomys texensis bakeri*, photograph by Robert D. Bradley; right, *Thomomys baileyi scotophilus*, photograph by Emily A. Wright.

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Layout and Design: Lisa Bradley
Cover Design: Photographs by Robert D. Bradley, Brandon A. Gross, and Emily A. Wright
Production Editor: Lisa Bradley

This book was set in Times New Roman and printed on acid-free paper that meets the guidelines for permanence and durability of the Committee on Production Guidelines for Book Longevity of the Council on Library Resources.

Printed: 1 November 2023

Library of Congress Cataloging-in-Publication Data

Special Publications of the Museum of Texas Tech University, Number 78
Series Editor: Robert D. Bradley

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ISSN 0149-1768
ISBN 1-929330-46-4
ISBN13 978-1-929330-46-1

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Lubbock, TX 79409-3191 USA
(806)742-2442

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ABSTRACT

Three genera of pocket gophers occur in Texas: *Cratogeomys* in the western third of the state, *Thomomys* in the montane regions of the Trans-Pecos Region and the southwestern portion of the Edwards Plateau, and *Geomys* statewide except for portions of the Trans-Pecos Region. However, due to considerable morphological conservation, differentiating among species and subspecies has been difficult, if not impossible. Advanced molecular markers such as DNA sequencing have proven useful in defining species boundaries and in generating phylogenetic relationships at the species level, but general taxon sampling and geographic representation has not been sufficient to provide a detailed assessment at the subspecific level. Herein, DNA sequence data obtained from the mitochondrial cytochrome-*b* gene was used to assess variation at the subspecific and species level for the three genera of pocket gophers occurring in Texas. Specimens collected from or adjacent to type localities were used to represent the genotype associated with each of the taxonomic names that have been proposed for Texas pocket gophers. Further, findings from previous morphometric, allozymic, karyotypic, and DNA studies were combined with DNA sequence data generated herein to assemble the broadest possible dataset for providing a taxonomic synthesis of each genus. In total, 22 taxonomic names were evaluated for *Cratogeomys*, 25 for *Geomys*, and 24 for *Thomomys*. For *Cratogeomys* occurring in Texas and immediate surrounding areas, 1 species and 13 subspecies were proposed; for *Geomys* occurring in Texas and immediate surrounding areas, 12 species and 18 subspecies were proposed; and for *Thomomys* occurring in Texas and immediate surrounding areas, 4 species and 22 subspecies were proposed. New distribution maps were provided to reflect the updated taxonomy. Forty-three original names were synonymized, elevated to species, or otherwise reassigned, and two new taxonomic entities were identified as needing official description.

Key words: *Cratogeomys*, cytochrome-*b* gene, *Geomys*, phylogenetics, pocket gophers, *Thomomys*

INTRODUCTION

In Texas, three genera of pocket gophers (*Cratogeomys*, *Geomys*, and *Thomomys*) are recognized (Schmidly and Bradley 2016), with species of *Cratogeomys* predominately occurring in the western third of the state, *Thomomys* in the southwestern fourth, primarily in the montane regions of the Trans-Pecos Region and the southwestern portion of the Edwards Plateau, and *Geomys* statewide except for portions of the Trans-Pecos Region. As a result of their adaptation for a fossorial lifestyle, pocket gophers exhibit considerable morphological divergence relative to other rodent groups. Among the three genera, morphological characteristics, such as the presence, absence, or number of grooves located on the incisors, easily differentiate each genus (Russell 1968a, b; Hall 1981; Schmidly and Bradley 2016): *Cratogeomys* have a single deep, median groove along the anterior surface of the incisors and are the largest in size of the three genera (Baird 1852); *Geomys* have two deep, median grooves along the anterior surface of the incisors and generally are smaller in size than *Cratogeomys* (Merriam 1895) but larger than *Thomomys*; *Thomomys* lacks conspicuous, deep, median grooves along the anterior surface of the incisors and are the smallest of the Texas pocket gophers (Eydoux and Gervais 1836).

Within the three genera of pocket gophers, there exists considerable morphological similarity (termed morphological conservation) resulting in difficulties differentiating among species and subspecies. Since the early 1900s, a vast literature has accumulated as researchers have attempted to decipher this morphological conservation, discern species boundaries, and document levels of variation (morphometric and genetic) among species. Many authors have examined a variety of morphological characters (Bangs 1898; Bailey 1915; Komarek and Spencer 1931; Hall 1932a, b, 1936, 1981; Goldman 1936, 1938, 1947; Davis 1938, 1940a, b; Hooper 1940; Swenk 1940; Sherman 1944; Durrant 1946; Villa-R. and Hall 1947; Baker 1950, 1953; Baker and Glass 1951; Dalquest 1953; Jackson 1957; McLaughlin 1958; Alvarez 1963; Anderson 1966; Russell 1968a, b; Baker and Genoways 1975; Smith et al. 1983; Mauk et al. 1999; Beauchamp-Martin et al. 2019). However, given their strictly fossorial lifestyle, adaptations to local soils, and tendency to be distributed in small, isolated populations, morphometric characters generally are unreliable in discriminating among species and subspecies (Baker et al. 2003). For example, Mauk et al. (1999) used sophisticated landmark-based morphometrics in an attempt to identify diagnostic characters that could be used to define species boundaries in seven species of *Geomys* in Texas. In that study, only *G. breviceps* could be distinguished, with statistical confidence, from the other six species examined therein, emphasizing the morphological conservatism among pocket gopher species.

Genetic characters such as chromosomes and allozymes (Patton and Dingman 1968; Berry and Baker 1971; Patton 1973; Baker and Genoways 1975; Hart 1978; Williams and Genoways 1980; Tucker and Schmidly 1981; Honeycutt and Williams 1982; Hafner and Geluso 1983; Heaney and Timm 1983, 1985; Burns et al. 1985; Lee and Baker 1987; Sudman et al. 1987; Qumsiyeh et al. 1988; Baker et al. 1989, 2003; Dowler 1989; Patton and Smith 1990, 1994; Block and Zimmerman 1991; Bradley et al. 1991; Smith and Patton 1993; Smolen and Bickham 1994, 1995; Smith 1998; Burt and Dowler 1999; Jones and Baxter 2004), as well as more advanced molecular markers (Sulentich et al. 1991; DeWalt et al. 1993; Smolen and Bickham 1995; Burt and Dowler 1999; Jolley et al. 2000; Demastes et al. 2002; Baker et al. 2003; Patton 2005; Wickliffe et al. 2005; Sudman et al. 2006; Chambers et al. 2008; Genoways et al. 2008; Hafner et al. 2008; Álvarez-Casteneda 2010) proved useful, in most cases, in defining species boundaries and in generating phylogenetic relationships at the species level. However, in general, taxon sampling and geographic representation have not been sufficient to provide a detailed assessment at the subspecific level. For example, the most recent taxonomic revisions and species lists (see Schmidly et al. 2022) for each group indicate that within Texas, the genus *Cratogeomys* contains a single species (*castanops* - 1 or 7 subspecies, Hollander 1990; Hafner et al. 2008); the genus *Geomys* contains nine species (*arenarius* - 1 subspecies, *attwateri* - 0 subspecies, *breviceps* - 1 subspecies, *bursarius* - 1 subspecies, *jugossicularis* - 1 subspecies, *knoxjonesi* - 0 subspecies, *personatus* - 6 subspecies, *streckeri* - 0 subspecies, and *texensis* - 2 subspecies (Sudman et al. 2006; Chambers et al. 2008); and the genus *Thomomys* also contains a single species (*bottae* - 9 or 14 subspecies, Beauchamp-Martin et al. 2019). See Table 1 for a list of species and subspecies, taxonomic history and designations, and type localities of pocket gophers occurring in Texas and adjacent regions in Louisiana, New Mexico, Oklahoma, and Mexico.

Consequently, despite being studied extensively for > 115 years since Vernon Bailey's first "statewide synopsis" of pocket gophers presented in the *Biological Survey of Texas* (Bailey 1905), species and subspecies identification, taxonomic and conservation status, and determination of phylogenetic relationships within these three genera remain challenging due to a combination of: conservative morphology, inappropriate character assessments, low taxon sampling, presence of both sibling and cryptic species, unclear intergrada-

Table 1. Original taxonomic names, type localities, locality referenced to distribution maps (Fig. 1), and DNA sequence status for the three genera of pocket gophers occurring in Texas and adjacent regions in Colorado (CO), Louisiana (LA), New Mexico (NM), Oklahoma (OK), and Mexico (MX). "Close" indicated that samples could not be obtained from the type locality; however, samples were obtained from nearby localities that were within the undisputed distribution of that taxon.

Original Description	Type Locality	Locality	Sequenced
Cratogeomys			
C. castanops angusticeps	Eagle Pass, Maverick Co., TX	(Loc 1)	Yes
C. castanops bullatus	2 mi S, 6.5 mi E Nava, 810 ft, Coahuila, MX	(Loc 2)	Yes
C. castanops consitus	Gallego, 5,500 ft, Chihuahua, MX	(Loc 5)	Yes
C. castanops convexus	7 mi E Las Vacas (= Acuna), Coahuila, MX	(Loc 6)	No
C. castanops dalquesti	1 mi N, 4 mi W Sterling City, Sterling Co., TX	(Loc 7)	Yes
C. castanops excelsus	10 mi W Laguna de Mayrán, Coahuila, MX	(Loc 8)	Yes
C. castanops hirtus	Albuquerque, 5,500 ft, Bernalillo Co., NM	(Loc 9)	No
C. castanops jucundus	Hermanas, 1,205 ft, Coahuila, MX	(Loc 10)	Yes
C. castanops lacrimalis	Roswell, 3,500 ft, Chaves Co., NM	(Loc 11)	Yes
C. castanops perplanus	Tascosa, Oldham Co., TX	(Loc 14)	Yes
C. castanops sordidulus	1.5 mi NW Ocampo, 3,300 ft, Coahuila, MX	(Loc 17)	Yes
C. castanops subsimus	Jaral (= San Antonio de Jaral), Coahuila, MX	(Loc 18)	Yes
C. castanops surculus	La Zarca, Durango, MX	(Loc 19)	Yes
C. castanops tamaulipensis	Matamoros, Tamaulipas, MX	(Loc 20)	Yes
C. castanops ustulatus	Don Martín, 800 ft, Coahuila, MX	(Loc 22)	No
Geomys clarkii	Ojinaga, Chihuahua, MX (old incorrect locality)	(Loc 4a)	Yes
Geomys clarkii	Presidio del Norte, Coahuila, MX (new locality as discussed herein)	(Loc 4b)	No
Pappogeomys castanops parviceps	18 mi SW Alamogordo, Otero Co., NM	(Loc 12)	Yes
Pappogeomys castanops perexiguus	6 mi E Jaco, 4,500 ft, Chihuahua, MX,	(Loc 13)	No
Pappogeomys castanops pratensis	8 mi W, 3 mi S Alpine, 5,100 ft, Brewster Co., TX	(Loc 15)	Yes
Pappogeomys castanops simulans	17 mi SE Washburn, Armstrong Co., TX	(Loc 16)	Yes
Pappogeomys castanops torridus	3 mi E Sierra Blanca, about 4,000 ft, Hudspeth Co., TX	(Loc 21)	Yes
Pseudostoma castanops	Prairie road to Bents Fort, near Las Animas, CO	(Loc 3)	Yes

Table 1. (cont.)

Original Description	Type Locality	Locality	Sequenced
Geomys			
G. arenarius	El Paso, El Paso Co., TX	(Loc 1)	Yes
G. arenarius brevirostris	9 mi W Tularosa, Hot Springs Rd., Otero Co., NM	(Loc 2)	Yes
G. breviceps	Prairie Mer Rouge, Morehouse Parish, LA	(Loc 4)	Yes
G. breviceps ammophilus	Cuero, DeWitt Co., TX	(Loc 6)	Yes
G. breviceps attwateri	Rockport, Matagorda Co., TX	(Loc 3)	Yes
G. breviceps brazensis	5 mi E Kurten, Grimes Co., TX	(Loc 7)	Yes
G. breviceps dutcheri	Fort Gibson, Muskogee Co., OK	(Loc 8)	Yes
G. breviceps llanensis	Llano, Llano Co., TX	(Loc 23)	Yes
G. breviceps ludemani	7 mi W Fannett, Jefferson Co., TX	(Loc 9)	No
G. breviceps pratincolus	2 mi E Liberty, Liberty Co., TX	(Loc 11)	Yes
G. breviceps sagittalis	Clear Creek, Galveston Co., TX	(Loc 5)	No
G. breviceps terricolus	1 mi N Texas City, Galveston Co., TX	(Loc 12)	No
G. bursarius knoxjonesi	4.1 mi N, 5.1 mi E Kermit, Winkler Co., TX	(Loc 13)	Yes
G. lutescens jugossicularis	Lamar, Prowers Co., CO	(Loc 14)	Yes
G. lutescens major	8 mi W Clarendon, Donley Co., TX	(Loc 10)	Yes
G. personatus	Padre Island, Cameron Co., TX	(Loc 20)	Yes, close
G. personatus davisi	3 mi N, 2.8 mi W Zapata, Zapata Co., TX	(Loc 15)	Yes
G. personatus fallax	South side Nueces Bay, Nueces Co., TX	(Loc 16)	No
G. personatus fuscus	Fort Clark, Kinney Co., TX	(Loc 17)	No
G. personatus maritimus	Flour Bluff, 11 mi SE Corpus Christi, Nueces Co., TX	(Loc 18)	Yes
G. personatus megapotamus	4 mi SE Oilton, Webb Co., TX	(Loc 19)	Yes
G. personatus streckeri	Carrizo Springs, Dimmit Co., TX	(Loc 21)	Yes
G. personatus tropicalis	Altamira, Tamaulipas, MX	(Loc 25)	Yes
G. texensis bakeri	1 mi E D'Hanis, Medina Co., TX	(Loc 22)	Yes
G. texensis	Mason, Mason Co., TX	(Loc 24)	Yes

Table 1. (cont.)

Original Description	Type Locality	Locality	Sequenced
Thomomys			
T. aureus lachuguilla	Arid foothills near El Paso, El Paso Co., TX	(Loc 9)	Yes
T. baileyi	Sierra Blanca, Hudspeth Co., TX	(Loc 3)	No
T. baileyi spatiosus	Alpine, 4,500 ft, Brewster Co., TX	(Loc 19)	Yes, close
T. baileyi tularosae	0.5 mi W Tularosa, Otero Co., NM	(Loc 23)	Yes, close
T. bottae actuosus	Corona, Lincoln Co., NM	(Loc 1)	Yes
T. bottae analogus	12 mi S General Cepeda, Coahuila, MX	(Loc 2)	Yes, close
T. bottae connectens	Clawson Dairy, 5 mi N Albuquerque, 4,943 ft, Bernalillo Co., NM	(Loc 5)	Yes, close
T. bottae cultellus	Hall's Peak, Mora Co., NM	(Loc 6)	Yes, close
T. bottae guadalupensis	McKittrick Canyon, 7,800 ft, Guadalupe Mts., TX	(Loc 7)	Yes
T. bottae humilis	3 mi W Hacienda San Miguel, 2,200 ft, Coahuila, MX	(Loc 8)	No
T. bottae limpiae	Limpia Canyon, 1 mi N Fort Davis, 4,700 ft, Jeff Davis Co., TX	(Loc 11)	Yes
T. bottae opulentus	Las Palomas on the Rio Grande, Sierra Co., NM	(Loc 12)	Yes, close
T. bottae pervarius	Lloyd Ranch, 35 mi S Marfa, 4,200 ft, Presidio Co., TX	(Loc 14)	Yes, close
T. bottae retractus	Fortin, 3.300 ft, 20 mi N, 2 mi E San Geronimo, Coahuila, MX	(Loc 15)	No
T. bottae robertbakeri	2.5 mi E McCamey, Upton Co., TX	(Loc 16)	Yes
T. bottae ruidosae	Ruidoso, Lincoln Co., NM	(Loc 17)	Yes
T. bottae scotophilus	1.5 mi W Bat Cave, Sierra Diablo, Hudspeth Co., TX	(Loc 18)	Yes
T. bottae toltecus	Colonia Juarez, 4,500 ft, Casas Grande River, Chihuahua, MX	(Loc 22)	Yes, close
T. bottae villai	7 mi S, 2 mi E Boquillas, 1,800 ft, Coahuila, MX	(Loc 24)	No
T. fulvus texensis	Head of Limpia Creek, 5,500 ft, Jeff Davis Co., TX	(Loc 21)	Yes
T. lachuguilla confinalis	35 mi E Rock Springs, 2,450 ft, Uvalde Co., TX	(Loc 4)	Yes, close
T. lachuguilla limitaris	4 mi W Boquillas, Brewster Co., TX	(Loc 10)	Yes
T. pectoralis	Carlsbad Cave, Eddy Co., NM	(Loc 13)	Yes, close
T. sturgisi	Sierra del Carmen 6,000 ft, Coahuila, MX	(Loc 20)	Yes, close

tion of boundaries between populations, and, in some instances, high degrees of chromosomal and allozymic variation (see Sudman et al. 2006, Beauchamp-Martin et al. 2019). As a result, pocket gophers are of a continual conservation and taxonomic concern because of the paucity of available information concerning intra- and interspecific, as well as intra- and intersubspecific, variation. Further, the lack of inclusion of type or topotype samples, in most studies, has precluded a true taxon-level assessment of genetic variation based on currently available or historic taxonomic names. Given the plethora of available taxonomic names for Texas pocket gophers (Table 1), a study incorporating samples obtained from type localities (or reasonably close) is required to link a taxonomic name to a representative genotype. This conceptual framework allows genotypes from across a proposed distribution to be compared to the genotype "representing" the type, much in the same manner that holotype specimens are used in morphometric studies. Therefore, the goal of this study was to delimit species and subspecific boundaries and determine taxon distributions by incorporating DNA sequence data from the mitochondrial cytochrome-*b* gene (*Cyt*b) of type or other accepted representatives of nominal names assigned to Texas pocket gophers. This allows researchers to compare a DNA sequence that is unassigned to a pocket gopher taxonomic name and extrapolate its taxonomic affiliation. Further, by examining all taxonomic entities (current and historic), this study will provide data for evaluating conservation and systematic concerns related to pocket gophers in Texas.

METHODS AND MATERIALS

Sampling.—Individuals representing three genera of pocket gopher (*Cratogeomys*, *Geomys*, and *Thomomys*) were collected from naturally-occurring populations in Texas and surrounding areas over a two-year period (2017–2019). Efforts were made to collect specimens from topotype or near type localities to establish the genotypic architecture for a particular taxonomic name (Figs. 1a–1c; Table 1). Further, to increase geographic and taxonomic sampling, tissue samples were borrowed from natural history collections and DNA sequences were obtained from GenBank. In total, 319 individuals representing three genera of pocket gopher (*Cratogeomys castanops*, n = 69; *Geomys* spp., n = 166; and *Thomomys bottae*, n = 84) were examined. In some cases, taxa occurring outside of Texas were included to help resolve taxonomic uncertainties. See Appendix I for a list of all specimens examined. Specimens were collected following methods outlined in the guidelines of the American Society of Mammalogists (Sikes et al. 2016) and protocols approved by the Texas Tech University Animal Care and Use Committee (protocol #17023-02).

DNA sequencing.—Genomic DNA (gDNA) was isolated from 0.1 g of frozen liver tissue using the Qiagen DNeasy blood and tissue extraction kit (Qiagen, Valencia, California). When possible, the complete *Cyt*b gene (1,143 bp) was amplified using the polymerase chain reaction (PCR) method (Saiki et al. 1988) with primers LGL765 (forward, Bickham et al. 1995) and LGL766 (reverse, Bickham et al. 2004) and MVZ05 (Smith and Patton 1991) and MVZ14 (Da Silva and Patton 1993), following the standard HotStarTaq (Qiagen, Valencia, California) protocol: 25 µL reactions containing 3 µL of gDNA, 12.5 µL HotStarTaq premix, 8.3 µL of distilled water, and 0.6 µL of each 10 µM primer. The thermal profile for PCR was as follows: hot start at 80°C, initial denaturation at 95°C for 2 min, followed by 34 cycles of denaturation at 95°C for 30 s, annealing at a range of 42–43°C for 45 s, and extension at 73°C for 1 min, with a final extension of 73°C for 15 min.

Tissue samples were unavailable for *T. b. sturgisi*; therefore, a small piece of a toe (approximately 5 mg excluding the toenail) was obtained from two museum voucher specimens and included in the dataset. DNA was isolated following Wright et al. (2020), in that toe clips initially were cleaned using a 95% ethanol rinse and then immediately treated with UV irradiation for 5 min. Each toe clip was washed with ddH_2O and incubated at 56°C for 15 minutes (3 repetitions). gDNA was isolated using the Qiagen DNeasy blood and tissue extraction kit (Qiagen, Valencia, California). A 423 bp fragment (position 400–823 bp aligned) of the *Cyt*b gene was amplified using PCR methods with primers 400F (Edwards et al. 2001) and Thomomys700H (5'-AAAAGTATCATTCAGGYTTAATGTGRGG-3'),

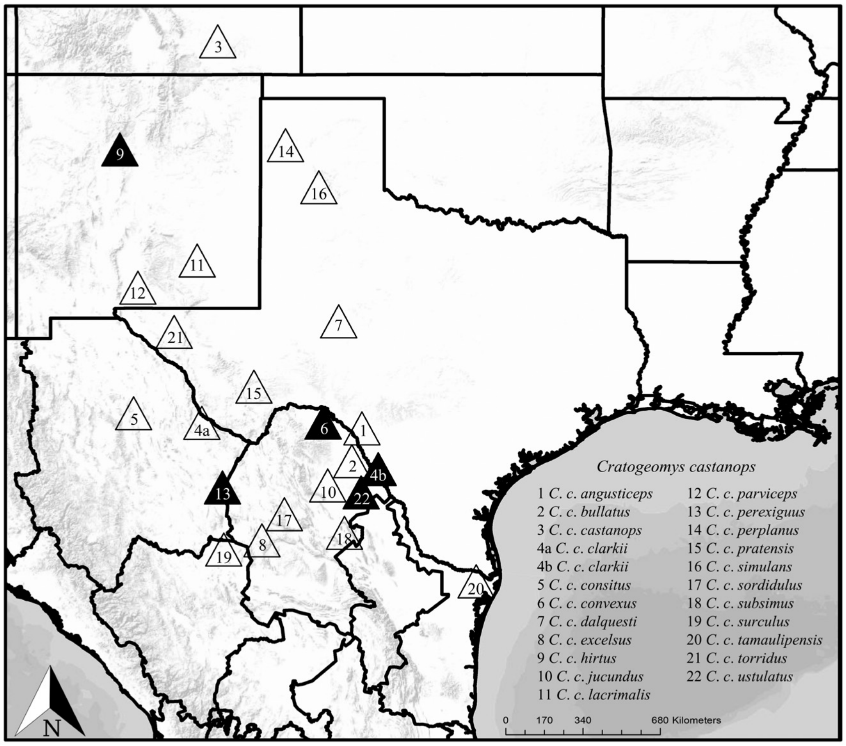


Figure 1a. Approximate location of the type localities for *Cratogeomys*. White triangles indicate localities that were sampled in this study; black triangles depict type localities for which no samples were available.

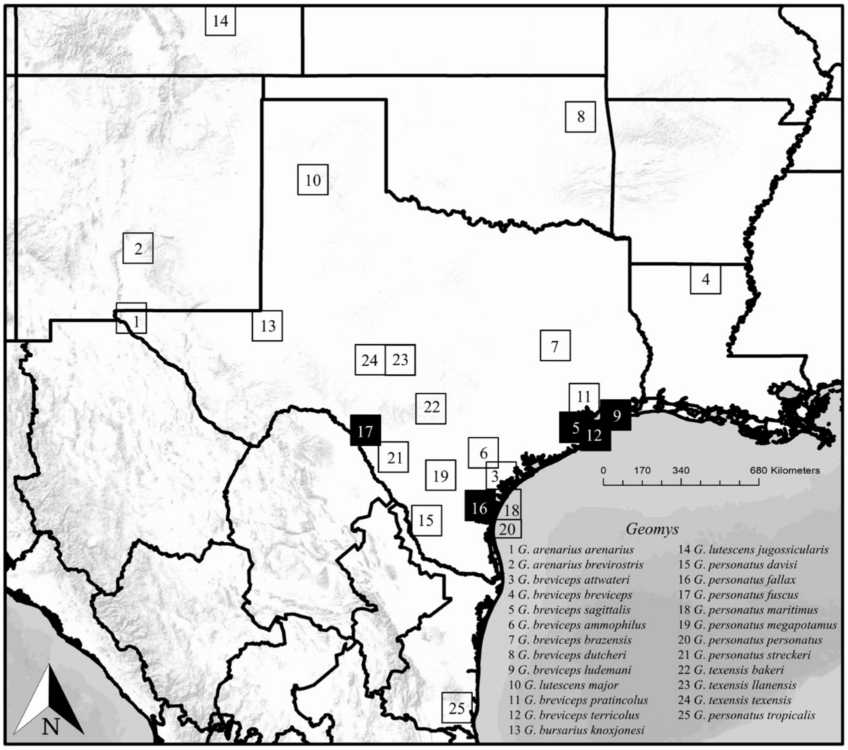


Figure 1b. Approximate location of the type localities for *Geomys*. White squares indicate localities that were sampled in this study; black squares depict type localities for which no samples were available.

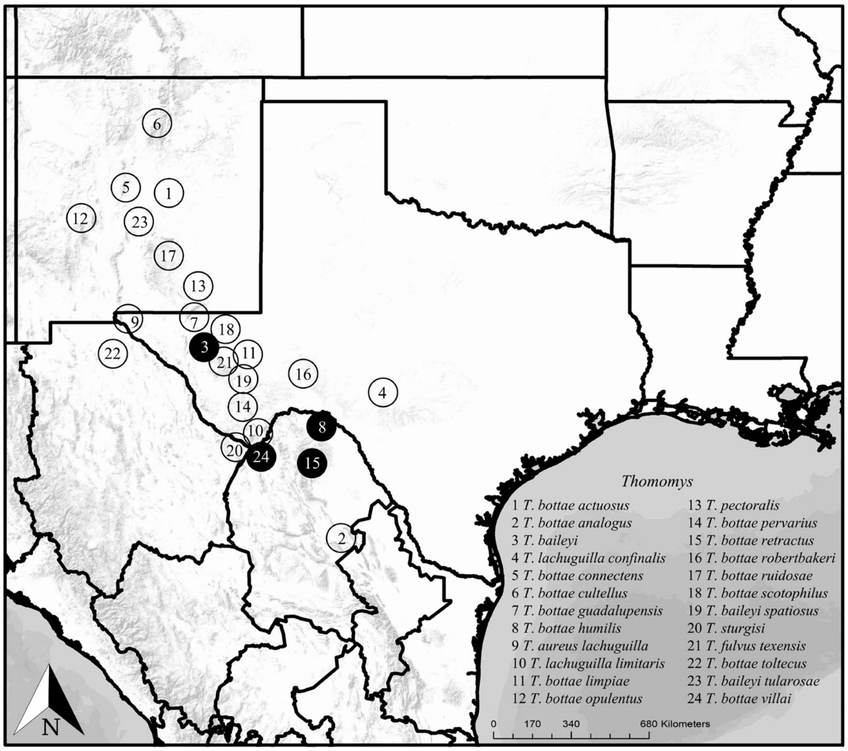


Figure 1c. Approximate location of the type localities for *Thomomys*. White circles indicate localities that were sampled in this study; black circles depict type localities for which no samples were available.

HotStarTaq (Qiagen Inc., Valencia, California), and the same thermal profile as described above was used for the tissue samples with the exception that the annealing temperature was 50°C.

PCR products were purified with ExoSAP-IT PCR Product Cleanup (Applied Biosystems, Foster City, California). Cycle sequencing was conducted with BigDye Terminator v3.1 (Applied Biosystems, Foster City, California) using the following 1 µM primers: LGL765 (Bickham et al. 1995) and LGL766 (Bickham et al. 2004), 870R (Peppers et al. 2002), F1 (Whiting et al. 2003), MVZ05 (Smith and Patton 1991), MVZ14 (Da Silva and Patton 1993), 400F (Edwards et al. 2001), and Thomomys700H. Cycle sequencing reactions were subsequently purified using Sephadex (Cytiva, Marlborough, Massachusetts) filtration and centrifugation methods, followed by dehydration (for samples sequenced at Eurofins see below) and resuspension in formamide (for samples sequenced at Cornell University see below). Purified sequencing products were analyzed on either an ABI Prism 310 automated sequencer (Biotechnology Resource Center, Institute of Biotechnology, Cornell University, Ithaca, New York) or an ABI 3730xl automated sequencer (Eurofins Genomics LLC, Louisville, Kentucky). Resulting sequences were proofed using Sequencher 4.10.1 software (Gene Codes Corporation, Ann Arbor, Michigan) and chromatograms generated from raw sequence reads were visually examined to authenticate all base changes. All *Cyt*b sequences generated herein were deposited in GenBank and are listed in Appendix I.

Phylogenetic analyses.—For each of the three analyses (Parsimony, Maximum Likelihood, and Bayesian Inference), a separate, pruned *Cyt*b dataset—*Cratogeomys* (n = 66), *Geomys* (n = 163), and *Thomomys* (n = 81)—was examined. *Cratogeomys fulvescens*, *C. merriami*, and *C. perotensis* served as the outgroups for the *Cratogeomys* dataset; *Geomys pinetis austrinus*, *Geomys pinetis floridanus*, and

Geomys pinetis mobilensis served as outgroups for the *Geomys* dataset; and *Thomomys bottae centralis*, *T. b. concisor*, and *T. b. mewa* served as the outgroups for the *Thomomys* dataset.

A parsimony analysis (PAUP* Version 4.0a167; Swofford 2003) was conducted for each dataset to identify synapomorphies indicative of taxonomic identifications. Parsimony characters were assigned equal weight and variable nucleotide positions were treated as unordered, discrete characters with four possible states: A, C, G, and T. Phylogenetically uninformative characters were removed from the analysis. The most-parsimonious trees were estimated using the heuristic search and tree-bisection-reconnection option. A strict consensus tree was generated from the pool of available trees and a bootstrap (BS) analysis (Felsenstein 1985) with 1,000 iterations and values ≥ 65 used to indicate moderate to strong nodal support.

Eighty-eight maximum likelihood models were evaluated using jModelTest-2.1.10 (Guindon and Gascuel 2003; Darriba et al. 2012) and the Akaike information criterion with a correction for finite sample sizes (AICc, Hurvich and Tsai 1989; Burnham and Anderson 2004) identified the TVM+I+G model of evolution (-lnL = 5344.8393) as the most appropriate for the *Cratogeomys* dataset, the TIM3+I+G model of evolution (-lnL = 12492.9378) as the most appropriate for the *Geomys* dataset, and the TPM1uf+I+G model of evolution (-lnL = 7350.0403) as the most appropriate for the *Thomomys* dataset. A likelihood analysis for each dataset was performed using RAxML (Version 8.2.12, Stamatakis 2014) and the following parameters: 1) *Cratogeomys* dataset: base frequencies (A = 0.3265, C = 0.2546, G = 0.1217, and T = 0.2972), proportion of invariable sites (I = 0.6314), gamma distribution (G = 0.2436), and the GTR+I+G (general time reversible plus proportion of invariable sites plus gamma) nucleotide substitution model; 2) *Geomys* dataset: base frequencies (A = 0.3358, C = 0.2766, G = 0.1013, and T = 0.28063), proportion of invariable sites (I = 0.5311), gamma distribution (G = 0.2651), and the GTR+I+G nucleotide substitution model; and 3) *Thomomys* dataset: base frequencies (A = 0.3133, C = 0.2719, G = 0.0970, and T = 0.3178), proportion of invariable sites (I = 0.6084), gamma distribution (G = 0.2022), and the GTR+I+G nucleotide substitution model. Nodal support was evaluated using the bootstrap method (1,000 iterations, Felsenstein 1985) with BS values ≥ 65 used to indicate moderate to strong nodal support.

A maximum likelihood analysis under a Bayesian Inference model (MrBayes v3.2.6; Ronquist et al. 2012) was conducted for each dataset to generate posterior probability values (PPV). The GTR+I+G nucleotide substitution model and the following parameters were used for each genus: two independent runs with four Markov-chains (one cold and three heated; MCMCMC), 1.0 x 10^6 generations, and sample frequency of every 1,000 generation. A visual inspection of likelihood scores resulted in the first 1,000,000 trees being discarded (10% burn-in) and a consensus tree (50% majority rule) constructed from the remaining trees. PPV ≥ 0.95 were used to designate nodal support (Huelsenbeck et al. 2002).

Genetic divergence.—The Kimura 2-parameter model of evolution (Kimura 1980) was utilized to estimate genetic distances among selected taxa and haplotypes. The resulting values were used to examine levels of genetic divergence pertaining to the genetic species concept outlined in Bradley and Baker (2001) and Baker and Bradley (2006).

Taxonomic decision-making process.—An attempt was made to review all relevant taxonomic and systematic studies conducted on the taxa addressed herein to develop a summary section entitled "Taxonomic Accounts and Interpretations" (see Appendix II). This section details the outcomes of prior morphologic and genetic synopses, incorporates data from the current study, and then combines all available data into a "Taxonomic Remarks" section that serves to present the best overall consensus of taxonomy and phylogenetic status. When possible, seven datasets were evaluated: morphologic characteristics used in the original taxonomic description of a taxon; morphometrics based on statistical analyses; allozymic, karyotypic, mtDNA, and nuclear DNA data; and genetic distances obtained from mtDNA sequences. Attempts were made to utilize statistically supported morphometric differences, monophyletic clades that were supported by nodal support values, and sister taxon relationships, especially if congruency across datasets could be identified, in assigning taxonomic groups. However, in most cases all seven datasets were not available, and in many instances only the mtDNA phylogenies and corresponding genetic distances were available for decision-making. Under those circumstances, levels of genetic variation within and between clades were compared to values obtained from other comparisons and were used as benchmarks for evaluating the magnitude of divergence between potential groups. When datasets were incongruent or where only mtDNA sequences and corresponding genetic divergence values were available, we were careful not to synonymize a taxon based on scarcity of data; instead, we deferred to the original or primary studies until additional data become available. In other words, our conservative approach allowed us to recognize and retain taxonomic names for future investigations. Our thoughts were that it was better to err in retaining a taxonomic name that might prove to be a synonym than it was to subsume a taxon and give the perception that the taxon was not valid.

RESULTS

Phylogenetic analyses.—All three phylogenetic analyses (Parsimony, Maximum Likelihood, and Bayesian Inference) implemented in the three datasets (*Cratogeomys*, *Geomys*, and *Thomomys*) produced similar topologies (except for a few mid-level nodes in the *Geomys* and *Thomomys* parsimony analyses); therefore only the topology obtained from the Bayesian Inference analysis are depicted herein (Figs. 2, 3a–3d, and 4). Bootstrap values obtained from the Parsimony and Maximum Likelihood analyses were superimposed onto the Bayesian Inference topologies, respectively. Results from each dataset are discussed below.

Following initial analyses to verify sequences, check for stop codons, or other abnormalities, the larger *Cyt*b datasets were pruned for final analyses. For taxa assigned (currently or historically) to *C. castanops* populations occurring in Texas and adjacent areas, complete nucleotide sequences from the mitochondrial *Cyt*b gene were obtained for individuals representing the 10 subspecies in Texas or adjacent areas (*angusticeps*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, *tamaulipensis*, and *torridus*). In addition, individuals representing eight other subspecies of *C. castanops* from Colorado and Mexico (*bullatus*, *castanops*, *consitus*, *excelsus*, *jucundus*, *sordidulus*, *subsimus*, and *surculus*), three subspecies of *C. goldmani* (*goldmani*, *rubellus*, and *subnubilus*), and three individuals representing *C. fulvescens*, *C. merriami*, and *C. perotensis* were included in the analyses as outgroup and references samples.

The topology of the phylogenetic tree obtained from the Bayesian Inference analysis of the *Cratogeomys* dataset is shown in Figure 2. Nodal support for other basal and mid-level clades generally were below our *a priori* threshold (bootstrap $\geq$ 65) resulting in all 51 individuals of *C. castanops* being contained in a single well-supported clade (Clade A). Within Clade A, four smaller clades were identified (B, C, D, and E). Clade B contained individuals representing four subspecies of *C. castanops* from Mexico (*excelsus*, *sordidulus*, *subsimus*, and *surculus*); Clade C contained one individual representing *jucundus* from Mexico; Clade D contained three individuals representing the subspecies *tamaulipensis*; and Clade E contained individuals representing 11 subspecies of *C. castanops* from Colorado, New Mexico, Oklahoma, Texas, and Mexico (*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, and *torridus*). Within Clade E, three well-supported subclades were recognized: Subclade F corresponding to individuals from south-central Texas and northern Coahuila (*angusticeps* and *bullatus*, respectively); Subclade G corresponding to individuals from southeastern Colorado (*castanops*), west-central Texas (*dalquesti*), from southwestern Oklahoma, northwestern Texas, and eastern New Mexico (*perplanus* and *simulans*); and Subclade H corresponding to individuals from southeastern New Mexico and southwestern Texas (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*).

For the genus *Geomys*, given the large number of *Cyt*b sequences (n = 166 individuals) and taxonomic groups (11 species and 24 subspecies), a condensed tree (Fig. 3a) was constructed to broadly visualize relationships among species. The topology of this tree revealed four supported clades (I–IV), with Clade I containing

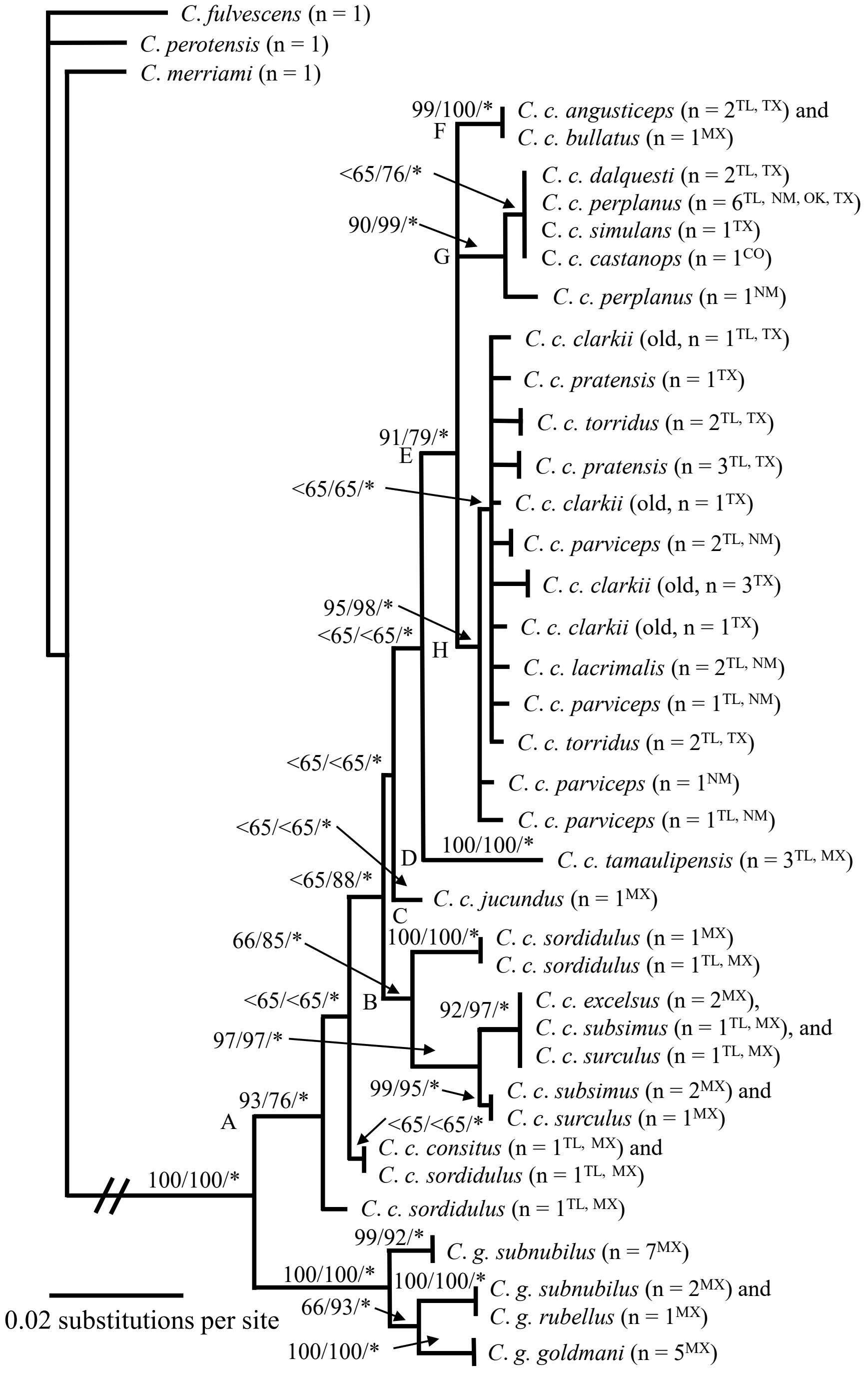


Figure 2. Phylogenetic relationships of samples of *Cratogeomys* examined in this study. The tree was generated using Bayesian methods (MrBayes; Ronquist et al. 2012) and the GTR+I+G model of evolution. Nodal support values obtained from the Parsimony, Maximum Likelihood, and Bayesian Inference analyses are depicted above branches, with bootstrap values obtained from the Parsimony analysis placed to the left of the first slash; bootstrap values for the Maximum Likelihood analysis placed between the two slashes; and posterior probability values for the Bayesian Inference were placed to the right of the second slash. Bootstrap values ≥ 65 and posterior probability values ≥ 0.95 (depicted by an asterick *), were considered as indicative of nodal support. Sample sizes (n) are placed in parentheses following a taxon name. Samples from Type Localities are denoted by TL (see Table 1), and samples from Colorado, New Mexico, Oklahoma, Texas, and Mexico are denoted by CO, NM, OK, TX, and MX, respectively.

3a.

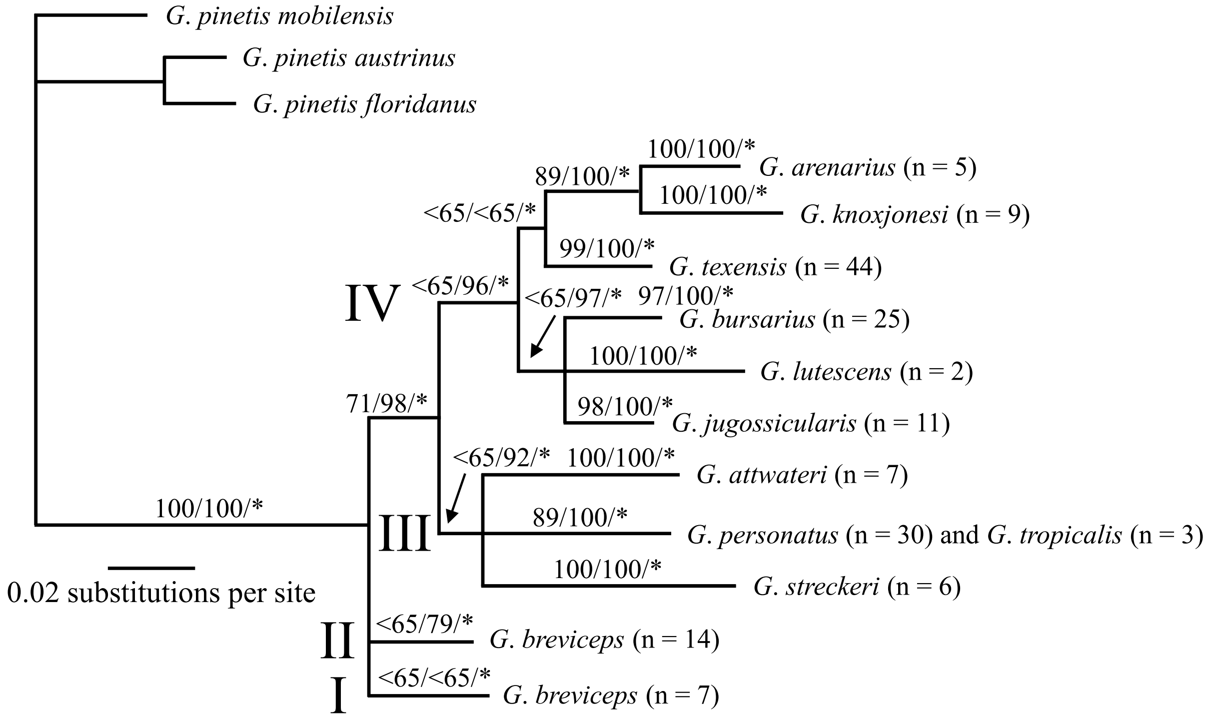
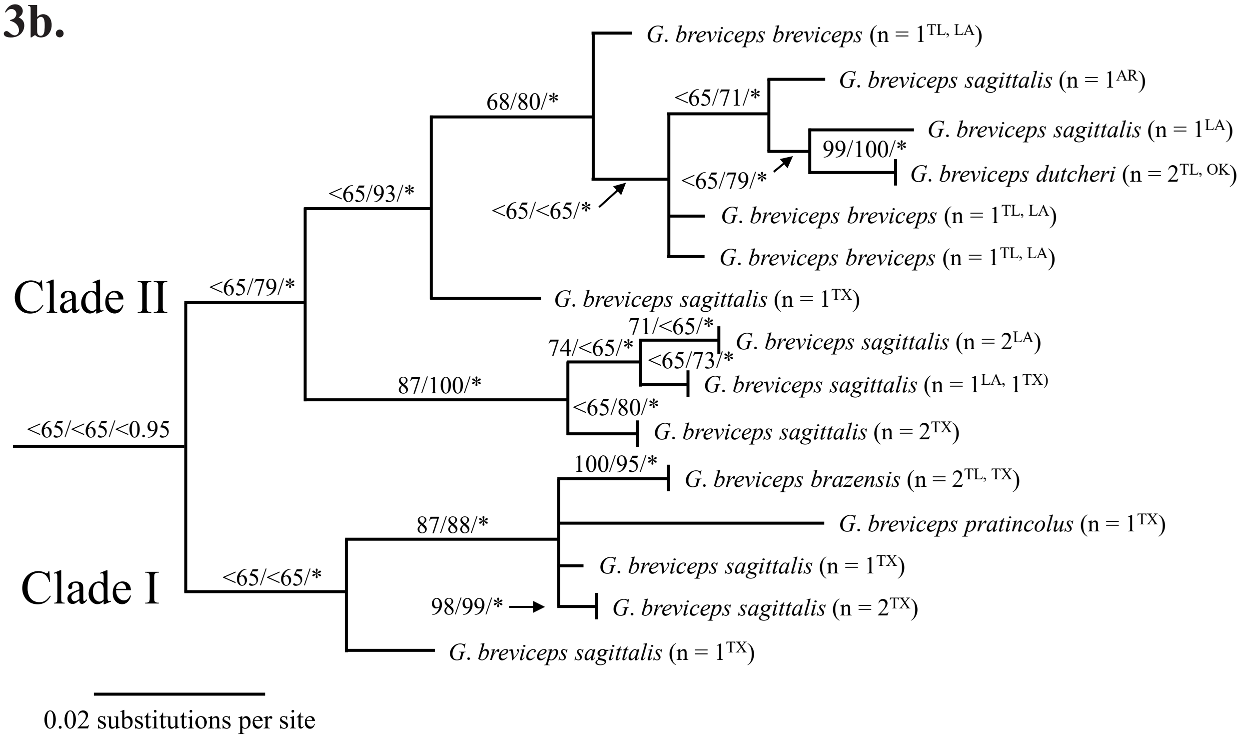
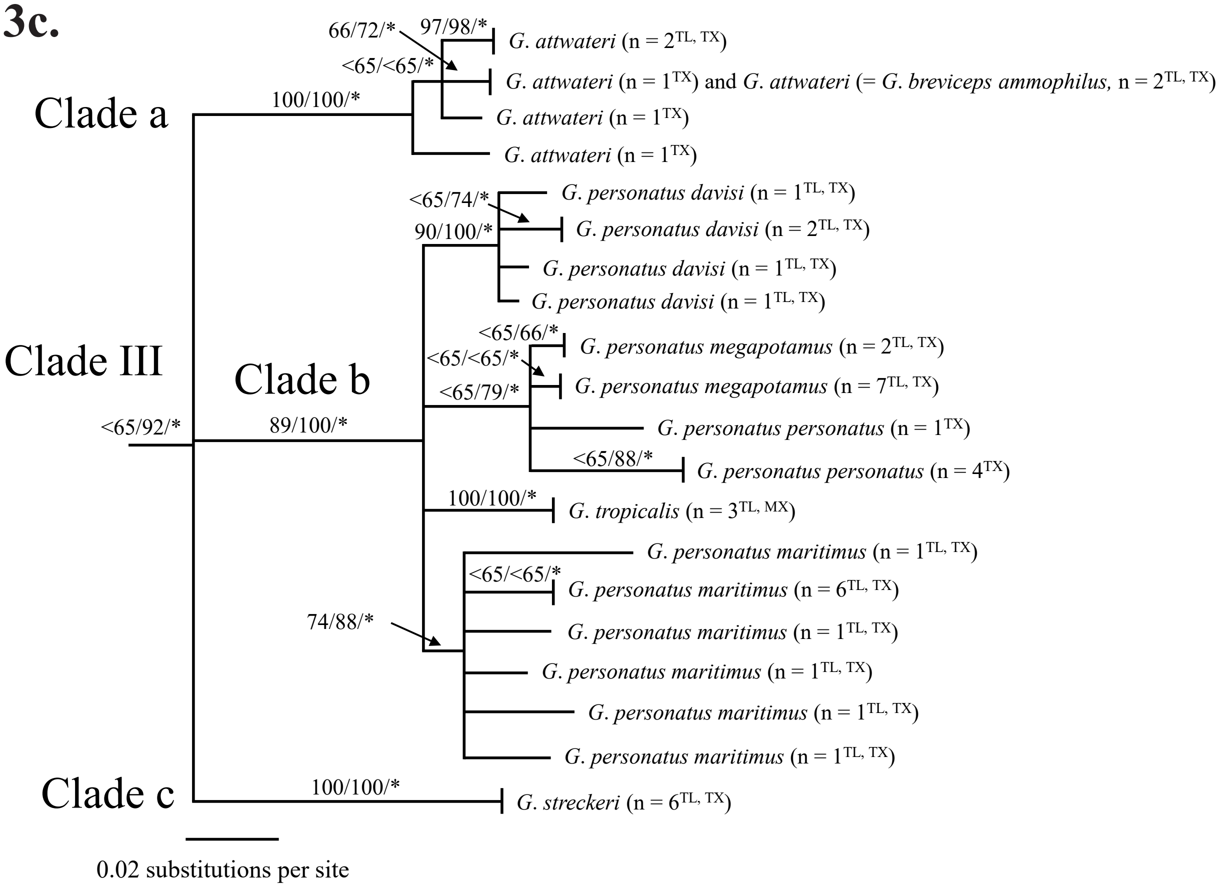


Figure 3a–d. Phylogenetic relationships of samples of *Geomys* examined in this study. The tree (depicted in four parts due to its size and complexity) was generated using Bayesian methods (MrBayes; Ronquist et al. 2012) and the GTR+I+G model of evolution. Nodal support values obtained from the Parsimony, Maximum Likelihood, and Bayesian Inference analyses are depicted above branches, with bootstrap values obtained from the Parsimony analysis placed to the left of the first slash; bootstrap values for the Maximum Likelihood analysis placed between the two slashes; and posterior probability values for the Bayesian Inference placed to the right of the second slash. Bootstrap values ≥ 65 and posterior probability values ≥ 0.95 (depicted by an asterick *) were considered as indicative of nodal support. Sample sizes (n) are placed in parentheses following a taxon name. Samples from Type Localities are denoted by TL (see Table 1), and samples from Arkansas, Colorado, Illinois, Iowa, Kansas, Loisiana, Minnesota, Missouri, Nebraska, New Mexico, Oklahoma, Texas, and Mexico are denoted by AR, CO, IL, IA, KS, LA, MN, MO, NE, NM, OK, TX, and MX, respectively. a) Depicts the 12 species of *Geomys* examined herein; b) depicts members formerly assigned to *G. breviceps* and *Geomys species novum*; c) depicts members formerly assigned to *G. attwateri*, *G. personatus*, *G. streckeri*, and *G. tropicalis*; and d) depicts members formerly assigned to *G. arenarius*, *G. bursarius*, *G. jugossicularis*, *G. knoxjonesi*, *G. lutescens*, and *G. texensis*.

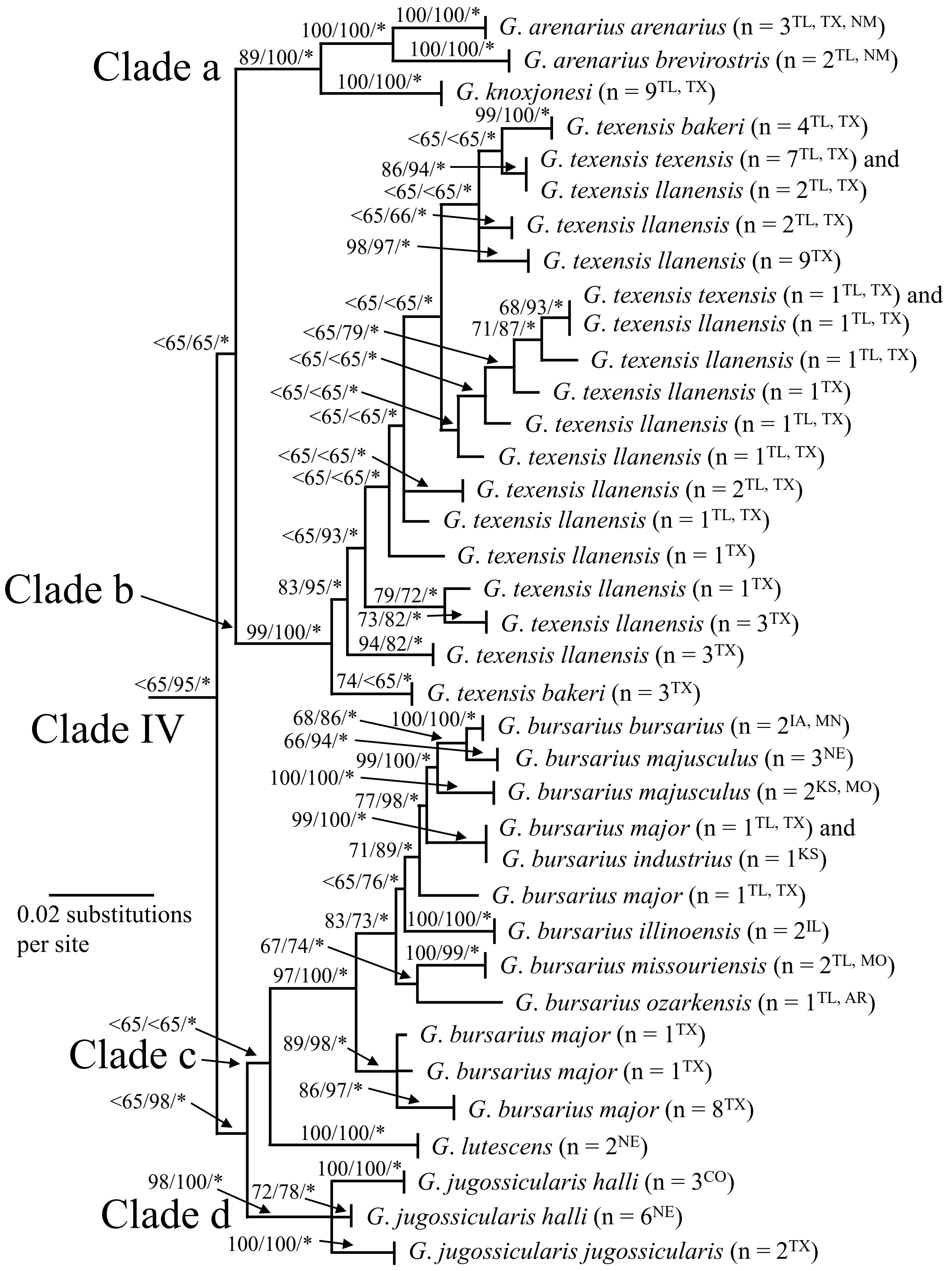
3b.


G. breviceps breviceps (n = 1$^{TL, LA}$)
68/80/*
<65/71/*
G. breviceps sagittalis (n = 1^{AR})
G. breviceps sagittalis (n = 1^{LA})
99/100/*
<65/79/*
G. breviceps dutcheri (n = 2$^{TL, OK}$)
<65/93/*
<65/<65/*
G. breviceps breviceps (n = 1$^{TL, LA}$)
G. breviceps breviceps (n = 1$^{TL, LA}$)
Clade II
<65/79/*
G. breviceps sagittalis (n = 1^{TX})
71/<65/*
74/<65/*
G. breviceps sagittalis (n = 2^{LA})
<65/73/*
87/100/*
G. breviceps sagittalis (n = 1^{LA,} 1^{TX})
<65/80/*
<65/<65/<0.95
G. breviceps sagittalis (n = 2^{TX})
100/95/*
G. breviceps brazensis (n = 2$^{TL, TX}$)
87/88/*
G. breviceps pratincolus (n = 1^{TX})
G. breviceps sagittalis (n = 1^{TX})
Clade I
<65/<65/*
98/99/*
G. breviceps sagittalis (n = 2^{TX})
G. breviceps sagittalis (n = 1^{TX})
0.02 substitutions per site

3c.


66/72/*
97/98/*
G. attwateri (n = 2$^{TL, TX}$)
<65/<65/*
G. attwateri (n = 1^{TX}) and *G. attwateri* (= *G. breviceps ammophilus,* n = 2$^{TL, TX}$)
Clade a
100/100/*
G. attwateri (n = 1^{TX})
G. attwateri (n = 1^{TX})
<65/74/*
G. personatus davisi (n = 1$^{TL, TX}$)
90/100/*
G. personatus davisi (n = 2$^{TL, TX}$)
G. personatus davisi (n = 1$^{TL, TX}$)
G. personatus davisi (n = 1$^{TL, TX}$)
<65/66/*
G. personatus megapotamus (n = 2$^{TL, TX}$)
Clade III
Clade b
<65/<65/*
G. personatus megapotamus (n = 7$^{TL, TX}$)
<65/79/*
<65/92/*
89/100/*
G. personatus personatus (n = 1^{TX})
<65/88/*
G. personatus personatus (n = 4^{TX})
100/100/*
G. tropicalis (n = 3$^{TL, MX}$)
G. personatus maritimus (n = 1$^{TL, TX}$)
<65/<65/*
G. personatus maritimus (n = 6$^{TL, TX}$)
74/88/*
G. personatus maritimus (n = 1$^{TL, TX}$)
G. personatus maritimus (n = 1$^{TL, TX}$)
G. personatus maritimus (n = 1$^{TL, TX}$)
G. personatus maritimus (n = 1$^{TL, TX}$)
Clade c
100/100/*
G. streckeri (n = 6$^{TL, TX}$)
0.02 substitutions per site

3d.


Clade a
100/100/*
100/100/*
G. arenarius arenarius (n = $3^{\text{TL, TX, NM}}$)
89/100/*
100/100/*
G. arenarius brevirostris (n = $2^{\text{TL, NM}}$)
100/100/*
G. knoxjonesi (n = $9^{\text{TL, TX}}$)
99/100/*
G. texensis bakeri (n = $4^{\text{TL, TX}}$)
<65/<65/*
86/94/*
G. texensis texensis (n = $7^{\text{TL, TX}}$) and
G. texensis llanensis (n = $2^{\text{TL, TX}}$)
<65/<65/*
<65/66/*
G. texensis llanensis (n = $2^{\text{TL, TX}}$)
98/97/*
G. texensis llanensis (n = 9^{TX})
<65/<65/*
68/93/*
G. texensis texensis (n = $1^{\text{TL, TX}}$) and
71/87/*
G. texensis llanensis (n = $1^{\text{TL, TX}}$)
<65/65/*
<65/79/*
<65/<65/*
G. texensis llanensis (n = $1^{\text{TL, TX}}$)
G. texensis llanensis (n = 1^{TX})
<65/<65/*
<65/<65/*
G. texensis llanensis (n = $1^{\text{TL, TX}}$)
G. texensis llanensis (n = $1^{\text{TL, TX}}$)
<65/<65/*
<65/<65/*
G. texensis llanensis (n = $2^{\text{TL, TX}}$)
G. texensis llanensis (n = $1^{\text{TL, TX}}$)
<65/93/*
G. texensis llanensis (n = 1^{TX})
Clade b
83/95/*
79/72/*
G. texensis llanensis (n = 1^{TX})
73/82/*
G. texensis llanensis (n = 3^{TX})
99/100/*
94/82/*
G. texensis llanensis (n = 3^{TX})
<65/95/*
74/<65/*
G. texensis bakeri (n = 3^{TX})
Clade IV
68/86/*
100/100/*
G. bursarius bursarius (n = $2^{\text{IA, MN}}$)
66/94/*
G. bursarius majusculus (n = 3^{NE})
99/100/*
100/100/*
G. bursarius majusculus (n = $2^{\text{KS, MO}}$)
77/98/*
99/100/*
G. bursarius major (n = $1^{\text{TL, TX}}$) and
G. bursarius industrius (n = 1^{KS})
71/89/*
G. bursarius major (n = $1^{\text{TL, TX}}$)
<65/76/*
0.02 substitutions per site
83/73/*
100/100/*
G. bursarius illinoensis (n = 2^{IL})
67/74/*
100/99/*
G. bursarius missouriensis (n = $2^{\text{TL, MO}}$)
97/100/*
G. bursarius ozarkensis (n = $1^{\text{TL, AR}}$)
<65/<65/*
G. bursarius major (n = 1^{TX})
Clade c
89/98/*
G. bursarius major (n = 1^{TX})
86/97/*
G. bursarius major (n = 8^{TX})
<65/98/*
100/100/*
G. lutescens (n = 2^{NE})
100/100/*
G. jugossicularis halli (n = 3^{CO})
98/100/*
72/78/*
Clade d
G. jugossicularis halli (n = 6^{NE})
100/100/*
G. jugossicularis jugossicularis (n = 2^{TX})

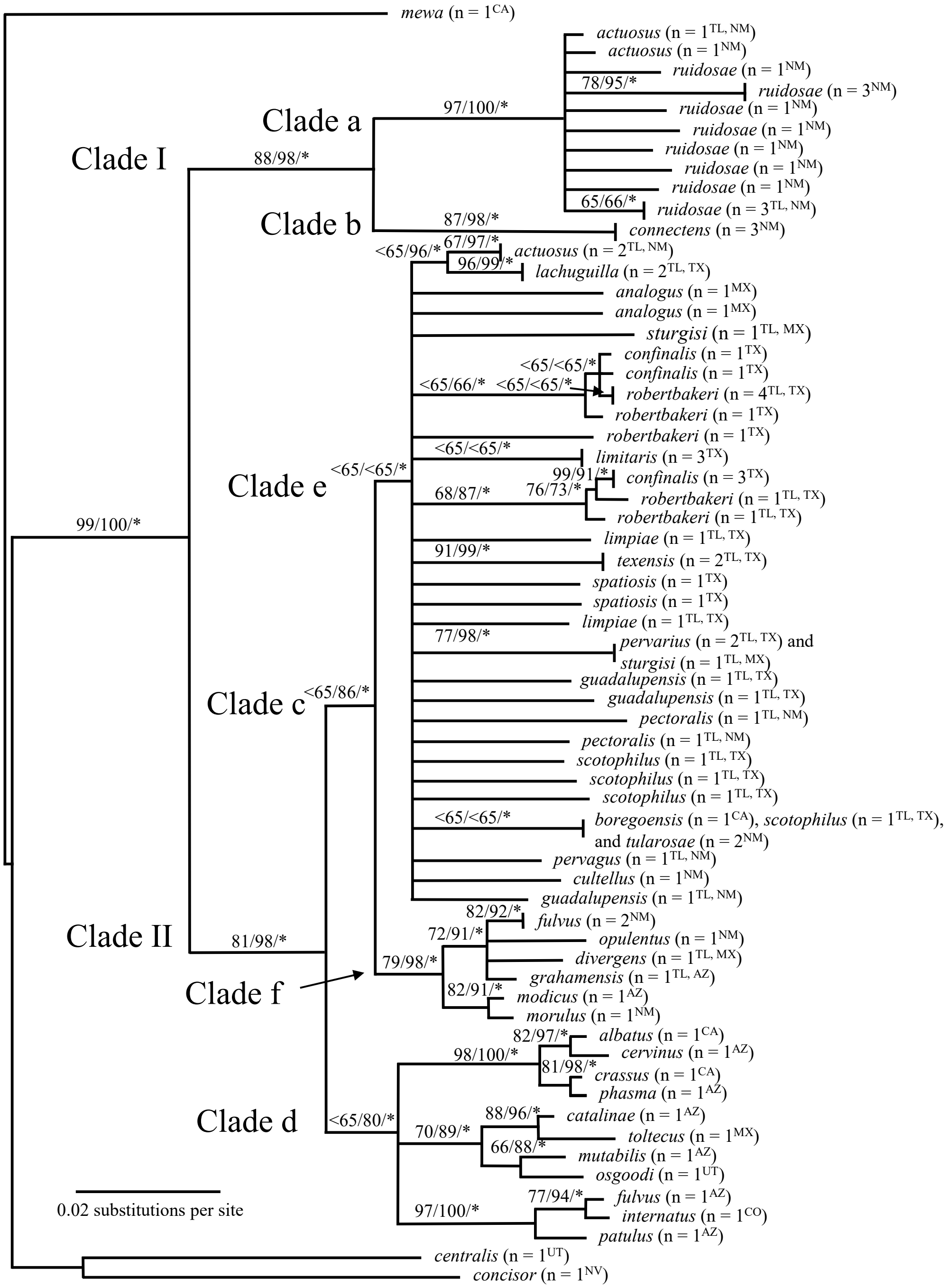


Figure 4. Phylogenetic relationships of samples of *Thomomys* examined in this study. The tree was generated using Bayesian methods (MrBayes; Ronquist et al. 2012) and the GTR+I+G model of evolution. Nodal support values obtained from the Parsimony, Maximum Likelihood, and Bayesian Inference analyses are depicted above branches, with bootstrap values obtained from the Parsimony analysis placed to the left of the first slash; bootstrap values for the Maximum Likelihood analysis placed between the two slashes; and posterior probability values for the Bayesian Inference analysis placed to the right of the second slash. Bootstrap values ≥ 65 and posterior probability values ≥ 0.95 (depicted by an asterick *), were considered as indicative of nodal support. Sample sizes (n) are placed in parentheses following a taxon name. Samples from Type Localities are denoted by TL (see Table 1), and samples from Arizona, California, Colorado, Nevada, New Mexico, Texas, and Mexico are denoted by AZ, CA, CO, NV, NM, TX, and MX, respectively.

7 representatives of *G. breviceps* from southeastern Texas; Clade II containing 14 representatives of *G. breviceps* from eastern Texas, Arkansas, Oklahoma, and Louisiana; Clade III containing *G. attwateri*, *G. personatus*, *G. streckeri*, and *G. tropicalis*; and Clade IV containing *G. arenarius*, *G. bursarius*, *G. jugossicularis*, *G. knoxjonesi*, *G. lutescens*, and *G. texensis*. Although the three major clades were well-resolved, phylogenetic relationships among some taxa within Clades II and III could not be determined. To better understand relationships among subspecies and to evaluate the geographic distribution of subspecies, each clade (I–IV) was expanded to its original topology to illustrate relationships among subspecies and geographic localities (Figs. 3b–d) and is discussed below.

Within the clade containing samples of *G. breviceps* (Fig. 3b), the topology obtained from the Bayesian Inference analysis depicted two clades of individuals that approximately corresponded to samples of *G. b. breviceps*, *G. b. dutcheri*, and *G. b. sagittalis*, from east-central Texas and west-central Louisiana (Clade I) and samples of *G. b. brazensis*, *G. b. pratincola*, and *G. b. sagittalis* from northeastern Texas, west-central and northern Louisiana, southwestern Arkansas, and east-central Oklahoma (Clade II). Varying levels of support were detected in the three analyses and are shown in Fig. 3b.

Within the clade containing samples of *G. attwateri, G. personatus, G. streckeri,* and *G. tropicalis* (Clade III; Fig. 3c), the topology obtained from the Bayesian Inference analysis depicted three clades of individuals (unresolved relative to each other) that approximately corresponded to samples of *G. attwateri* and samples formerly assigned to *G. breviceps ammophilus* from southeastern Texas (Clade a); samples of *G. p. davisi*, *G. p. maritimus*, *G. p. megapotamus*, *G. p. personatus*, and *G. tropicalis* from southeastern Texas and northeastern Mexico (Clade b); and samples of *G. streckeri* from southern Texas (Clade c). Varying levels of support were detected among taxa and geographic localities in the three analyses and are shown in Fig. 3c.

Within the clade containing samples of *G. arenarius*, *G. bursarius*, *G. jugossicularis*, *G. knoxjonesi*, *G. lutescens*, and *G. texensis* (Clade IV; Fig. 3d), the topology obtained from the Bayesian Inference analysis depicted four clades (a–d) of individuals (unresolved relative to each other). Clade a corresponded to samples from eastern New Mexico and western Texas represented by *G. arenarius* and *G. knoxjonesi* with the two subspecies of *G. arenarius* (*arenarius* and *brevirostris*) forming a monophyletic group. Clade b corresponded to samples of *G. texensis* from central and south-central Texas with the three subspecies of *G. texensis* (*bakeri*, *llanensis*, and *texensis*) being paraphyletic. Clade c corresponded to samples of *G. bursarius* and *G. lutescens* from north-central Texas and the upper midwestern portion of the United States, with the seven subspecies of *G. bursarius* (*bursarius*, *illinoensis*, *industrus*, *major*, *majusculus*, *missouriensis*, and *ozarkensis*) forming a monophyletic group that was sister to *G. lutescens*. Clade d corresponded to samples of *G. jugossicularis* from northwestern Texas with the two subspecies (*halli* and *jugossicularis*) being paraphyletic.

For taxa assigned (currently or historically) to *T. bottae* populations occurring in Texas and adjacent areas (New Mexico and Mexico), complete or nearly complete nucleotide sequences from the mitochondrial *Cyt*b gene were obtained for 32 individuals representing the 11 Texas subspecies (*confinalis*, *guadalupensis*, *lachuguilla*, *robertbakeri*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, *spatiosis*, *sturgisi*, and *texensis*). In addition, 48 individuals representing 26 other subspecies of *T. bottae* from Arizona, California, Colorado, New Mexico, Utah, and Mexico (*actuosus*, *albatus*, *analogus*, *boregoensis*, *catalinae*, *cervinus*, *connectens*, *crassus*, *cultellus*, *divergens*, *fulvus*, *grahamensis*, *internatus*, *modicus*, *morulus*, *mutabilis*, *opulentus*, *osgoodi*, *patulus*, *pectoralis*, *pervagus*, *phasma*, *ruidosae*, *sturgisi*, *toltecus*, and *tularosae*) were used as reference samples, and three individuals representing *centralis*, *concisor*, and *mewa* were included in the analyses as outgroup samples.

The topology of the phylogenetic tree obtained from the Bayesian Inference analysis of the *Thomomys* dataset produced two major clades (Clades I and II) and is shown in Figure 4. Clade I contained three subspecies from northern and eastern New Mexico which were arranged into two Subclades (a and b); Subclade a contained individuals representing *actuosus* and *ruidosae*, and Subclade b contained individuals representing *connectens*. Clade II contained 34 subspecies occurring in Arizona, California, Colorado, New Mexico, Texas, Utah, and Mexico. This large clade was divided into four unresolved subclades (c–f). Subclade c was further comprised of two subclades (e and f) containing subspecies occurring primarily in Texas and surrounding states. Subclade e contained 18 subspecies from eastern New Mexico, Texas, and northern Mexico (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *pectoralis*, *pervagus, pervarius*, *robertbakeri*, *scotophitus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*). Subclade f contained primarily subspecies (*fulvus*, *divergens*, *grahamensis*, *modicus*, *morulus*, and *opulentus*) adjacent to Texas populations of *Thomomys* (Arizona, New Mexico, and Mexico); whereas, subclade d contained primarily the reference subspecies (*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *patulus*, *phasma*, and *toltecus*) from the western distribution of *Thomomys* (Arizona, California, Colorado, Utah, and Mexico).

Genetic distances.—To ascertain the significance of genetic differentiation between and among taxa, average genetic distance values (Tables 2–7), for selected taxa, were obtained from the Kimura 2-parameter model of evolution (Kimura 1980). Subspecific comparisons ranged within *Cratogeomys* from 0.57% to 3.93%; within *Geomys* from 1.89% to 10.55%; and within *Thomomys* from 0.44% to 5.73%. Additional comparisons of select taxa of *Cratogeomys* are presented in Table 2. Additional comparisons of select taxa of *Geomys* are as follows: 10.02% to 16.44% for species; 8.81% for *breviceps*, *dutcheri*, and *sagittalis*-in part versus *brazensis*, *pratincola*, and *sagittalis*-in part; 12.25% for *davisi*, *maritimus*, *megapotamus*, *personatus*, and *tropicalis* versus *streckeri*; and 11.01% for *arenarius*, *brevirostris*, and *knoxjonesi* vs *bursarius*, *illinoensis*, *industrius*, *lutescens*, *major*, *majusculus*, *missouriensis*, and *ozarkensis* (Tables 3–6). Additional comparisons of *Thomomys* ranged from 4.64% to 12.48% for various combinations of putative subspecies (Table 7).

Table 2. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) were obtained for selected comparisons of clades and/or taxa of *Cratogeomys*. The northern versus southern group of taxa roughly corresponds to the Hafner et al. (2008) vision of a *castanops* subspecies and a *consitus* subspecies. AGD = Average Genetic Distance.

Comparison		AGD
Within Selected Clades		
A	*angusticeps*, *bullatus*, *castanops*, *clarkii*, *consitus*, *dalquesti*, *excelsus*, *jucundus*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, *sordidulus*, *subsimus*, *surculus*, *tamaulipensis*, and *torridus*	3.93%
B	*excelsus*, *sordidulus*, *subsimus*, and *surculus*	2.37%
C	*jucundus*	NA
D	*tamaulipensis*	0.73%
E	*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, and *torridus*	1.85%
F	*angusticeps* and *bullatus*	0.57%
G	*castanops*, *dalquesti*, *perplanus*, and *simulans*	0.96%
H	*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*	0.61%
Between Selected Clades		
B and C	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs *jucundus*	3.79%

Table 2. (cont.)

Comparison		AGD
B vs D	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs *tamaulipensis*	7.64%
B vs E	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs (*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, and *torridus*)	6.15%
B vs F	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs (*angusticeps* and *bullatus*)	5.93%
B vs G	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs (*castanops*, *dalquesti*, *perplanus*, and *simulans*)	6.42%
B vs H	(*excelsus*, *sordidulus*, *subsimus*, and *surculus*) vs (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*)	6.04%
C vs D	*jucundus* vs *tamaulipensis*	7.08%
C vs E	*jucundus* vs (*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, and *torridus*)	3.99%
C vs F	*jucundus* vs (*angusticeps* and *bullatus*)	3.76%
C vs G	*jucundus* vs (*castanops*, *dalquesti*, *perplanus*, and *simulans*)	4.98%
C vs H	*jucundus* vs (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*)	3.50%
D vs E	*tamaulipensis* vs (*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, and *torridus*)	6.41%
D vs F	*tamaulipensis* vs (*angusticeps* and *bullatus*)	6.50%
D vs G	*tamaulipensis* vs (*castanops*, *dalquesti*, *perplanus*, and *simulans*)	6.33%
D vs H	*tamaulipensis* vs (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*)	6.44%
F vs G	(*angusticeps* and *bullatus*) vs (*castanops*, *dalquesti*, *perplanus*, and *simulans*)	2.80%
F vs H	(*angusticeps* and *bullatus*) vs (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*)	2.47%
G vs H	(*castanops*, *dalquesti*, *perplanus*, and *simulans*) vs (*clarkii*, *lacrimalis*, *parviceps*, *pratensis*, and *torridus*)	2.90%
Between Selected Taxa		
	castanops vs *dalquesti*	2.51%
	castanops vs *perplanus*	2.43%
	castanops vs *simulans*	2.39%
	dalquesti vs *perplanus*	0.74%
	dalquesti vs *simulans*	0.49%
	perplanus vs *simulans*	0.40%
Other Selected Groups		
Northern vs Southern	(*angusticeps*, *bullatus*, *castanops*, *clarkii*, *dalquesti*, *jucundus*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *simulans*, *tamaulipensis*, and *torridus*) vs (*consitus*, *excelsus*, *sordidulus*, *subsimus*, and *surculus*)	6.09%

Table 3. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of clades and/or taxa of *Geomys*. AGD = Average Genetic Distance.

Comparison		AGD
Between Selected Clades		
I vs II	*breviceps* (*brazensis*, *pratincolus*, and *sagittalis*) vs *breviceps* (*breviceps*, *dutcheri*, and *sagittalis*)	8.95%
I vs III	*breviceps* (*brazensis*, *pratincolus*, and *sagittalis*) vs (*attwateri*, *personatus*, *streckeri*, and *tropicalis*)	12.99%
I vs IV	*breviceps* (*brazensis*, *pratincolus*, and *sagittalis*) vs (*arenarius*, *bursarius*, *jugossicularis*, *knoxjonesi*, *lutescens*, and *texensis*)	13.02%
II vs III	*breviceps* (*breviceps*, *dutcheri*, and *sagittalis*) vs (*attwateri*, *personatus*, *streckeri*, and *tropicalis*)	13.98%
II vs IV	*breviceps* (*breviceps*, *dutcheri*, and *sagittalis*) vs (*arenarius*, *bursarius*, *jugossicularis*, *knoxjonesi*, *lutescens*, and *texensis*)	14.44%
III vs IV	(*attwateri*, *personatus*, *streckeri*, and *tropicalis*) vs (*arenarius*, *bursarius*, *jugossicularis*, *knoxjonesi*, *lutescens*, and *texensis*)	12.93%
Between Selected Species		
	arenarius vs *attwateri*	14.26%
	arenarius vs *bursarius*	12.37%
	arenarius vs *jugossicularis*	11.28%
	arenarius vs *knoxjonesi*	10.37%
	arenarius vs *lutescens*	11.24%
	arenarius vs *personatus*	14.82%
	arenarius vs *streckeri*	14.01%
	arenarius vs *texensis*	11.94%
	arenarius vs *tropicalis*	15.82%
	attwateri vs *bursarius*	12.96%
	attwateri vs *jugossicularis*	12.10%
	attwateri vs *knoxjonesi*	13.49%
	attwateri vs *lutescens*	12.58%
	attwateri vs *personatus*	11.46%
	attwateri vs *streckeri*	12.13%
	attwateri vs *texensis*	13.08%
	attwateri vs *tropicalis*	12.10%
	breviceps vs *arenarius*	14.67%
	breviceps vs *attwateri*	13.96%
	breviceps vs *bursarius*	14.57%

Table 3. (cont.)

Comparison	AGD
breviceps vs *jugossicularis*	13.78%
breviceps vs *knoxjonesi*	15.32%
breviceps vs *lutescens*	13.86%
breviceps vs *personatus*	13.53%
breviceps vs *streckeri*	13.37%
breviceps vs *texensis*	13.32%
breviceps vs *tropicalis*	14.58%
bursarius vs *jugossicularis*	8.34%
bursarius vs *knoxjonesi*	11.70%
bursarius vs *lutescens*	8.79%
bursarius vs *personatus*	12.81%
bursarius vs *streckeri*	12.59%
bursarius vs *texensis*	9.82%
bursarius vs *tropicalis*	14.12%
jugossicularis vs *knoxjonesi*	10.86%
jugossicularis vs *lutescens*	8.13%
jugossicularis vs *personatus*	12.04%
jugossicularis vs *streckeri*	12.00%
jugossicularis vs *texensis*	9.15%
jugossicularis vs *tropicalis*	12.95%
lutescens vs *personatus*	13.72%
lutescens vs *streckeri*	11.75%
lutescens vs *texensis*	9.88%
lutescens vs *tropicalis*	13.92%
personatus vs *streckeri*	12.22%
personatus vs *texensis*	12.88%
personatus vs *tropicalis*	5.20%
streckeri vs *texensis*	11.52%
streckeri vs *tropicalis*	12.56%
texensis vs *tropicalis*	13.05%

Table 4. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of clades and/or taxa of the *Geomys breviceps* group. AGD = Average Genetic Distance.

Comparison		AGD
Between Clades		
I vs II	(*brazensis*, *pratincolus*, and *sagittalis*-in part) vs (*breviceps*, *dutcheri*, and *sagittalis*-in part)	8.81%
Between Subspecies		
	brazensis vs *breviceps*	9.39%
	brazensis vs *dutcheri*	8.41%
	brazensis vs *pratincolus*	4.04%
	brazensis vs *sagittalis* (from Clade I)	2.64%
	brazensis vs *sagittalis* (from Clade II)	8.59%
	breviceps vs *dutcheri*	3.45%
	breviceps vs *pratincolus*	10.23%
	breviceps vs *sagittalis* (from Clade I)	9.27%
	breviceps vs *sagittalis* (from Clade II)	7.27%
	dutcheri vs *sagittalis* (from Clade I)	8.54%
	dutcheri vs *sagittalis* (from Clade II)	7.96%
	pratincolus vs *sagittalis* (from Clade I)	4.79%
	pratincolus vs *sagittalis* (from Clade II)	8.97%
	sagittalis (from Clade I) vs *sagittalis* (from Clade II)	8.89%
	brazensis and *pratincolus* vs *sagittalis* (from Clade I)	3.35%
	breviceps and *dutcheri* vs *sagittalis* (from Clade II)	6.85%

Table 5. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of clades and/or taxa of the *Geomys personatus* group. AGD = Average Genetic Distance.

Comparison		AGD
Between Clades		
a vs b	*attwateri* vs (*davisi*, *maritimus*, *megapotamus*, *personatus*, and *tropicalis*)	11.52%
a vs c	*attwateri* vs *streckeri*	12.13%
b vs c	(*davisi*, *maritimus*, *megapotamus*, *personatus*, and *tropicalis*) vs *streckeri*	12.25%

Table 5. (cont.)

Comparison		AGD
Between Select Clades and Taxonomic Groups		
	attwateri vs *ammophilus*	2.31%
	davisi vs *maritimus*	6.34%
	davisi vs *megapotamus*	4.33%
	davisi vs *personatus*	5.05%
	davisi vs *tropicalis*	4.48%
	maritimus vs *megapotamus*	5.25%
	maritimus vs *personatus*	5.30%
	maritimus vs *tropicalis*	5.81%
	megapotamus vs *personatus*	1.97%
	megapotamus vs *tropicalis*	4.86%
	personatus vs *tropicalis*	5.15%
Within Selected Clades and Taxonomic Groups		
	attwateri	2.22%
	davisi	0.62%
	maritimus	0.98%
	megapotamus	1.27%
	personatus	1.58%
	tropicalis	1.06%
	b (*davisi*, *maritimus*, *megapotamus*, *personatus*, and *tropicalis*)	4.03%

Table 6. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of clades and/or taxa of the *Geomys bursarius* group. AGD = Average Genetic Distance.

Comparison		AGD
Between Selected Clades		
a vs b	(*arenarius*, *brevirostris*, and *knoxjonesi*) vs (*bakeri*, *llanensis*, and *texensis*)	11.63%
a vs c	(*arenarius*, *brevirostris*, and *knoxjonesi*) vs (*bursarius*, *illinoensis*, *industrius*, *lutescens*, *major*, *majusculus*, *missouriensis*, and *ozarkensis*)	11.01%
a vs d	(*arenarius*, *brevirostris*, and *knoxjonesi*) vs (*halli* and *jugossicularis*)	11.91%
b vs c	(*bakeri*, *llanensis*, and *texensis*) vs (*bursarius*, *illinoensis*, *industrius*, *lutescens*, *major*, *majusculus*, *missouriensis*, and *ozarkensis*)	9.85%
b vs d	(*bakeri*, *llanensis*, and *texensis*) vs (*halli* and *jugossicularis*)	9.15%

Table 6. (cont.)

Comparison		AGD
c vs d	(*bursarius*, *illinoensis*, *industrius*, *lutescens*, *major*, *majusculus*, *missouriensis*, and *ozarkensis*) vs (*halli* and *jugossicularis*)	8.33%
a and b vs c and d	(*arenarius*, *brevirostris*, *knoxjonesi*, *bakeri*, *llanensis*, and *texensis*) vs (*bursarius*, *illinoensis*, *industrius*, *lutescens*, *major*, *majusculus*, *missouriensis*, *ozarkensis*, *halli* and *jugossicularis*)	10.12%
Between Selected Subspecies (and Species)		
	arenarius vs *brevirostris*	6.74%
	arenarius vs *knoxjonesi*	10.02%
	brevirostris vs *knoxjonesi*	10.88%
	bakeri vs *llanensis*	3.83%
	bakeri vs *texensis*	3.82%
	llanensis vs *texensis*	2.13%
	bursarius vs *halli*	8.63%
	bursarius vs *illinoensis*	4.10%
	bursarius vs *industrius*	3.07%
	bursarius vs *jugossicularis*	8.25%
	bursarius vs *lutescens*	9.10%
	bursarius vs *major*	5.22%
	bursarius vs *majusculus*	1.29%
	bursarius vs *missouriensis*	5.37%
	bursarius vs *ozarkensis*	4.74%
	halli vs *illinoensis*	9.04%
	halli vs *industrius*	8.92%
	halli vs *jugossicularis*	2.46%
	halli vs *lutescens*	8.10%
	halli vs *major*	8.10%
	halli vs *majusculus*	8.40%
	halli vs *missouriensis*	9.32%
	halli vs *ozarkensis*	8.54%
	illinoensis vs *industrius*	3.72%
	illinoensis vs *jugossicularis*	8.46%
	illinoensis vs *lutescens*	9.12%

Table 6. (cont.)

Comparison	AGD
illinoensis vs *major*	4.76%
illinoensis vs *majusculus*	3.94%
illinoensis vs *missouriensis*	5.09%
illinoensis vs *ozarkensis*	4.37%
industrius vs *jugossicularis*	8.47%
industrius vs *lutescens*	8.80%
industrius vs *major*	4.87%
industrius vs *majusculus*	2.82%
industrius vs *missouriensis*	5.28%
industrius vs *ozarkensis*	4.46%
jugossicularis vs *lutescens*	8.27%
jugossicularis vs *major*	7.61%
jugossicularis vs *majusculus*	8.09%
jugossicularis vs *missouriensis*	8.49%
jugossicularis vs *ozarkensis*	8.03%
lutescens vs *major*	8.51%
lutescens vs *majusculus*	9.12%
lutescens vs *missouriensis*	8.97%
lutescens vs *ozarkensis*	8.89%
major vs *majusculus*	5.07%
major vs *missouriensis*	6.38%
major vs *ozarkensis*	5.33%
majusculus vs *missouriensis*	5.18%
majusculus vs *ozarkensis*	4.30%
missouriensis vs *ozarkensis*	4.32%

Table 7. Average genetic distances estimated using the Kimura 2-parameter model of evolution (Kimura 1980) for selected comparisons of clades and/or taxa of the *Thomomys* group. AGD = Average Genetic Distance; * = samples for which limited sequence data were available for comparison.

Comparison		AGD
Between Clades		
I vs II	(*actuosus*-like, *connectens*, and *ruidosae*) vs (*actuosus*, *albatus*, *analogus*, *boregoensis*, *catalinae*, *cervinus*, *confinalis*, *crassus*, *cultellus*, *divergens*, *fulvus*, *grahamensis*, *guadalupensis*, *internatus*, *lachuguilla*, *limitaris*, *limpiae*, *modicus*, *morulus*, *mutabilis*, *opulentus*, *osgoodi*, *patulus*, *pectoralis*, *pervagus*, *pervarius*, *phasma*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, *toltecus*, and *tularosae*)	11.10%
a vs b	(*actuosus* and *ruidosae*) vs *connectens*	7.70%
a vs c	(*actuosus* and *ruidosae*) vs (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *divergens*, *fulvus*, *grahamensis*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *modicus*, *morulus*, *opulentus*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*)	11.07%
a vs d	(*actuosus* and *ruidosae*) vs (*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *phasma*, and *toltecus*)	12.09%
a vs e	(*actuosus* and *ruidosae*) vs (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*)	10.95%
a vs f	(*actuosus* and *ruidosae*) vs (*divergens*, *fulvus*, *grahamensis*, *modicus*, *morulus*, and *opulentus*)	11.91%
b vs c	*connectens* vs (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *divergens*, *fulvus*, *grahamensis*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *modicus*, *morulus*, *opulentus*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*)	9.93%
b vs d	*connectens* vs (*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *phasma*, and *toltecus*)	12.58%
b vs e	*connectens* vs (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*)	9.80%
b vs f	*connectens* vs (*divergens*, *fulvus*, *grahamensis*, *modicus*, *morulus*, and *opulentus*)	10.80%
c vs d	(*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *divergens*, *fulvus*, *grahamensis*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *modicus*, *morulus*, *opulentus*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*) vs (*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *phasma*, and *toltecus*)	7.22%
d vs e	(*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *phasma*, and *toltecus*) vs (*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*)	7.13%
d vs f	(*albatus*, *catalinae*, *cervinus*, *crassus*, *fulvus*, *internatus*, *mutabilis*, *osgoodi*, *phasma*, and *toltecus*) vs (*divergens*, *fulvus*, *grahamensis*, *modicus*, *morulus*, and *opulentus*)	7.80%
e vs f	(*actuosus*, *analogus*, *boregoensis*, *confinalis*, *cultellus*, *guadalupensis*, *lachuguilla*, *limitaris*, *limpiae*, *osgoodi*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri*, *scotophilus*, *spatiosis*, *sturgisi*, *texensis*, and *tularosae*) vs (*divergens*, *fulvus*, *grahamensis*, *modicus*, *morulus*, and *opulentus*)	4.64%

Table 7. (cont.)

Comparison	AGD
Between Subspecies (and species)	
actuosus vs *analogus*	5.29%
actuosus vs *boregoensis*	5.19%
actuosus vs *confinalis*	3.94%
actuosus vs *cultellus*	4.68%
actuosus vs *guadalupensis*	3.88%
actuosus vs *lachuguilla*	3.15%
actuosus vs *limitaris*	3.83%
actuosus vs *limpiae*	3.60%
actuosus vs *pectoralis*	4.03%
actuosus vs *pervagus*	4.33%
actuosus vs *pervarius*	4.68%
actuosus vs *robertbakeri*	3.85%
actuosus vs *scotophilus*	3.95%
actuosus vs *spatiosis*	3.69%
actuosus vs *sturgisi*	2.33%
actuosus vs *texensis*	3.93%
actuosus vs *tularosae*	3.91%
analogus vs *boregoensis*	3.84%
analogus vs *confinalis*	3.48%
analogus vs *cultellus*	4.27%
analogus vs *guadalupensis*	3.47%
analogus vs *lachuguilla*	5.15%
analogus vs *limitaris*	3.11%
analogus vs *limpiae*	2.89%
analogus vs *pectoralis*	3.58%
analogus vs *pervagus*	3.61%
analogus vs *pervarius*	4.18%
analogus vs *robertbakeri*	3.30%
analogus vs *scotophilus*	3.38%
analogus vs *spatiosis*	2.96%
analogus vs *sturgisi*	1.93%

Table 7. (cont.)

Comparison	AGD
analogus vs *texensis*	2.91%
analogus vs *tularosae*	3.14%
boregoensis vs *confinalis*	2.11%
boregoensis vs *cultellus*	2.93%
boregoensis vs *guadalupensis*	1.58%
boregoensis vs *lachuguilla*	4.27%
boregoensis vs *limitaris*	2.17%
boregoensis vs *limpiae*	2.02%
boregoensis vs *pectoralis*	1.23%
boregoensis vs *pervagus*	2.95%
boregoensis vs *pervarius*	3.29%
boregoensis vs *robertbakeri*	2.49%
boregoensis vs *scotophilus*	1.47%
boregoensis vs *spatiosis*	1.86%
boregoensis vs *sturgisi*	0.00%*
boregoensis vs *texensis*	1.86%
boregoensis vs *tularosae*	0.92%
confinalis vs *cultellus*	2.97%
confinalis vs *guadalupensis*	1.92%
confinalis vs *lachuguilla*	4.44%
confinalis vs *limitaris*	1.23%
confinalis vs *limpiae*	1.34%
confinalis vs *pectoralis*	2.12%
confinalis vs *pervagus*	2.31%
confinalis vs *pervarius*	2.31%
confinalis vs *robertbakeri*	1.07%
confinalis vs *scotophilus*	1.69%
confinalis vs *spatiosis*	1.45%
confinalis vs *sturgisi*	4.61%
confinalis vs *texensis*	1.78%
confinalis vs *tularosae*	1.83%
cultellus vs *guadalupensis*	2.29%

Table 7. (cont.)

Comparison	AGD
cultellus vs *lachuguilla*	4.72%
cultellus vs *limitaris*	3.10%
cultellus vs *limpiae*	2.78%
cultellus vs *pectoralis*	2.78%
cultellus vs *pervagus*	1.58%
cultellus vs *pervarius*	4.30%
cultellus vs *robertbakeri*	3.19%
cultellus vs *scotophilus*	2.85%
cultellus vs *spatiosis*	2.78%
cultellus vs *sturgisi*	0.00%*
cultellus vs *texensis*	2.65%
cultellus vs *tularosae*	2.38%
guadalupensis vs *lachuguilla*	4.15%
guadalupensis vs *limitaris*	1.78%
guadalupensis vs *limpiae*	1.66%
guadalupensis vs *pectoralis*	1.01%
guadalupensis vs *pervagus*	2.51%
guadalupensis vs *pervarius*	2.83%
guadalupensis vs *robertbakeri*	1.82%
guadalupensis vs *scotophilus*	0.93%
guadalupensis vs *spatiosis*	1.81%
guadalupensis vs *sturgisi*	2.59%
guadalupensis vs *texensis*	2.07%
guadalupensis vs *tularosae*	0.99%
lachuguilla vs *limitaris*	4.38%
lachuguilla vs *limpiae*	3.96%
lachuguilla vs *pectoralis*	4.38%
lachuguilla vs *pervagus*	4.31%
lachuguilla vs *pervarius*	5.05%
lachuguilla vs *robertbakeri*	4.27%
lachuguilla vs *scotophilus*	4.10%

Table 7. (cont.)

Comparison	AGD
lachuguilla vs *spatiosis*	4.29%
lachuguilla vs *sturgisi*	5.73%
lachuguilla vs *texensis*	4.76%
lachuguilla vs *tularosae*	4.14%
limitaris vs *limpiae*	1.20%
limitaris vs *pectoralis*	1.95%
limitaris vs *pervagus*	2.22%
limitaris vs *pervarius*	2.10%
limitaris vs *robertbakeri*	0.96%
limitaris vs *scotophilus*	1.48%
limitaris vs *spatiosis*	1.29%
limitaris vs *sturgisi*	4.35%
limitaris vs *texensis*	1.48%
limitaris vs *tularosae*	1.62%
limpiae vs *pectoralis*	1.78%
limpiae vs *pervagus*	2.05%
limpiae vs *pervarius*	2.10%
limpiae vs *robertbakeri*	1.20%
limpiae vs *scotophilus*	1.31%
limpiae vs *spatiosis*	1.06%
limpiae vs *sturgisi*	4.04%
limpiae vs *texensis*	1.20%
limpiae vs *tularosae*	1.38%
pectoralis vs *pervagus*	2.44%
pectoralis vs *pervarius*	2.88%
pectoralis vs *robertbakeri*	1.90%
pectoralis vs *scotophilus*	0.91%
pectoralis vs *spatiosis*	1.78%
pectoralis vs *sturgisi*	4.54%
pectoralis vs *texensis*	2.28%
pectoralis vs *tularosae*	1.06%

Table 7. (cont.)

Comparison	AGD
pervagus vs *pervarius*	3.37%
pervagus vs *robertbakeri*	2.31%
pervagus vs *scotophilus*	2.57%
pervagus vs *spatiosis*	2.18%
pervagus vs *sturgisi*	0.00%*
pervagus vs *texensis*	2.05%
pervagus vs *tularosae*	2.31%
pervarius vs *robertbakeri*	2.00%
pervarius vs *scotophilus*	2.28%
pervarius vs *spatiosis*	2.15%
pervarius vs *sturgisi*	3.47%
pervarius vs *texensis*	2.37%
pervarius vs *tularosae*	2.37%
robertbakeri vs *scotophilus*	1.43%
robertbakeri vs *spatiosis*	1.25%
robertbakeri vs *sturgisi*	3.96%
robertbakeri vs *texensis*	1.54%
robertbakeri vs *tularosae*	1.55%
scotophilus vs *spatiosis*	1.40%
scotophilus vs *sturgisi*	3.83%
scotophilus vs *texensis*	1.71%
scotophilus vs *tularosae*	0.44%
spatiosis vs *sturgisi*	3.98%
spatiosis vs *texensis*	1.38%
spatiosis vs *tularosae*	1.42%
sturgisi vs *texensis*	4.95%
sturgisi vs *tularosae*	4.02%
texensis vs *tularosae*	1.74%

Discussion

Over the last two centuries, several datasets have been generated in hopes of contributing to the understanding of taxonomy and nomenclature of pocket gophers. Each study has contributed, in its own manner, toward: identifying diagnostic or informative characters; resolving phylogenetic relationships; proposing taxonomic changes; or in many cases, identifying new questions for pursuit. Given the differences between and resolution provided by different types of data (morphology, allozymes, chromosomes, and DNA sequences), access to an ever-increasing pool of specimens, tissues, and other research materials, and changes in philosophies of taxonomic categories such as species and subspecies, the time has come for a thorough synopsis that uses all available data in an attempt to construct a conceptual framework that serves as a hypothesis for governing decisions on conservation and taxonomy for pocket gophers in Texas and surrounding areas.

Herein, 22 taxonomic names associated with *Cratogeomys* occurring in Texas or adjacent areas, 25 for *Geomys*, and 24 for *Thomomys*, were evaluated (Table 1, Appendix II). Efforts were made to obtain DNA sequences from samples collected at type localities (topotypes) or as nearby as possible to establish a genotype that could be referenced to each taxonomic name (Figs. 5–7). For each taxonomic name, an account was prepared that provides: 1) the scientific name used in the original description, current name usage, and scientific name proposed resulting from the synopsis provided herein; 2) a brief taxonomic history reflecting any name changes and the authority; 3) the type locality for each taxon and locality of samples examined in this study; 4) a morphological synopsis based on the original description and any comparative information gleaned from subsequent studies; 5) a synopsis of available genetic data (karyotypic, allozymic, and DNA) based on the broadest possible dataset for providing a taxonomic synthesis of each name; 6) taxa in need of additional research and possible taxonomic revision; and 7) new distribution maps reflecting the updated taxonomy (Appendix II, Figs. 8–10).

Several criteria were outlined in the Methods and Materials section and those were considered during the development of the taxonomic synopses. First, monophyly and sister relationships were used to evaluate the cohesiveness of a potential group. Second, levels of genetic variation within and between clades were used as benchmarks for evaluating the magnitude of divergence between potential groups (see below). Third, congruency of the dataset presented herein with other datasets (morphometric, allozymic, karyotypic, DNA sequences, etc.) was considered. Together, these three criteria were used to critically review proposed taxonomic groups relative to the newly presented data. Although the taxonomic scheme proposed herein may be controversial and open to question, it is the best synopsis available to date and provides a series of hypotheses to be tested in the future. Further, we recognize that caution is necessary when applying phylogenetic methods solely on the basis of genetic identification to determine the taxonomic status of subspecies. Researchers have argued that genetic differentiation is insufficient, by itself, to diagnose a subspecies; morphological diagnosability is required as well (Mousseau and Sikes 2011; Patten 2015). This especially is a problem when phenotypic and genetic differentiation yield different answers for allopatric populations (Mousseau and Sikes 2011), which often is the case for pocket gophers. Certainly, additional data (increased taxonomic and geographic representations) are needed to provide a more thorough resolution; therefore, the arrangements provided herein are meant to serve as placeholders and hypotheses until more data become available. There were a few examples of this throughout this study; and in situations such as these, we were conservative in proposing taxonomic changes that could result in some subspecies being unnecessarily treated as junior synonyms (see Appendix II).

Although the debate surrounding the retention and utility of subspecies in taxonomy recently has resurfaced (Phillimore and Owens 2006; Braby et al. 2012; Patten 2015; de Queiroz 2020, 2021; Hillis 2020, 2021; Reydon and Kunz 2021; Burbrink et al. 2022), we: 1) follow the premise of Hillis (2020) that subspecies represent formerly isolated lineages, and 2) recognize that efforts to define populations or geographically varying units in a regional context is probably best achieved by using subspecific designations. Clearly,

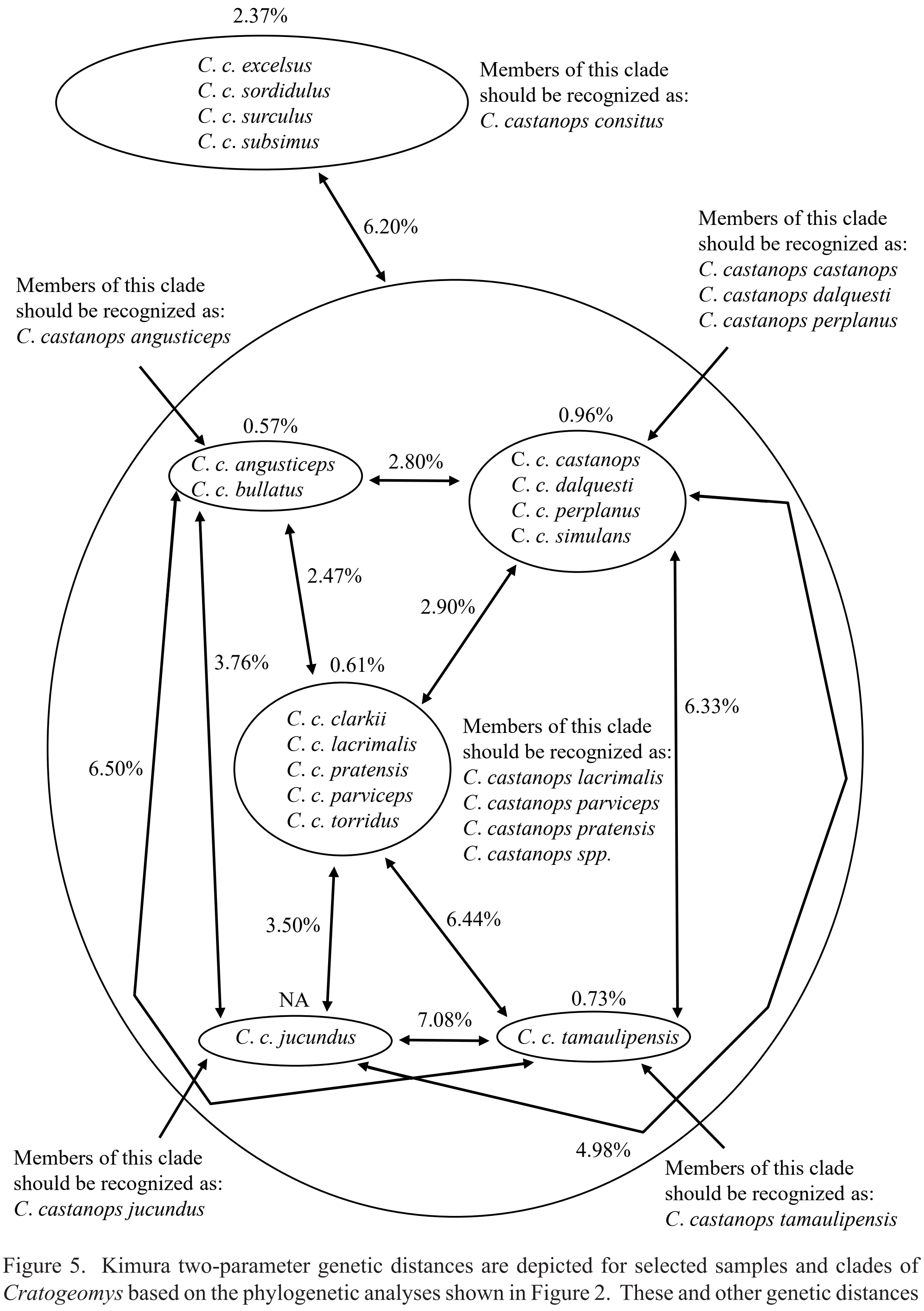


Figure 5. Kimura two-parameter genetic distances are depicted for selected samples and clades of *Cratogeomys* based on the phylogenetic analyses shown in Figure 2. These and other genetic distances are shown in Table 2.

6a.

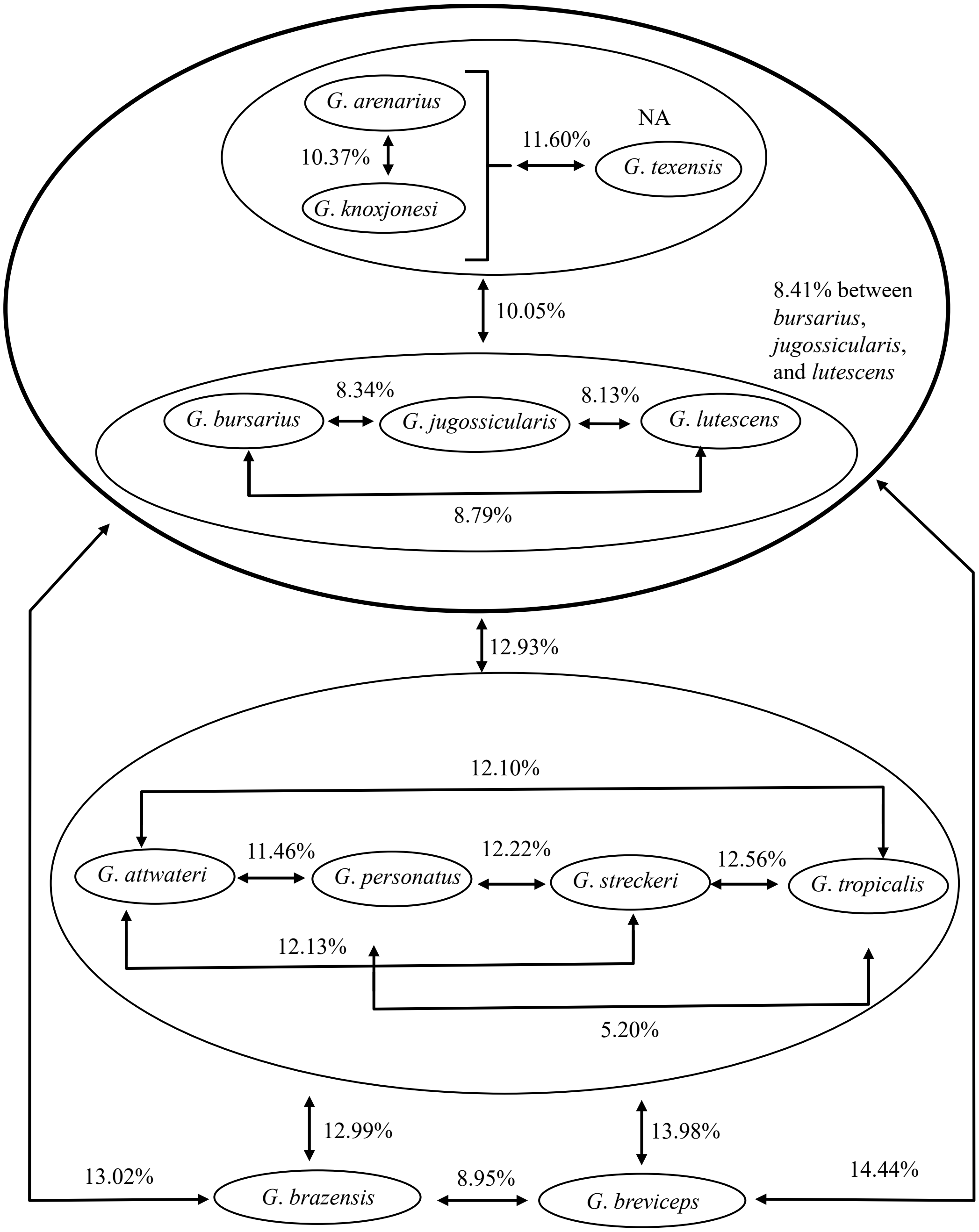
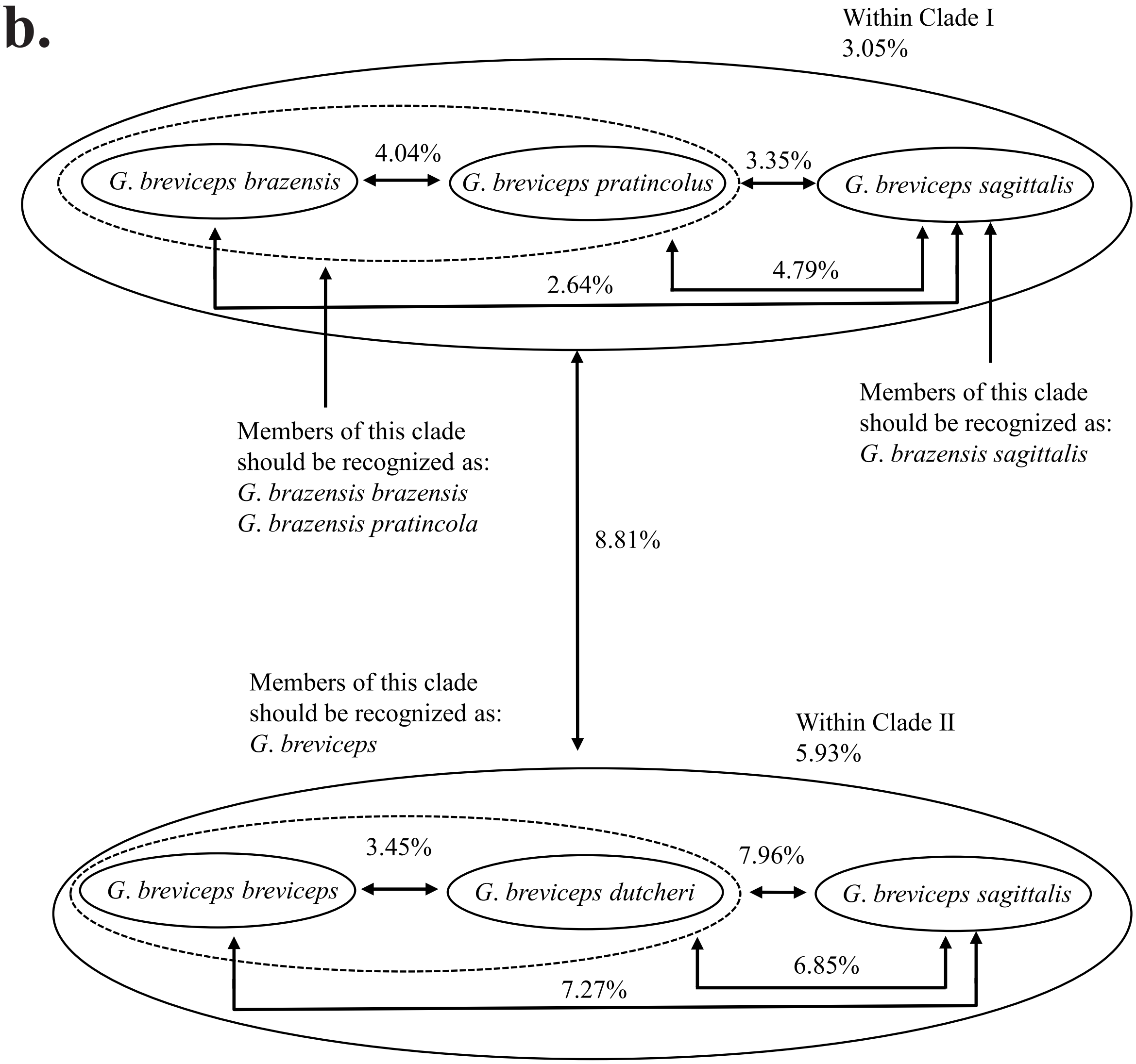
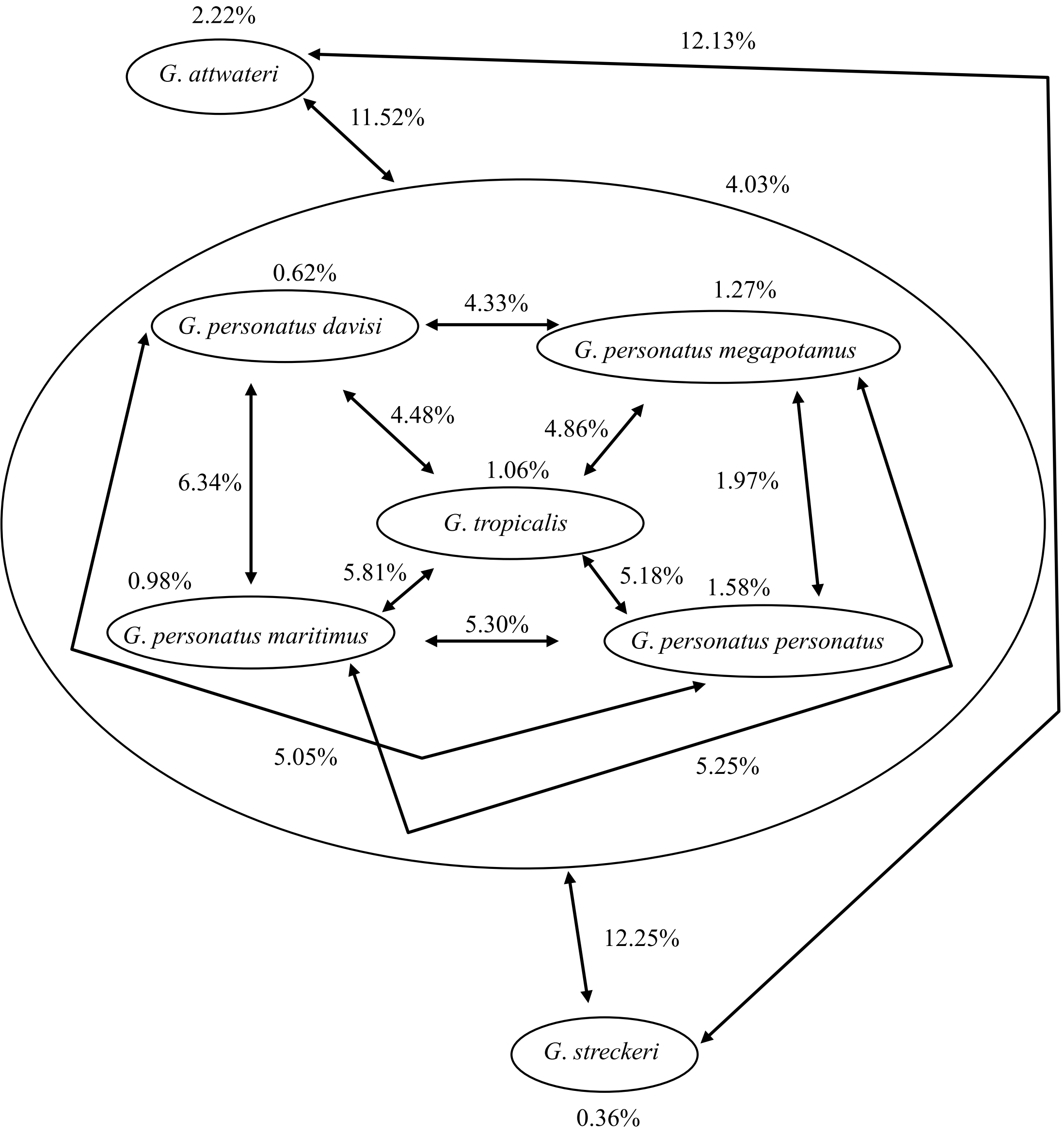


Figure 6a–d. Kimura two-parameter genetic distances are depicted for selected samples and clades of *Geomys* based on: a) the phylogenetic analyses shown in Figure 3a; b) the phylogenetic analyses shown in Figure 3b; C) the phylogenetic analyses shown in Figure 3c; and d) the phylogenetic analyses shown in Figure 3d. These and other genetic distances are shown in Tables 3–6.

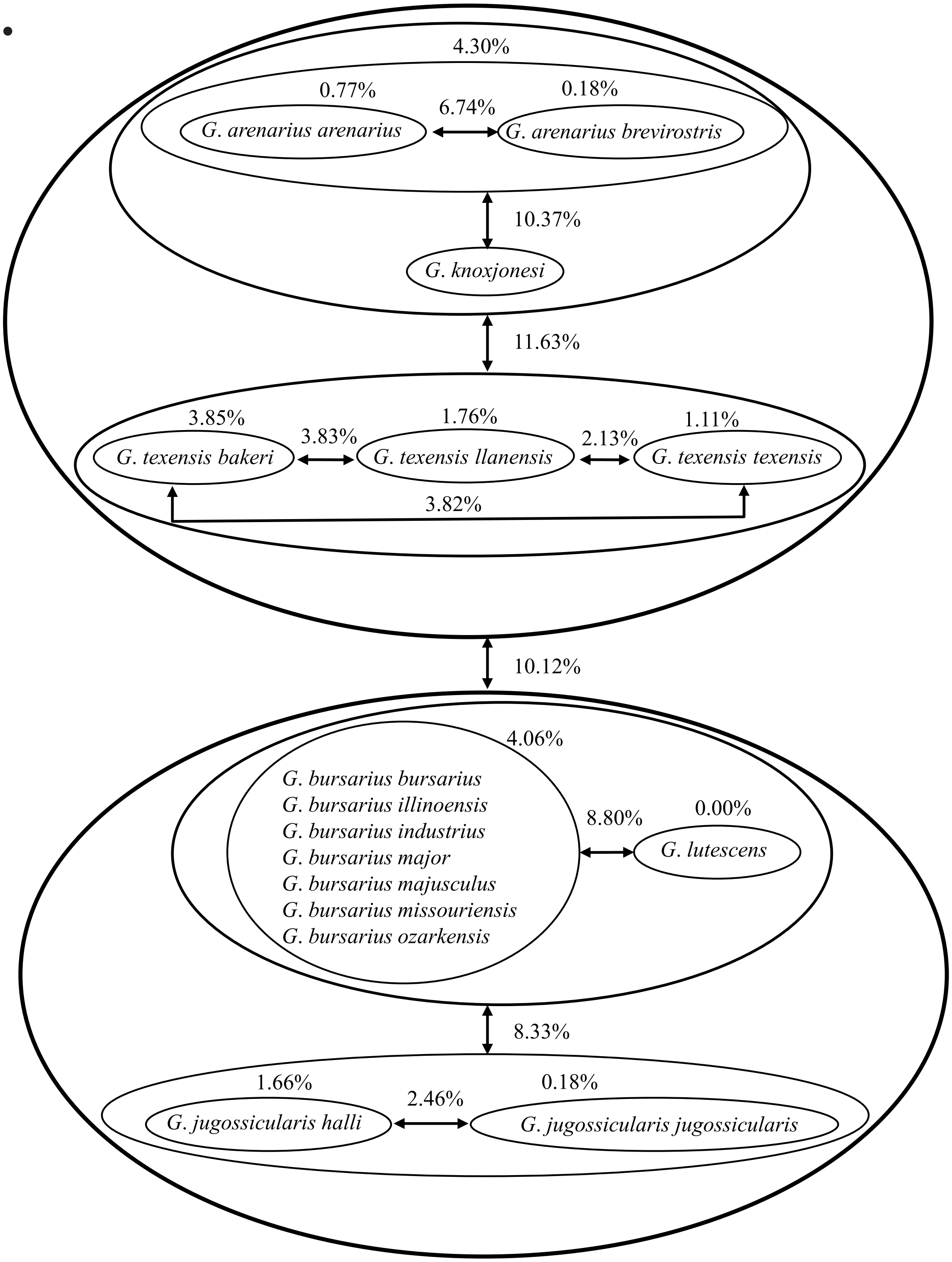
6b.


Within Clade I
3.05%
G. breviceps brazensis
4.04%
G. breviceps pratincolus
3.35%
G. breviceps sagittalis
4.79%
2.64%
Members of this clade
should be recognized as:
G. brazensis brazensis
G. brazensis pratincola
Members of this clade
should be recognized as:
G. brazensis sagittalis
8.81%
Members of this clade
should be recognized as:
G. breviceps
Within Clade II
5.93%
G. breviceps breviceps
3.45%
G. breviceps dutcheri
7.96%
G. breviceps sagittalis
6.85%
7.27%

6c.


2.22%
G. attwateri
12.13%
11.52%
4.03%
0.62%
G. personatus davisi
4.33%
1.27%
G. personatus megapotamus
4.48%
4.86%
6.34%
1.06%
G. tropicalis
1.97%
0.98%
5.81%
5.18%
1.58%
G. personatus maritimus
5.30%
G. personatus personatus
5.05%
5.25%
12.25%
G. streckeri
0.36%

6d.


4.30%
0.77%
0.18%
6.74%
G. arenarius arenarius
G. arenarius brevirostris
10.37%
G. knoxjonesi
11.63%
3.85%
1.76%
1.11%
3.83%
2.13%
G. texensis bakeri
G. texensis llanensis
G. texensis texensis
3.82%
10.12%
4.06%
G. bursarius bursarius
G. bursarius illinoensis
G. bursarius industrius
G. bursarius major
G. bursarius majusculus
G. bursarius missouriensis
G. bursarius ozarkensis
8.80%
0.00%
G. lutescens
8.33%
1.66%
0.18%
2.46%
G. jugossicularis halli
G. jugossicularis jugossicularis

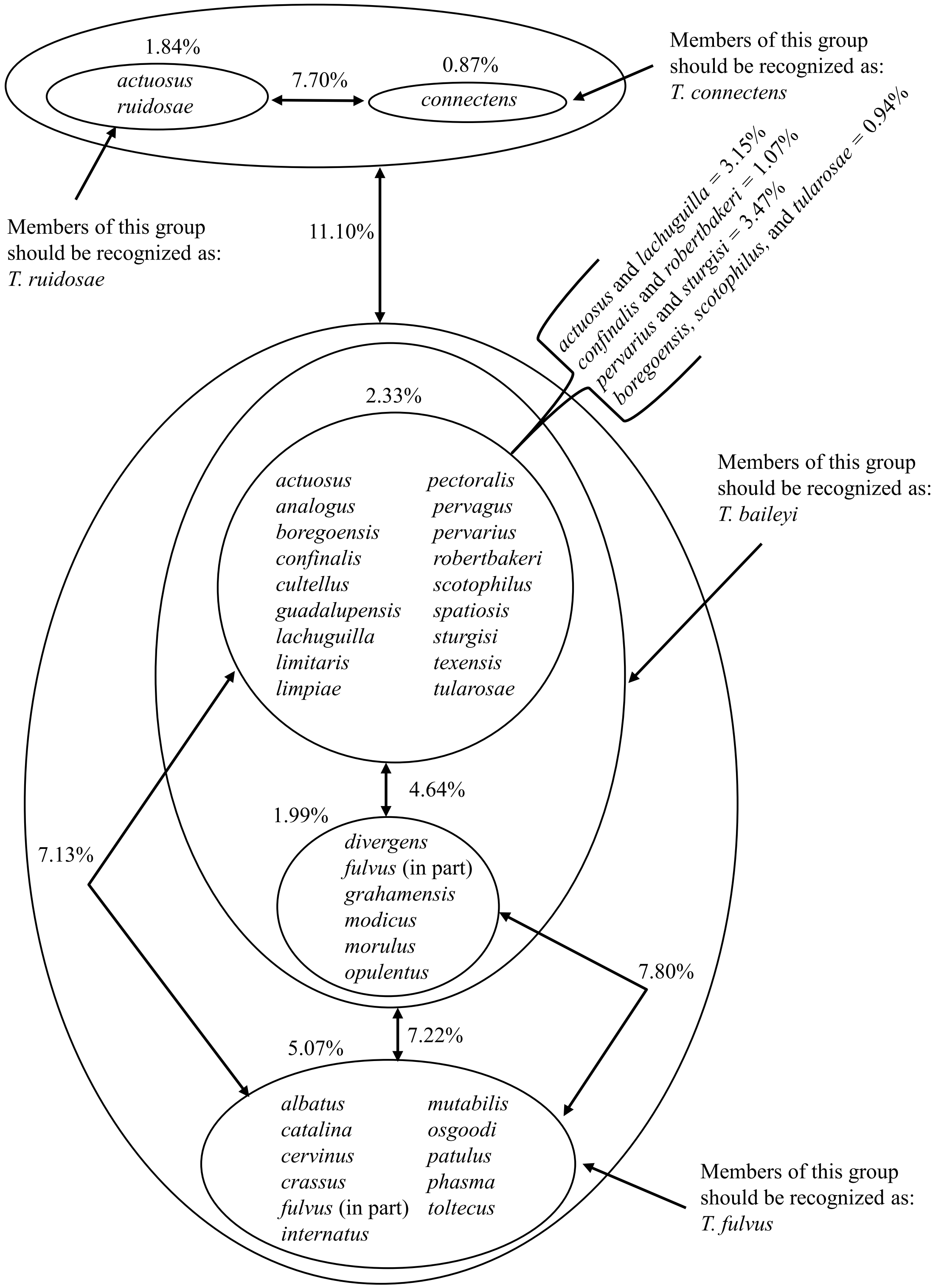


Figure 7. Kimura two-parameter genetic distances are depicted for selected samples and clades of *Thomomys* based on the phylogenetic analyses shown in Figure 2. These and other genetic distances are shown in Table 7.
]

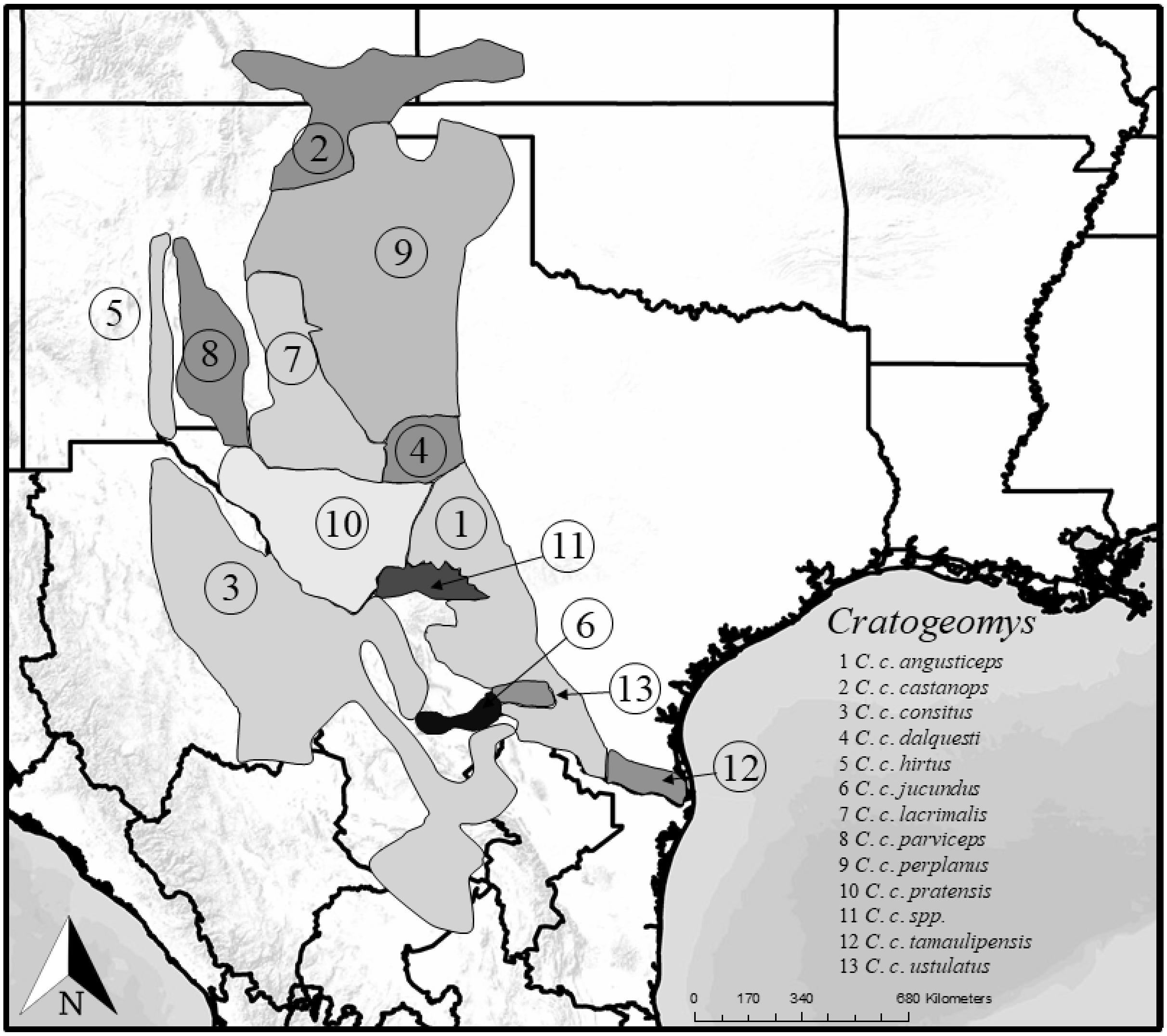


Figure 8. Map depicting approximate geographic distributions of taxa for *Cratogeomys*. Proposed distributions are based on a summation of the current and previous studies as discussed in Appendix II.

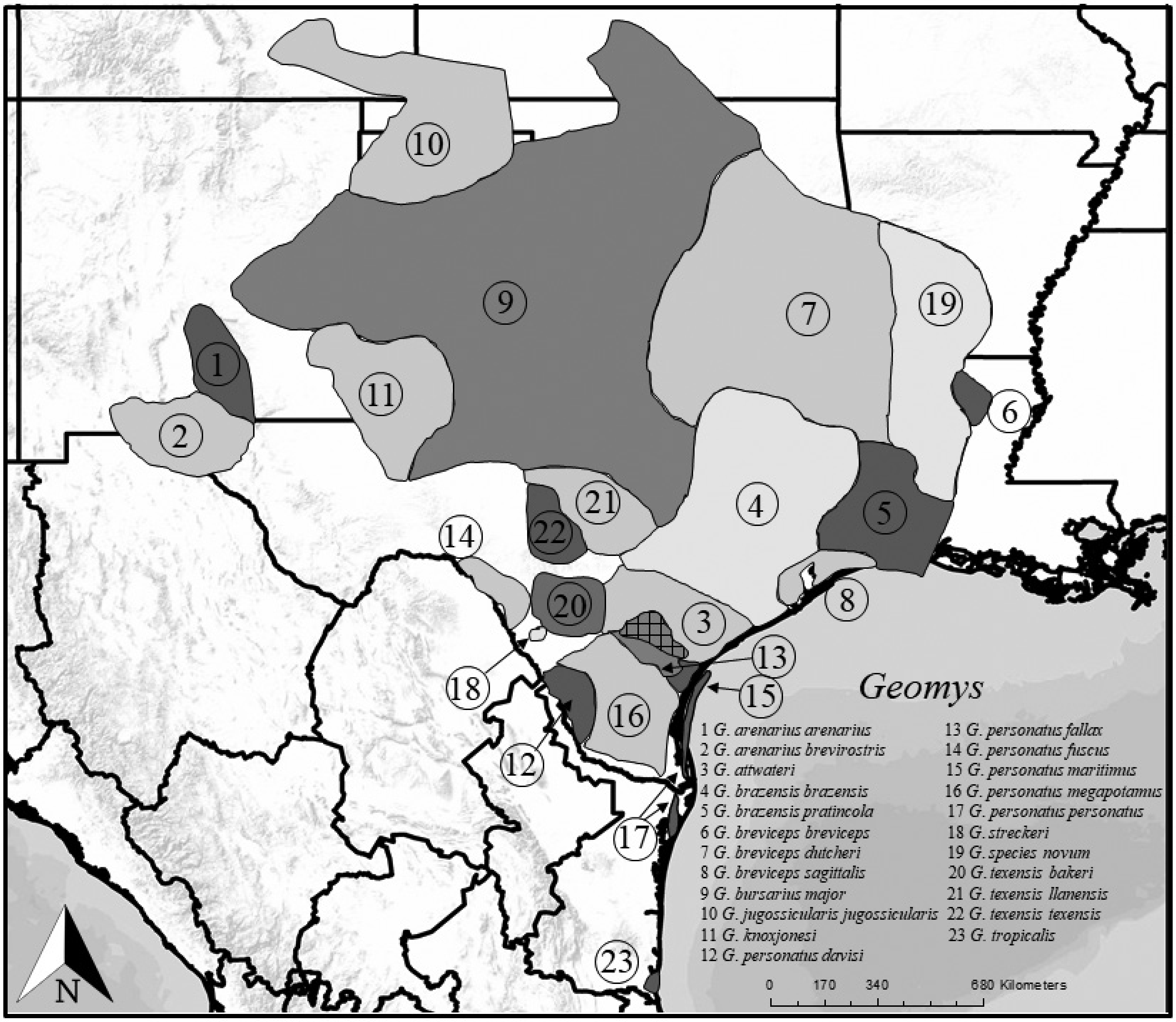


Figure 9. Map depicting approximate geographic distributions of taxa for *Geomys*. Proposed distributions are based on a summation of the current and previous studies as discussed in Appendix II.

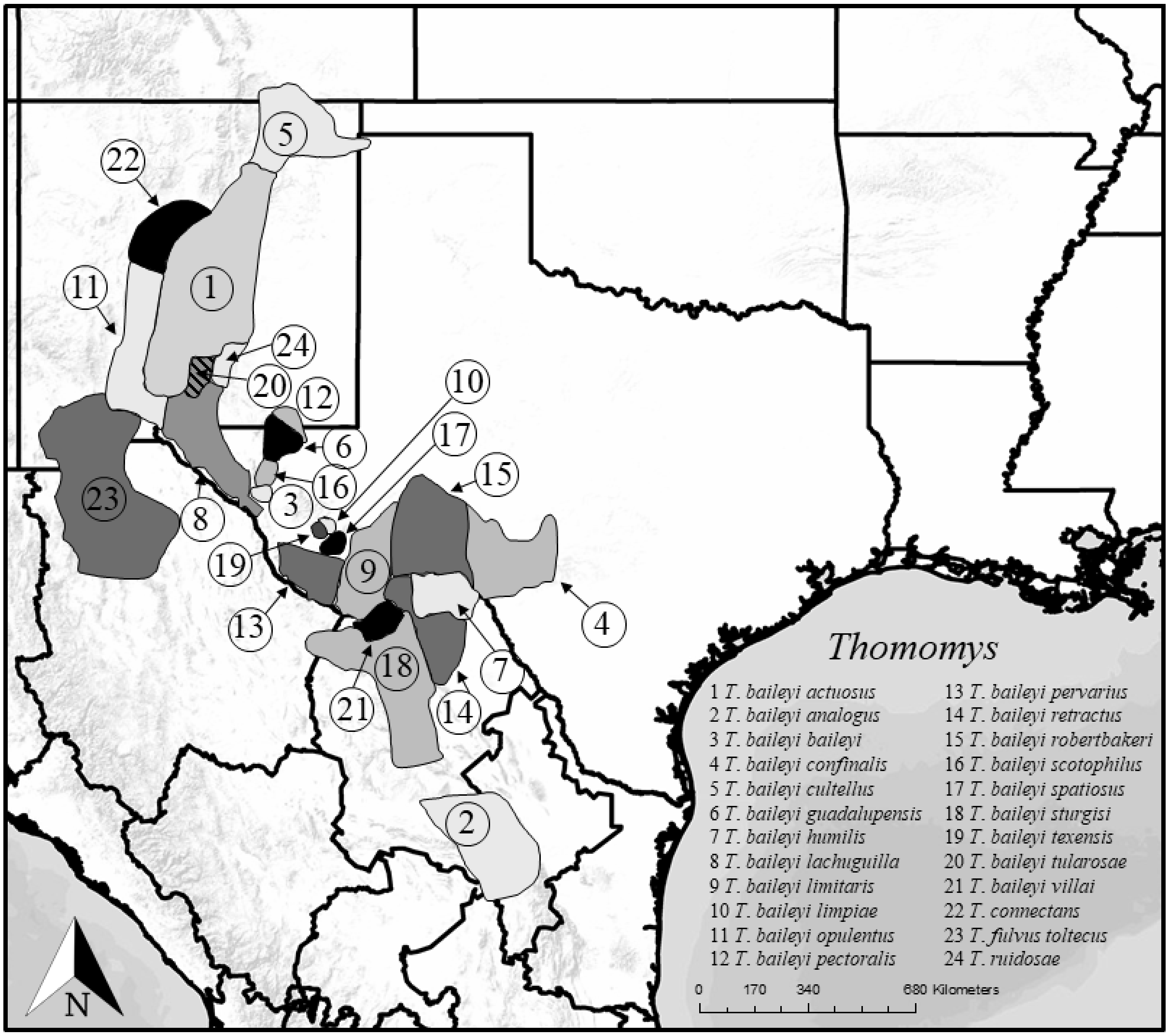


Figure 10. Map depicting approximate geographic distributions of taxa for *Thomomys*. Proposed distributions are based on a summation of the current and previous studies as discussed in Appendix II.

both of these points become important in the realm of conservation efforts where decisions to recognize and ultimately offer legal protection to a biological unit necessitates the use of a descriptor such as "subspecies" or "geographic variant". We have chosen to follow the traditional use of subspecies because: 1) generally there are multiple studies that have investigated, compared, and vetted the scientific usage and significance of the subspecies in question relative to other subspecies, and 2) the physical boundaries or distributions are typically well-defined.

When invoking genetic distances as a proxy for evaluating the magnitude of genetic differentiation of pocket gophers within the study area (type localities in Texas, western Louisiana, eastern New Mexico, southern Oklahoma, and northern Mexico), we followed the premises outlined in Bradley and Baker (2001) and Baker and Bradley (2006). Under the genetic species concept, populations are recognized as species when said populations can be demonstrated to be genetically isolated. Further, levels of genetic divergence among taxa or populations can be indicative of time since genetic isolation was established. In establishing an *a priori* benchmark that is representative of the magnitude of genetic divergence between two taxa, one should use entities that most systematists would agree represent valid taxa (species or subspecies, in this study). For example, if one considers *Geomys*, most systematists would agree that, based on numerous studies and datasets, *arenarius*, *attwateri*, *breviceps*, *bursarius*, *knoxjonesi*, *personatus*, and *tropicalis* deserve species recognition. For these taxa, the pair-wise genetic differences range from 10.37% to 15.82%. The only conundrum in this benchmark is the *personatus* to *tropicalis* comparison (5.20%), which is much lower than the "standard" differentiation among *Geomys* species. However, given the considerable chromosomal evolution possessed by *tropicalis* (Davis et al. 1971), it is clear that its divergence from *personatus* has been rather recent (and complicated by the major chromosomal rearrangements present in *tropicalis*). If those values are meaningful, then other taxa such as *jugossicularis*, *lutescens*, *streckeri*, and *texensis* display similar levels of genetic differentiation (8.34% to 14.01%); and in fact these recently have been suggested to represent species by several studies, as discussed in Appendix II. Further, in this study, we recommend that *brazensis* be elevated to species status given its genetic divergence from other populations of *G. breviceps* by 8.95% and from other species of *Geomys* by approximately 13.00% (Fig. 6A). Similarly, *G. b. sagittalis* differed from other populations of *G. breviceps* by values ranging from 6.85 to 7.96%; however, we are reluctant to formerly revise this taxon until additional samples from eastern Texas, Louisiana, and Arkansas can be included in a genetic analysis. An identical rationale/approach was invoked for evaluating genetic divergences among subspecies, with well-established subspecies serving as the indicators of "typical genetic differentiation". In those comparisons, subspecies of *Geomys* ranged from 1.29% to 6.38% (see Tables 4–6, Figs. 5–7). Based on this rationale, we used the following approximations: NA% for species level (monotypic, so no comparisons available) and 2.5–7% for subspecies level recognition within *Cratogeomys*; 7–14% for species level and 1.5–6.5% for subspecies level recognition within *Geomys*; and 7–11% for species level and 1–5% for subspecies level recognition within *Thomomys*.

The phylogenetic tree (Fig. 2) obtained from the analysis of *Cratogeomys* produced a topology similar to that presented in Hafner et al. (2008). The analyses primarily differed in that Hafner et al. (2008) recognized a northern and a southern group; however, only a few of the northern subspecies were included in their study. Results from the current analysis indicated a northern group (Clade E), a southern group (Clades B–D), and three samples (one individual of *C. c. consitus* and two of *C. c. sordidulus*) that were not affiliated with any clade. Further, Hafner et al. (2008) reduced the number of subspecies within this geographic region from 25 to two, resulting in all populations north of the Rio Grande being considered as *C. c. castanops* and those to the south of the Rio Grande as *C. c. consitus*. In the current study, we used a genetic divergence rate estimated for subspecies of *Cratogeomys* (>2.5%; discussed above, Fig. 5, Table 2) to recognize 10 subspecies (*angusticeps*, *castanops*, *consitus*, *dalquesti*, *jucundus*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, and *tamaulipensis*) plus three subspecies (*hirtus*, spp. nov., and *ustulatus*) that we were not included in our study but based on other evidence presumably deserve subspecific status.

Because Hafner et al. (2008) gave little consideration to morphological differences previously used to describe subspecies and because their sample size was small (only three specimens from two of the Texas subspecies), we did not adopt their proposed taxonomic arrangement of subspecies *in toto* and instead continued to recognize multiple subspecies based on the morphological study of these taxa by Hollander (1990). In addition, we did not recognize any additional species of *Cratogeomys* because the genetic distances between and among the clades of the various taxa revealed relatively low levels of genetic divergence. However, *C. c. tamaulipensis*, whose genetic divergence approached a level (7%) seen between other species of pocket gophers, may prove to be a distinct species. Further, our study focused on taxa occurring in Texas, eastern New Mexico, and northern Mexico; and clearly material from central and southern Mexico will be critical in more completely assessing the taxonomy of *Cratogeomys*; consequently, the low level of genetic divergences detected in the "northern" complex may not apply to the "southern" complex.

The phylogenetic tree obtained from the analysis of *Geomys* revealed a topology similar to that presented in Sudman et al. (2006) and Chambers et al. (2009), with the recognition of a basal *G. breviceps* group followed by a sister relationship between the *G. personatus* group and the *G. bursarius* group. The primary difference between the current study and Sudman et al. (2006) and Chambers et al. (2008) is the discovery of at least one unrecognized species in the *G. breviceps* group. Using the level of genetic divergence among species of *Geomys* (>7%), members of Clade I (referred to as *Geomys breviceps*) appear to be a different species from members of Clade II (referred to as *Geomys brazensis*). Further, the topology and level of genetic divergence (7.96%; Figs. 3b and 6b) between the clade containing samples of *G. b. breviceps* and *G. b. dutcheri* (II-A) and the clade containing samples of *G. b. sagittalis* (II-b), as well as the inconsistent placement of samples of *G. b. sagittalis* from extreme northeastern Texas, southeastern Oklahoma, Arkansas, and northern Arkansas in both Clade I and II, makes a final determination difficult and suggests more research needs to be done before elevating an unrecognized taxon (see Taxonomic Remarks for *G. b. sagittalis*). A second difference involves the inconsistent placement of the three subspecies of *G. texensis* (Fig. 3d) and suggests a case for synonymizing all three subspecies into a single taxon; however, given the breadth of genetic diversity among *G. t. bakeri*, *G. t. llanensis*, and *G. t. texensis*, precludes a simple combination. Given that *G. t. llanensis* and *G. t. texensis* are morphologically diagnosable but genetically very similar, we await a more detailed geographic study to determine more precise distributions of these taxa. Although the low level of genetic divergence (4.5–5.8%) between *G. tropicalis* and *G. personatus* suggests that they may be conspecific, the magnitude of chromosomal evolution (Davis et al. 1971) precludes that assumption and argues for retention of *G. tropicalis* as a species.

Although the level of taxonomic sampling was different, the phylogenetic tree obtained in the analysis of *Thomomys* taxa (Figs. 4, 7) recovered several of the relationships depicted in Alvarez-Castaneda (2010). Basically, Alvarez-Castaneda (2010) identified eight major clades within *Thomomys bottae*, several of which have been elevated to species level. One of these clades, referred by Alvarez-Castaneda (2010) as the "southwestern group", was especially relevant to this study, although we were only able to include 37 of the 80 or so subspecies comprising this group. Within Alvarez-Castaneda's (2010) southwestern group we recognize two major clades (I and II) and 5 minor clades (a–f). The level of genetic divergence between Clades I and II was >11%, exceeding values separating most species of gophers (Sudman et al. 2006) and indicating that Clades I and II probably represent different species. Within Clades I and II, a similar level of genetic divergence was apparent, with *actuosus* and *ruidosae* differing from *connectens* by a value of 7.70% and taxa associated with *baileyi* differing from those assigned to *fulvus* by 7.13%. Based on the breadth of information contained in this study, it appears that *baileyi*, *connectens*, *fulvus*, and *ruidosae* should be elevated to specific status (detailed explanations for these taxonomic determinations are provided in Appendix II). Genetic distances within the five minor clades (a–f) ranged from 0.87% to 5.07% (Fig. 7) and reflect varying levels of genetic divergence that could be assumed to represent separate subspecies in some cases or could be used to synonymize some taxa into a few subspecies. Certainly, many of the subspecific names should be synonymized (see Beauchamp-Martin et al. 2019 for an alternative view); however, we await a more inclusive dataset (broader taxon and geographic sampling), especially from Alvarez-Castaneda's (2010) "southwestern group," before further revising this group.

In summary (see Appendix II, Figs. 8–10), for *Cratogeomys* occurring in Texas and immediate surrounding areas, one species (*Cratogeomys castanops*) and 13 subspecies (*angusticeps*, *castanops*, *consitus*, *dalquesti*, *hirtus*, *jucundus*, *lacrimalis*, *parviceps*, *perplanus*, *pratensis*, *species novum*, *tamaulipensis*, and *ustulatus*) are proposed; for *Geomys* occurring in Texas and immediate surrounding areas, 12 species (*arenarius, attwateri*, *brazensis*, *breviceps*, *bursarius*, *jugossicularis, knoxjonesi, personatus, streckeri*, *species novum, texensis*, and *tropicalis*) and 18 subspecies (*arenarius arenarius*, *arenarius brevirostris*, *brazensis brazensis*, *brazensis pratincola*, *breviceps breviceps*, *breviceps dutcheri*, *breviceps sagittalis, bursarius major, jugossicularis jugossicularis*, *personatus davisi*, *personatus fallax*, *personatus fuscus*, *personatus maritimus, personatus megapotamus*, *personatus personatus*, *texensis bakeri, texensis llanensis*, and *texensis texensis*) are proposed; and for *Thomomys* occurring in Texas and immediate surrounding areas, four species (*baileyi*, *connectens*, *fulvus*, and *ruidosae*) and 22 subspecies (*baileyi actuosus*, *baileyi analogus*, *baileyi baileyi*, *baileyi confinalis*, *baileyi cultellus*, *baileyi guadalupensis*, *baileyi humilis*, *baileyi lachuguilla*, *baileyi limitaris*, *baileyi limpiae*, *baileyi opulentus*, *baileyi pectoralis, baileyi pervarius*, *baileyi retractus*, *baileyi robertbakeri*, *baileyi scotophilus*, *baileyi spatiosus*, *baileyi sturgisi*, *baileyi texensis*, *baileyi tularosae*, *baileyi villai*, and *fulvus toltecus*) are proposed. Forty-three original names were synonymized, elevated to species, or otherwise reassigned (see Appendix II for details): *Cratogeomys* (*bullatus*, *clarkii*, *convexus*, *excelsus*, *perexiguus*, *simulans*, *sordidulus*, *subsimus*, *surculus*, and *torridus*), *Geomys* (*breviceps ammophilus*, *breviceps attwateri*, *breviceps brazensis*, *breviceps llanensis*, *breviceps ludemani*, *breviceps pratincolus*, *breviceps terricolus*, *bursarius knoxjonesi*, *lutescens jugossicularis*, *lutescens major*, *personatus streckeri*, and *personatus tropicalis*), and *Thomomys* (*aureus lachuguilla*, *bottae actuosus*, *bottae analogus*, *bottae connectens*, *bottae cultellus*, *bottae guadalupensis*, *bottae humilis*, *bottae limpiae*, *bottae opulentus*, *bottae pervarius*, *bottae retractus*, *bottae robertbakeri*, *bottae ruidosae*, *bottae scotophilus*, *bottae toltecus*, *bottae villai*, *fulvus texensis*, *lachuguilla confinalis*, *lachuguilla limitaris*, *pectoralis*, and *sturgisi*). New taxonomic categories need to be recognized for samples previously recognized as *Cratogeomys castanops clarkii* and as *Geomys breviceps sagittalis*.

Although this study represents, by far, the most intensive compilation of data, it is far from being the final authority on pocket gopher systematics and taxonomy. For example, some individuals of *T. baileyi actuosus* from the type locality in Corona, NM, possessed a mtDNA haplotype reflective of *T. baileyi actuosus*, whereas others possessed a haplotype associated with *T. baileyi ruidosae*. This finding supports the study of Ruedi et al. (1997) who assumed hybridization between the two subspecies. Clearly, the presence of hybridization at a type locality of a taxon presents a challenge for future taxonomic studies. Given the close proximity of several sampling sites for supposedly different taxa and the propensity for pocket gophers to hybridize (several previously documented hybrid zones), it would be reasonable to assume there are other regions where hybridization is occurring.

Another limitation of the current study in producing a conclusive dataset involves missing taxa. Despite our efforts, we could not obtain any samples for 14 taxa (*C. castanops convexus*, *C. castanops hirtus*, *C. castanops ustulatus*, *C. castanops* spp., *C. castanops perexiguus*, *G. breviceps ludemani*, *G. breviceps sagittalis*, *G. breviceps terricolus*, *G. personatus fallax*, *G. personatus fuscus*, *T. bottae baileyi*, *T. bottae humilis*, *T. bottae retractus*, and *T. bottae villai*). Obviously, future studies should target those taxa, as well as focus on topotype samples for additional taxa.

In addition to missing data, limited sampling, especially across the geographic distribution of taxa, presented a challenge in data analyses, especially within *Thomomys*. In most cases, only two or three samples were available to represent the geographic variability within a taxon. This lack of coverage in conjunction with the apparent isolation and *in situ* evolution resulted in many of the subspecies of *Thomomys* failing to show genetic structure that could be used in establishing phylogenetic relationships, and consequently relationships among most subspecies were unresolved. Although this study provides a synoptic overview of several data types and datasets, taxa were not equally represented. For some taxa, few data points were available beyond the original descriptive data based on simple morphological observations. For those taxa, no genetic or intricate morphometric data were available. Despite these limitations, we were able to provide a phylogenetic resolution for many taxa and a taxonomic synopsis for the three genera. Therefore, this study provides a map forward for addressing systematic and conservation issues pertaining to the diversity of pocket gophers in Texas.

ACKNOWLEDGMENTS

Thanks to H. Garner and K. MacDonald of the Natural Science Research Laboratory, Museum of Texas Tech University, for assisting with tissue loans. Thanks to C. Garcia, B. Gross, J. Korstian, N. Paulat, K. Sullivan, C. Tipton and others for help with fieldwork and specimen collection. Thanks to the Field Methods classes of 2017–2022 for additional help with collecting samples. Special thanks to M. Janis, M. Mitchell, C. McEntire, and the late D. Stockbridge for securing access to Texas Parks and Wildlife Department properties and private ranches. Additional thanks to Jonah Evans and Texas Parks and Wildlife Department for funding various aspects of this project. Additional funding was provided by a State Line Item to Texas Tech University.

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Appendix I

*Specimens examined.—*Specimens examined in this study are listed below. Scientific names in brackets reflect the taxonomic status as determined by the data and interpretations presented herein. For each specimen, the collecting locality is provided; all specimens were collected from the United States unless otherwise noted. For most taxa, the museum catalog number and GenBank accession numbers for *Cyt*b are provided in parentheses and are separated by slashes, respectively. Multiple specimens from the same locality are separated by a semicolon. Abbreviations for museum catalog numbers are as follows: Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA); Louisiana State University Museum of Natural Science (LSUMZ); Museum of the High Plains, Fort Hays State University (MHP); Museum of Vertebrate Zoology (MVZ); Museum of Texas Tech University (TTU); New Mexico Museum of Natural History (NMMNH); and University of Arkansas, Little Rock (UALR). If museum numbers were not available (samples provided by individuals), abbreviations for samples are as follows: Henke et al. 2014 (Hap); Troy L. Best (Las Vegas Tissue, LVT); Museum of Texas Tech University (TK); Phillip Sudman (PDS); Scott B. Block (SBB); Scott K. Davis (SKD); Tarleton State University (A.N. Kozora, ANH); and Texas Cooperative Wildlife Collection, Texas A&M University (AK). For some specimens (designated BL, HY, NA, or PC) in DeWalt et al. (1993), Demastes (1994), Elrod et al. (2000), and Ruedi et al. (1997), there were no locality, museum number, or collector number available.

***Cratogeomys* (n = 69)**

Cratogeomys castanops angusticeps [= *Cratogeomys castanops angusticeps*].—Texas; Maverick Co., SSE on Loop 480 Eagle Pass, UTM 14R-354956-3171265 (TTU154633/OQ692170, TTU154634/OQ692171).

Cratogeomys castanops bullatus [= *Cratogeomys castanops angusticeps*].—Mexico: Coahuila; 1.7 km N Primero de Mayo, 390 m (LSUMZ36453/EF607265).

Cratogeomys castanops consitus [= *Cratogeomys castanops consitus*].—Mexico: Chihuahua; Gallego, 1,627 m (NMMNH5106/EF607273).

Cratogeomys castanops dalquesti [= *Cratogeomys castanops dalquesti*].—Texas; Sterling Co., Hwy 163, W Sterling City, 31.956496 N, 101.035489 W (TTU156682/OQ692172); 31.953721 N, 101.035489 W (TTU156683/OQ692173).

Cratogeomys castanops excelsus [= *Cratogeomys castanops consitus*].—Mexico: Durango; 5 km SW Lerdo, 1,158 m (NMMNH4472/EF607253, NMMNH2488/AF302172).

Cratogeomys castanops jucundus [= *Cratogeomys castanops jucundus*].—Mexico: Coahuila; Santa Teresa de Sofía, 2,500 feet (NMMNH3615/EF607246).

Cratogeomys castanops lacrimalis [= *Cratogeomys castanops lacrimalis*].—New Mexico; Chaves Co., Roswell along railroad track, 13S-546844-3691856 (TTU154604/OQ692174); 13S-546093-3693334 (TTU154605/OQ692175).

Cratogeomys castanops perplanus [= *Cratogeomys castanops perplanus*].—New Mexico; Chaves Co., 6.5 mi W Caprock, 4,300 feet (NMMNH4317/EF607274); Roosevelt Co., 2.5 mi E Tolar, 1,306 m (NMMNH4341/EF607252); Oklahoma; Cimarron Co., 1.5 mi S, 3 mi E Kenton (TTU43257/EF607276); Texas; Cochran Co., Yoakum Dunes Wildlife Management Area, 13S-716632-3699001 (TTU154754/OQ692176), 0.5 mi W Morton, 1,172 m (NMMNH4340/EF607251); Moore Co., 3 mi S Dumas (TTU42767/EF607275); Oldham Co., Boys Ranch, Horse Pasture, 35.530043 N, 102.255365 W (TTU156685/OQ692177).

Cratogeomys castanops sordidulus [= *Cratogeomys castanops consitus*].—Mexico: Coahuila; 1.5 miles NW Ocampo, 3,300 feet (NMMNH3626/EF607247, NMMNH3627/EF607248, NMMNH3628/EF607249); 2 km (by road) NW Cuatro Ciénegas, 776 m (LSUMZ36456/EF607266).

Cratogeomys castanops subsimus [= *Cratogeomys castanops consitus*].—Mexico: Coahuila; San Lorenzo, 1,380 m (NMMNH5104/EF607272); 7 km S, 14 km W General Cepeda, 1,710 m (LSUMZ36446/EF607261); Plan de Guadalupe, 1,040 m (LSUMZ36448/EF607264).

Cratogeomys castanops surculus [= *Cratogeomys castanops consitus*].—Mexico: Durango; 7 mi NNW La Zarca, 5,700 ft (NMMNH2467/AF302171); Hacienda Atotonilco, 1,976 m (NMMNH4482/EF607254).

Cratogeomys castanops tamalupensis [= *Cratogeomys castanops tamaulipensis*].—Mexico: Tamaulipas; 1.4 km upriver from old bridge on Rio Grande in Matamoros (TTU44881/OQ692178, TTU44882/OQ692179); Matamoros (TTU44883/L11908).

Cratogeomys castanops clarkii [= *Cratogeomys castanops pratensis*].—Texas; Presidio Co., Big Bend Ranch State Natural Area, 13R-601105-3260471 (TTU68426/EF607277); 35 mi S Marfa, 13R-595064-3307271 (TTU154639/OQ692180); El Carmen Land and Conservation Company (CEMEX USA), 13R-709868-3255299 (TTU156678/OQ692181), 13R-709713-3255388 (TTU156679/OQ692182), 13R-704122-3256046 (TTU156680/OQ692183), 13R-709829-3255144 (TTU156681/OQ692184).

Cratogeomys castanops parviceps [= *Cratogeomys castanops parviceps*].—New Mexico; Otero Co., US 70 0.5 mi E MM 192, 32.697 N, 106.235 W (TTU156684/OQ692185); 18 mi SW Alamogordo on Hwy 70, 13S-387486-3623169 (TTU154612/OQ692186); 40 km S Alamogordo (LSUMZ31455/L11902); 25 miles SW Alamogordo, 3,800 feet (LSUMZ31454/EF607255); 1.5 mi NE White Sands National Monument (UTM 13S-393476-3629302) (TTU154619/OQ692187).

Cratogeomys castanops pratensis [= *Cratogeomys castanops pratensis*].—Texas; Brewster Co., Alpine, Kokernot Municipal Park, UTM 13R-628377-3360903) (TTU154625/OQ692188, TTU154626/OQ692189, TTU154627/OQ692190); Elephant Mountain Wildlife Management Area, 13R-638181-3323673 (TTU154622/OQ692191).

Pappogeomys castanops simulans [= *Cratogeomys castanops perplanus*].—Texas; Lubbock Co., Lubbock (TTU111188/OQ692192).

Pappogeomys castanops torridus [= *Cratogeomys castanops pratensis*].—Texas; Hudspeth Co., 6.4 mi N, 2 mi E Sierra Blanca 14-101635-3478963 (TTU69278/OQ692193, TTU69279/OQ692194; TTU69280/OQ692195); 1.5 mi S Sierra Blanca 13R-466342-3445937 (TTU154628/OQ692196).

Pseudostoma castanops [= *Cratogeomys castanops castanops*].—Colorado; Otero, La Junta (TTU6776/OQ692197).

***Cratogeomys* outgroup and reference samples:**

Cratogeomys fulvescens.—Mexico: Tlaxcala; Huamantia, 2,380 m (CNMA41908/AY649462).

Cratogeomys goldmani goldmani.—Mexico: Coahuila; 1 km NW La Flor de Jimulco, 1,295 m (NMMNH5072/EF607267); Zacatecas; 30 km NW Río Grande, 2,095 m (NMMNH5078/EF607269); 20 km E, 2 km N Río Grande (DeWalt 1993/L11904); 0.5 km N Cañitas, 2,018 m (NMMNH5075/EF607268); 25 km S Concepción del Oro, 1,864 m (LSUMZ36442/EF607262).

Cratogeomys goldmani subnubilus.—Mexico: Coahuila; 44 km SSW Saltillo (NMMNH3629/EF607250); 19 km S, 18 km W General Cepeda (NMMNH5101/EF607270; NMMNH5102/EF607271); 17 km S, 16 km W General Cepeda, 2,064 m (LSUMZ36434/EF607258, LSUMZ36435/EF607259, LSUMZ36436/EF607260); 2 mi E Agua Nueva, 2,017 m (LSUMZ36444/EF607263).

Cratogeomys goldmani rubellus.—Mexico: San Luis Potosí; Rancho Ejido Montebello (DeWalt 1993/L11907); 6 km E Río Verde, 3350 ft (LSUMZ36089/AF302176, LSUMZ36086/EF607257).

C. merriami.—Mexico: Puebla; 1 km S Atlixco (LSUMZ36068/AY649464).

C. perotensis.—Mexico: Veracruz; 9 km NE Perote, 2,440 m (CNMA41911/AY649456).

***Geomys* (n = 166)**

Geomys arenarius [= *Geomys arenarius arenarius*].— New Mexico; Doña Ana Co., E bank Rio Grande W of Las Cruces (LSUMZ31456/AY393935); Texas; El Paso Co., 1 mi S, 0.25 mi W Fabens, 13R-179902-3507540 (TTU69205/OQ692198, TTU69207/OQ692199).

Geomys arenarius brevirostris [= *Geomys arenarius brevirostris*].—New Mexico; White Sands National Monument, 32.79117 N, 106.22664 W (ANH5/OQ692200, ANH6/OQ692201).

Geomys breviceps [= *Geomys breviceps breviceps*].—Arkansas; Little River Co., 3 miles NW Alleene (LVT5500/AY926386, UALR4532/AF158689); Louisiana; Morehouse Parish, 3.1 mi E Bastrop (LSUMZ31603/AY393939); 5.0 km E Bastrop (no voucher number, Demestes 1994/L28733); Collinston (no voucher number, Demestes 1994/L28734); Texas; Wood Co., 3.5 mi SE Quitman, 14-837069-3630019 (TTU69299/FJ210793).

Geomys breviceps ammophilus [= *Geomys attwateri*].—Texas; DeWitt Co., 1.13 mi SE Cuero (TTU143392/OQ692202, TTU143393/OQ692203).

Geomys breviceps attwateri [= *Geomys attwateri*].—Texas; Aransas Co., 0.57 mi SE Rockport (TTU143471/OQ692204, TTU143387/OQ692205); Bastrop County; no other data (AK5455/AY393937); Gonzales County; 0.8 miles S Ottine (LSUMZ29596/AY393936); Wilson County; 10 miles W Floresville (AK7920/AY393938).

Geomys breviceps brazensis [= *Geomys brazensis brazensis*].—Texas; Grimes Co., 5.81 mi E Kurten, CR 101 (TTU143407/OQ692206, TTU143408/OQ692207).

Geomys breviceps dutcheri [= *Geomys breviceps dutcheri*].—Oklahoma; Muskogee Co., Fort Gibson Historic Site (TTU143398/OQ692208, TTU143399/OQ692209).

Geomys breviceps llanensis [= *Geomys texensis llanensis*].—Texas; Gillespie Co., 9 mi E Fredericksburg (LSUMZ29604/AY393965); 14.6 mi N Fredericksburg, Texas 16 (PDS521/AY395304, PDS523/AY395305, PDS524/AY395306); Lampasas Co., 1 mi N Bend (PDS502/AY395295, PDS503/AY395296, PDS504/AY395297, PDS505/AY395298); 2.5 mi NE Bend (PDS506/AY395299, PDS510/AY395300); Llano Co., 2.11 mi W Llano, Llano River Golf Course, FM 152 (TK200137/OQ692210, TTU143480/OQ692211); Llano Golf Course (PDS529/AY395311, PDS530/AY395312, PDS531/AY395313, PDS532/AY395314, PDS533/AY395315); 1.8 mi W

Buchanan Dam (PDS537/AY395317, PDS538/AY395318); 5.1 mi W Buchanan Dam (PDS541/AY395319); McLennan Co., 3.46 mi SE Waco, Garden Drive (TTU143465/OQ692212, TTU143466/OQ692213, TTU143467/OQ692214); 3.52 mi SE Waco, Garden Drive (TTU155660/OQ692215); 3.65 mi SE Waco, University RV Park (TTU155664/OQ692216); 2.8 mi SE Waco, Garden Drive (TTU127928/OQ692217, TTU127931/OQ692218, TTU127932/OQ692219); McLennan Co., 3.64 mi SE Waco, Donaldson Road (TTU155663/OQ692220).

Geomys breviceps pratincolus [= *Geomys brazensis pratincola*].—Texas; Polk Co., 0.5 mi E Livingston, Hwy 90 (TTU143428/OQ692221).

Geomys breviceps sagittalis [= *Geomys sagittalis*].—Louisiana; Vernon Parish; 2 mi S, 3 mi W Rosepine (LSUMZ30723/AY393940); 0.5 km N Ranger Station (LSUMZ29336/U65297, LSUMZ29337/U65298); Fort Polk National Forest, 0.8 km N Ranger Station (no voucher specimen, Demestes 1994/L28736); Texas; Jasper Co., 1.4 km S Kirbyville (no voucher specimen, Demestes 1994/L28738); Smith Co., 6.8 km N Lindale (no voucher specimen, Demestes 1994/L28737); Reagan, Waite Cemetery, CR252 (TTU119230/OQ692222, TTU155642/OQ692223, TTU155643/OQ692224); Reagan, intersection of Hwy 6 and CR 251 (TTU119231/OQ692225).

Geomys knoxjonesi [= *Geomys knoxjonesi*].—Texas; Cochran Co., Yoakum Dunes WMA, 13S-716949-3698048 (TTU154726/OQ692226); 13S-716609-3697831 (TTU154731/OQ692227); 13S-715395-3698775 (TTU154732/OQ692228); 13S-714378-3698605 (TTU154733/OQ692229); 13S-713711-3698394 (TTU154734/OQ692230); 13S-716937-3698048 (TTU154777/OQ692231); Winkler Co., TX 18, 1 mi S Kermit, 314855.51 N, 103428.98 W (TTU156673/OQ692232, TTU156674/OQ692233), 3.2 miles S Kermit (SBB8/AY393947).

Geomys lutescens jugossicularis [= *Geomys jugossicularis jugossicularis*].—Texas; Dallam Co., 12 mi NE Texline, Thompson Grove Campground, Rita Blanca National Grassland, 13S-696734-4032226 (TTU156671/OQ692234); 12 mi NE Texline, Thompson Grove Campground, Rita Blanca National Grassland, 13S-693049-4032082 (TTU156672/OQ692235).

Geomys lutescens major [= *Geomys bursarius major*].—Texas; Donley Co., TX 70 near Clarendon, 34.876098 N, 100.877093 W (TTU156669/OQ692236), TX 70, S Clarendon (TTU156670/OQ692237); Hood Co., 7.5 mi N Granbury (LSUMZ29606/AY393944); 12.0 km N Granbury (no voucher specimen, Demestes 1994/L28735); McLennan Co., 3.4 mi SE Waco, FM 434 (TTU127930/OQ692238); Waco, 14-673833-3487957 (TTU53714/OQ692239, TTU53713/OQ692240); 0.5 mi SE Downsville, FM 434 (TTU139477/OQ692241, TTU139478/OQ692242, TTU139479/OQ692243); 2.8 mi SE Waco Garden Road (TTU127929/OQ692244); 3.54 mi SE Waco, Garden Drive (TTU155661/OQ692245).

Geomys personatus [= *Geomys personatus personatus*].—Texas; Nueces Co., Mustang Island State Park (AK7964, AY393960); Padre Island (Hap4/KC567287, Hap5/KC567285); San Patricio Co., Padre Island, Jct. Park Road 22 and 53, 14-680928-3056470 (TTU53737/OQ692246, TTU53738/OQ692247).

Geomys personatus davisi [= *Geomys personatus davisi*].—Texas; Zapata Co., Zapata Airfield, 14R-475262-2982566 (TTU154748/OQ692248, TTU154749/OQ692249, TTU154750/OQ692250, TTU154751/OQ692251); 2.5 mi N, 4 mi E San Ignacio (AK5362/AY393951).

Geomys personatus maritimus [= *Geomys personatus maritimus*].—Texas; Nueces Co., Flour Bluff, Corpus Christi, 27.64219 N, 97.31947 W (TTU154735/OQ692252, TTU154736/OQ692253); Flour Bluff, Graham Road (SKD176/AY393952, AK7924/AY393953, AK5431/AY393954); Mainland Nueces Co. and/or Flour Bluff (Hap1/KC567282), Flour Bluff (Hap3/KC567284, Hap8/KC567288); Mainland Nueces Co. (Hap6/KC567289, Hap7/KC567286, Hap9/KC567290).

Geomys personatus megapotamus [= *Geomys personatus megapotamus*].—Texas; Brooks Co., 5 mi S Falfurrias (AK5432/AY393957); Jim Hogg Co., 8 mi S Hebbronville (AK5439/AY393958); Webb Co., 4.5 mi SE Oilton, 14R-507688-3037070 (TTU154738/OQ692254, TTU154739/OQ692255, TTU154740/OQ692256), 4.5 mi SE Oilton, 14R-507688-3037072 (TTU154741/OQ692257); Kleberg Co., 1.5 mi S Riviera (LSUMZ31458/AY393959); Willacy Co., 6 mi N Raymondville (AK5242/AY393955, AK5241/AY393956).

Geomys streckeri [= *Geomys streckeri*].—Texas; Dimmitt Co., Carrizo Springs (TTU154755/OQ692258, TTU154756/OQ692259, TTU154757/OQ692260, SKD47/AY393967; AK5417/AY393968, AK4803/AY393969).

Geomys tropicalis [= *Geomys tropicalis*].—Mexico: Tamaulipas; 3.5 km S Altamira (TTU44885/OQ692261; TTU44886/AY393971, SKD143/AY393970).

Geomys texensis bakeri [= *Geomys texensis bakeri*].—Texas; Uvalde Co., 13 mi S Sabinal, 14-454486-3222273 (TTU69260/AY393964); 11 mi S Sabinal, FM 187 near Sabinal River, 14R-453276-3225125 (TTU154766/OQ692262, TTU154767/OQ692263, TTU154768/OQ692264); 15.4 mi S Sabinal (PDS515/AY395301; PDS517/AY395302); 16.4 mi S Sabinal (PDS518/AY395303).

Geomys texensis [= *Geomys texensis texensis*].—Texas; Mason Co., Mason Mountain WMA, 14-478532-3410990 (TTU98559/OQ692265, TTU98560/OQ692266); 2 mi W Mason (LSUMZ29605/AY393966); 2.5 mi W Mason on Highway 377 (PDS525/AY395307); 9.2 mi W Mason on Highway 377 (PDS526/AY395308, PDS527/AY395309, PDS528/AY395310); Pontotoc (PDS536/AY395316).

Geomys **outgroup and reference samples**

Geomys bursarius bursarius.—Minnesota; Anoka Co., Cedar Creek Biological Station (SKD407/AY393941); Iowa, Jasper Co., 2.7 mi N Oakland Acres (MHP29082/AF158693).

Geomys bursarius illinoensis.—Illinois; Madison Co., 1 mi N, 2 mi W Collinsville (LSUMZ35274/AY393942); Madison Co. (voucher at UALR/AF158691).

Geomys bursarius industrius.—Kansas; Reno Co., 2 mi N, 4 mi W Arlington (MHP24799/AY393943).

Geomys bursarius majusculus.—Kansas, Riley Co. (voucher at UALR/AF158694); Missouri; Holt Co., 6 mi S, 2 mi E Mound City (LSUMZ31448/AY393945); Nebraska, Saunders Co., 1 mi N, 4 mi E Cedar Bluffs (MHP24869, AF158694); Madison Co., 1.0 mi E Tilden, 14-599288-4655150 (TTU76065/EU332153); 1.0 mi E Tilden, 14-599333-4655044 (TTU76066/EU332154).

Geomys bursarius missouriensis.—Missouri; St. Louis Co. (voucher at UALR/AF158688); 1.0 mi S Creve Coeur Lake (LSUMZ31450/AY393946).

Geomys bursarius ozarkensis.—Arkansas; Izard Co., 3 mi W Melbourne (UALR4352/AF158697).

Geomys jugossicularis halli.—Colorado, Fremont Co., 3 mi S, 4 mi E Canon City (LSUMZ29284/AY393949); Fremont Co. (voucher at UALR/AF158692); 5 km S, 6 km E Canon City (deposited at LSUMZ/L11901); Nebraska; Harlan Co, 2 mi W Alma (LSUMZ31464/AY393948; LSUMZ31463/L38472); Harlan Co. (voucher at UALR/AF158695); Lincoln Co., 0.7 mi N Sutherland, 14-322330-4559659 (TTU76069/EU332155);

1.6 mi N Sutherland, 14-322370-4560542 (TTU76071/EU332156); 0.9 mi S Maxwell, 14-371907-4546014 (TTU76077/EU332157).

Geomys lutescens lutescens.—Nebraska; Custer Co.,; 8.5 mi N, 0.8 mi W Miller (Buffalo County) (LSUMZ31447/AY393950); Elrod et al. (2000) no locality (voucher at ULAL/AF158696).

Geomys pinetis mobilensis.—Florida; Santa Rosa Co., 0.8 mi N, Rt. 90 on Rt. 87 (LSUMZ29340/AY393961).

Geomys pinetis austrinus.—Georgia; Camden Co., 1.7 mi S Kingsland, rt. 17 (LSUMZ29327/AY393962).

Geomys pinetis floridanus.—Florida; Baker Co., 4.5 mi N Maclenny, Rt. 121 (LSUMZ29331/AY393963).

***Thomomys* (n = 84)**

Thomomys aureus lachuguilla [= *Thomomys baileyi lachuguilla*].—Texas; El Paso Co., Franklin Mountain State Park, Tom Mays Unit, 31.928609 N, 106.508308 W (TTU156675/OQ692267, TTU156676/OQ692268).

Thomomys baileyi spatiosus [= *Thomomys baileyi spatiosus*].—Texas; Brewster Co., Elephant Mountain Wildlife Management Area, UTM: 13R-640132-3322640 (TTU150134/OQ692269); Pecos Co., 22 mi N Marathon, 30.4080409 N, 102.9849812 W (TTU156677/OQ692270).

Thomomys baileyi tularosae [= *Thomomys baileyi tularosae*].—New Mexico; Otero Co., Fort Bliss, UTM: 13S-434087-3592888 (TTU76371/OQ692271); Fort Bliss, UTM: 13S-429746-3593710 (TTU76383/ AF445053).

Thomomys bottae actuosus [= *Thomomys baileyi actuosus*].—New Mexico; Lincoln Co., Corona, UTM: 13S-444950-3788586 (TTU150121/OQ692272, TTU150122/OQ692273), Gallinas Mountains (GA1/U64970); Mora Co., Pecos Mountains (PE1/U64969).

Thomomys bottae analogus [= *Thomomys baileyi analogus*].—Mexico: Coahuila; Bella Unión (NA/U64977); 1 km N Bella Unión (MVZ158017/U65273).

Thomomys bottae connectens [= *Thomomys connectens*].—New Mexico Socorro Co., Bernardo (NA/U64983); W side Rio Grande, 3.5 mi S La Joya (MVZ158634/U65270); Bernalillo Co., Albuquerque (NA/U64982).

T. bottae cultellus [= *Thomomys baileyi cultellus*].—New Mexico; Union Co., Des Moines (no voucher specimen, Ruedi et al. 1997/U64980).

Thomomys bottae guadalupensis [= *Thomomys baileyi guadalupensis*].—New Mexico; Otero Co., Guadalupe Mountains (NA/U64978); Texas, Culberson Co., Guadalupe Mountains National Park, McKittrick Canyon, UTM: 13R-523302-3538030 (TTU150135/OQ692274); Guadalupe Mountains National Park, McKittrick Canyon, UTM: 13R-523388-3538014 (TTU150136/OQ692275).

Thomomys bottae limpiae [= *Thomomys baileyi limpiae*].—Texas; Jeff Davis Co., 13.8 mi NE Fort Davis on HWY 17 (TTU136500/AF445058); 11 mi N Fort Davis on Hwy 17, 13R-615947-3395850 (TTU155154/ OQ692276).

Thomomys bottae opulentus [= *Thomomys baileyi opulentus*].—New Mexico; Socorro Co., Socorro (no voucher specimen, Ruedi et al 1997/U64981).

Thomomys bottae pervarius [= *Thomomys baileyi pervarius*].—Texas; Presidio Co., 1.7 mi N Shafter, UTM: 13R-567153-3301317 (TTU150133/OQ692277); Big Bend Ranch State Natural Area, UTM: 13-577321-3287548 (TTU67236/AF445052).

Thomomys bottae robertbakeri [= *Thomomys baileyi robertbakeri*].—Texas; Crockett Co., 14 mi N, 16 mi W Ozona, UTM: 14-262563-3422133 (TTU44476/AF445044); Irion Co., 0.5 mi W Barnhart, UTM: 14-293874-3447641 (TTU44477/AF445051); Reagan Co., 1.0 mi W Best, UTM: 14-250580-3458489 (TTU44478/AF445043); 3 mi W Big Lake, UTM: 14-260851-3453606 (TTU44480/AF445050); Upton Co., 2.5 mi E McCamey, UTM: 13-769136-3447857 (TTU43116/AF445042); 1.5 mi E McCamey, UTM: 13-767506-3447769 (TTU44654/OQ692278, TTU44655/OQ692279); 4 mi N, 4 mi E McCamey, UTM: 13-771227-3454511 (TTU44656/AF445047).

Thomomys bottae ruidosae [= *Thomomys ruidosae*].—New Mexico; Lincoln Co., Ruidoso, Schoolhouse Park, UTM: 13S-440244-3687181 (TTU150126/OQ692280); Bonita Lake (BL1/U64971, BL3/U64972); Bonita Lake, 14 mi N Ruidoso (MVZ147023/U65272), Nogal Canyon in the Sacramento Mountains (HY5/U64975); Otero Co., Lincoln National Forest, Deerhead Campground (TTU78860/AF445062, TTU78861/AF445061, TTU78862/AF445063), Deerhead Park (TTU109267/OQ692281, TTU109268/AF445064); Peñasco Canyon (PC1/U64973, PC2/U64974).

Thomomys bottae scotophilus [= *Thomomys baileyi scotophilus*].—Texas; Culberson Co., Sierra Diablo Wildlife Management Area, UTM: 13-508596-3459591 (TTU75824/AF445054); Sierra Diablo Wildlife Management Area, UTM: 13-508543-3460050 (TTU75866/AF445055); Hudspeth Co., Sierra Diablo Wildlife Management Area Headquarters, 5860 ft (TTU155152/OQ692282, TTU155153/OQ692283).

Thomomys fulvus texensis [= *Thomomys baileyi texensis*].—Texas; Jeff Davis Co., Mount Livermore Preserve (MLP-13), UTM: 13-580230-3390355 (TTU81072/AF445060); Mount Livermore Preserve, 6,280 FT, UTM: 13R-580697-3392220 (TTU127500/AF445059).

Thomomys lachuguilla confinalis [= *Thomomys baileyi confinalis*].—Texas; Kimble Co., 2 mi S London, UTM: 14-445631-3391234 (TTU44473/OQ692284); 4 mi SSW London, UTM: 14-443149-3388491 (TTU45539/AF445048); 1.13 mi SW London, UTM: 14R-443455-3388546 (TTU144979/OQ692285); Sutton Co., 13 mi W Sonora on FM 1989 (TK26933/OQ692286; TK26934/OQ692287).

Thomomys lachuguilla limitaris [= *Thomomy baileyi limitaris*].—Texas; Brewster Co., Big Bend Ranch State Park, UTM: 13R-618185-3257611 (TTU75658/AF445056, TTU75659/AF445057); Presidio Co., 14 mi N, 3 mi E Candelaria (TK26999/OQ692288).

Thomomys pectoralis [= *Thomomys baileyi pectoralis*].—New Mexico; Eddy Co., 7 mi E of Queen at junction of NM 137 and CR 410, UTM: 13S-535163-3563369 (TTU150118/OQ692289); UTM: 13S-535228-3562925 (TTU150119/OQ692290).

Thomomys sturgisi [= *Thomomys baileyi sturgisi*].—Mexico: Coahuila; 85 mi NW Ciudad Muzquiz, Canon del Hillcoat, Santa Rosa Mountains (TTU91522/OQ692291, TTU91523/OQ692292).

***Thomomys* outgroup and reference samples**

Thomomys bottae albatus.—California; Imperial Co., 2 mi S Holtville (MVZ156116/ U65260).

Thomomys bottae centralis.—Utah; Millard Co., 7 mi SW Skull Rock Pass (MVZ179591/U65266).

Thomomys bottae cervinus.—Arizona; Maricopa Co., 5 mi W, 3 mi N Gila Bend (MVZ156025/U65267).

Thomomys bottae concisor.—Nevada; Nye County, Wilson Ranch [=Monitor Ranch], Monitor Valley (MVZ163235/U65264).

Thomomys bottae grahamensis.—Arizona; Graham Co., Hospital Flat, Graham Mountains (MVZ146961/U65268).

Thomomys bottae mewa.—California; Fresno Co., 1.6 mi NW Academy (MVZ162920/U65254).

Thomomys bottae pervagus.—New Mexico; Rio Arriba Co., Alcalde (no voucher specimen, Ruedi et al. 1997/U64979).

Thomomys fulvus boregoensis.—California; Riverside Co., Mecca (MVZ156074/EU240742).

Thomomys fulvus catalinae.—Arizona; Pima Co., Soldier Camp, Santa Catalina Mountains (MVZ146822/EU240745).

Thomomys fulvus crassus.—California,;Imperial Co., 3.7 mi S Niland (MVZ156105/EU240743)

Thomomys fulvus divergens.—Mexico: Sonora; 1 mi N Huachinera (MVZ146861/EU240747).

T. fulvus fulvus.—New Mexico; Grant Co., Iron Creek, Black Range (MVZ146927/U65271); Black Range (no voucher specimen, Ruedi et al. 1997/U64976); Arizona, Yavapai Co., Wolf Creek, 0.5 mi E Ponderosa Park, Bradshaw Mountains (MVZ146880/U65269).

Thomomys fulvus internatus.—Colorado; Huerfano Co., 4.1 mi W Walsenburg (MVZ150313/EU240738).

Thomomys fulvus modicus.—Arizona; Santa Cruz Co., Sycamore Canyon, Patagonia Mountains (MVZ184977/EU240786).

Thomomys fulvus morulus.—New Mexico; Valencia Co., 13.1 mi S San Rafael on Hwy 53 (MVZ158511/EU240739).

Thomomys fulvus mutabilis.—Arizona; Gila Co., Rose Creek, Sierra Ancha (MVZ147002/EU240741).

Thomomys fulvus osgoodi.—Utah; Grand Co., 13.3 mi N Moab (MVZ150383/EU240737).

Thomomys fulvus patulus.—Arizona; Maricopa Co., Hassayampa River, 5.3 mi SE Wickenberg (MVZ156002/EU240740).

Thomomys fulvus phasma.—Arizona; Yuma Co., 1 mi N Tacna (MVZ156062/EU240744).

Thomomys fulvus toltecus.—Mexico: Chihuahua; Rancho El Peñasco, 5.6 mi E Janos (MVZ150183/EU240746).

Appendix II. Taxonomic Accounts and Interpretations

List of taxonomic names associated with gophers residing in Texas and adjacent areas. Comparisons are based on characterizations from original taxonomic descriptions. An asterisk (*) indicates the type locality is either in New Mexico or Mexico but the taxon is relevant to other taxonomic names applied to Texas gophers. An equal sign enclosed in parentheses (=) indicates a synopsis based on the most recent classifications as they pertain to Texas pocket gophers: for *Cratogeomys* (Hafner et al. 2008; Hollander 1990); *Thomomys* (Reudi et al. 1997; Álvarez-Castañeda 2010; Beauchamp-Martin et al. 2019); and *Geomys* (Jolley et al. 2000; Chambers et al. 2008; Sudman et al. 2006). An equal sign enclosed in brackets [=] indicates the classification-based data generated in this current study, as well as an overall synopsis of all previous studies. Figures 1–10 and Tables 1–7 were used as supporting data for the taxonomic decisions.

Names applied to *Cratogeomys*

As a result of the historical back and forth application of the generic designations, *Pappogeomys* and *Cratogeomys*, taxa have been described under both generic names. Hollander (1990) recognized 7 subspecies in Texas, but Hafner et al. (2008) subsumed all seven into a single subspecies, *C. c. castanops*, a taxonomic determination called into question in this study. Unlike the situation in *Geomys* and *Thomomys*, the levels of genetic divergence among taxa do not support the recognition of cryptic species. Multiple subspecies of the wide-ranging species, *C. castanops*, are recognized as presented below.

Cratogeomys castanops angusticeps (= *C. castanops castanops*) [= *C. castanops angusticeps*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in *P. castanops* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Eagle Pass, Maverick Co., Texas. Topotype sample included in this study (Locality 1).

Morphologic synopsis.—*C. c. angusticeps* generally is paler than other subspecies and smaller in cranial measurements compared to *tamaulipensis* (Nelson and Goldman 1934).

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *angusticeps* as sister to *bullatus* with only 0.57% genetic divergence between them, whereas *angusticeps* is genetically divergent from other members of the *C. castanops* clades (11 other subspecies) by genetic distances > 2.5%.

Taxonomic remarks.—*C. c. angusticeps* is most closely related to the subspecies *bullatus* and although separated by the Rio Grande, the two form a clade separate from other clades containing subspecies of *C. castanops*. The magnitude of genetic divergence between the *angusticeps*/*bullatus* clade and the other clades is probably indicative of subspecific divergence; consequently, in contrast to Hafner et al. (2008), we continue to recognize *angusticeps* as a subspecies separate from *C. castanops*. However, given the extremely low genetic divergence detected between *angusticeps* and *bullatus*, these two taxa should be synonymized under *angusticeps* which has priority over *bullatus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops bullatus** (= *C. castanops castanops*) [= *C. castanops angusticeps*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Russell and Baker 1955); placed in *P. castanops* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—2 mi S, 6.5 mi E Nava, 810 ft, Coahuila. No topotype sample included in this study; however, a sample from Primero de Mayo, Coahuila, located approximately 123 km SW of type locality, was included (Locality 2).

Morphologic synopsis.—This is a medium-sized gopher that resembles *tamaulipensis* except for larger cranial features. It is smaller than *convexus* and paler than *angusticeps* (Russell and Baker 1955).

Genetic synopsis.—No karyological or allozymic data are available. Hafner et al. (2008) placed *bullatus* in a clade containing other individuals of *C. c. castanops*. Our study of the mtDNA *Cyt*b gene depicts *bullatus* as sister to *angusticeps* with only 0.57% divergence between the two taxa. However, *bullatus* is genetically divergent from other members of the *C. castanops* clades (11 other subspecies) with genetic distances > 2.5%.

Taxonomic remarks.—*C. c. bullatus* is most closely related to *angusticeps* and although separated by the Rio Grande, the two form a clade separate from other clades containing subspecies of *C. castanops*. The magnitude of genetic divergence between the *angusticeps*/*bullatus* clade and the other clades is probably indicative of subspecific divergence; consequently, in contrast to Hafner et al. (2008) we propose that *bullatus* should be recognized as a subspecies separate from *C. castanops*. However, given the extremely low level of genetic divergence detected between *bullatus* and *angusticeps*, *bullatus* should be synonymized under *angusticeps* which has priority over *bullatus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops consitus** (= *C. castanops consitus*) [= *C. castanops consitus*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); later recognized as a subspecies of *P. castanops* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); recognized as a senior synonym of *C. c. consitus* (Hafner et al. 2008). Hafner et al. (2008) treated it as a broad ranging morphotype that includes several other formerly recognized subspecies.

Type locality.—Gallego, 5,500 feet, Chihuahua, Mexico. Topotype sample included in this study (Locality 5).

Morphologic synopsis.—*C. c. consitus* is similar to *clarkii*, but it has a smaller, lighter, and narrower skull. The auditory bullae bulge farther below the level of the basioccipital bone and the maxillary toothrow is shorter than in *C. c. lacrimalis*.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted some populations of *consitus* as sister to *sordidulus*, whereas other populations were members of a clade containing *convexus, excelsus, sordidulus*, *subsimus*, and *surculus*. Our study of the mtDNA *Cyt*b gene depicts *consitus* as paraphyletic and as a member of at least two clades containing *excelsus*, *subsimus* and *surculus*, and *sordidulus*, respectively. The sample of *consitus* forms a sister relationship to a sample of *sordidulus* with a genetic distance of 2.46%, but we cannot infer that *consitus* is phylogenetically related to *sordidulus* as three other samples of *sordidulus* were sister to a clade containing samples of *excelsus, subsimus*, and *surculus* or were basal to all other samples of *C.*

castanops. However, the *consitus* group substantially differs from the other clade of *Cratogeomys* by a genetic level (6.11%) approaching a magnitude that is seen between some species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—A thorough review is necessary to sort out the phylogenetic affinities and taxonomy of *consitus*, *excelsus*, *sordidulus*, *subsimus*, and *surculus*. At this time, given the low level of genetic divergence (2.26%) among these taxa (*consitus*, *excelsus*, *sordidulus*, *subsimus*, and *surculus*), we concur with Hafner et al. (2008) in synonymizing all four subspecies into *consitus*, which has priority. The magnitude of genetic distance between the *consitus* group and the other clades of *Cratogeomys* supports the conclusion of Hafner et al. (2008) that *consitus* should be recognized as a separate subspecies within *C. castanops*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops convexus **(=** ***C. castanops castanops*****) [=** ***C. castanops*** **spp.]**

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in synonymy as a subspecies of *P. castanops clarkii* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); considered morphologically indistinct from *C. c. castanops* and placed in synonymy with *C. c. castanops* by Hafner et al. (2008).

Type locality.—7 mi E Las Vacas, Rio Grande Valley, Coahuila, Mexico (opposite Del Rio, Texas). No topotype or other sample was included in this study (Locality 6).

Morphologic synopsis.—This subspecies is similar to *clarkii* and *tamaulipensis* except for its paler coloration and convex skull. It is similar to *angusticeps* except for its paler underparts and broader and more massive skull.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *convexus* as a member of a clade containing *consitus* and *subsimus*.

Taxonomic remarks.—Given that we were unable to obtain genetic material for this taxon, we cannot provide any additional taxonomic remarks beyond those presented in Hafner et al. (2008), who placed *convexus* in synonymy with *castanops*. Based on its geographic distribution and the genetic differences identified herein, the affinity of *convexus* could align with either *C. castanops castanops* or *C. castanops angusticeps*. Efforts to acquire genetic samples from the type locality of *convexus* will be necessary in order for a final taxonomic assignment to be made. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops dalquesti **(=** ***C. castanops castanops*****) [=** ***C. castanops dalquesti*****]**

Taxonomic history.—Described as a subspecies of *C. castanops* (Hollander 1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—1 mi N, 4 mi W Sterling City, Sterling Co., Texas. Topotype sample included in this study (Locality 7).

Morphologic synopsis.—Compared to *perplanus* and *clarkii*, *dalquesti* is darker, with distinguished shaped lacrimal bones, and is larger in all cranial measurements.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *dalquesti* as a member of a clade containing *castanops*, *perplanus*, and *simulans,* but with little genetic divergence between *dalquesti* and these other taxa (0.96%).

Taxonomic remarks.—Based on the moderate level of genetic divergence (2.4–2.5%) between *dalquesti* and the other three taxa (*castanops, perplanus*, and *simulans*), we initially agreed with Hafner et al. (2008) that genetically *dalquesti* should be placed in synonymy with *castanops, perplanus*, and *simulans* (*castanops* has priority). However, the morphometric distinction identified by Hollander (1990) should be considered in providing a taxonomic assignment; therefore, until a more detailed study is undertaken we are retaining *dalquesti* as a valid subspecies. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops excelsus** (= *C. castanops consitus*) [= *C. castanops consitus*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in *P. castanops* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008). *Cratogeomys c. excelsus* is treated as morphologically indistinct from *C. c. consitus* by Hafner et al. (2008).

Type locality.—10 mi W Laguna de Mayrán, Coahuila, Mexico. No topotype sample included in this study; however, a sample from Lerdo, Durango, located approximately 108 km WSW of the type locality was included (Locality 8).

Morphologic synopsis.—This is the largest subspecies within *castanops*. It is larger in size, paler in color, with a large and more angular skull, and relatively longer nasals than *consitus*, *clarkii*, *goldmani*, and *tamaulipensis*. The skull is heavier and more wedge-shaped than in *tamaulipensis*.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *excelsus* as a member of a clade containing *consitus* and *surculus*. Our study of the mtDNA *Cyt*b gene depicts *excelsus* is a member of a clade containing a sample of *subsimus* and *surculus* from their respective type localities. The sequence data indicate little genetic divergence (0.61%) between *excelsus* and the other two taxa. Further, there is a low level of genetic divergence (2.37%) among *consitus*, *excelsus*, *sordidulus, subsimus*, and *surculus*. However, the *consitus* group substantially differs from the other clade of *Cratogeomys* by a genetic level of 6.11%.

Taxonomic remarks.—Based on the mtDNA sequence data and the low levels of genetic divergence, we concur with Hafner et al. (2008) and propose synonymizing *excelsus* into *consitus*, which has priority. Further, because of the high level of genetic divergence between the *consitus* group and other clades of *Cratogeomys*, which approach a magnitude that is seen between some species of *Geomys* (Sudman et al. 2006), we concur with Hafner et al. (2008) that *consitus* should be recognized as a separate subspecies within *C. castanops*. Clearly, a more thorough study with genetic samples is needed to discern taxonomic assignments of populations from the type locality of *excelsus*, as well as to sort out the phylogenetic affinities and taxonomy of *consitus*, *excelsus*, *sordidulus*, *subsimus*, and *surculus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops hirtus** (= *C. castanops castanops*) [= *C. castanops hirtus*]

Taxonomic history.—described as a subspecies of *C. castanops* (Nelson and Goldman 1934); later recognized as a subspecies of *P. castanops* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Albuquerque, 5,500 ft, Bernalillo Co., New Mexico. No topotype or other sample available for this study (Locality 9).

Morphologic synopsis.—This subspecies is dark-colored, with long and dense pelage. It is similar to *lacrimalis* but upper parts are more heavily mixed and overlaid with black and the skull is generally shorter and narrower.

Genetic synopsis.—No karyological, allozymic, or DNA data are available.

Taxonomic remarks.—Given that we were unable to obtain genetic material for this taxon, we cannot provide any additional taxonomic remarks beyond those presented in Hollander (1990) and Hafner et al. (2008), who retained *hirtus* as a morphologically distinct subspecies or placed it in synonymy with *C. c. castanops*, respectively. However, the morphometric distinction identified by Hollander (1990) should not be ignored and precludes a confident taxonomic assignment. Efforts to acquire genetic samples from the type locality of *hirtus* will be necessary before a final taxonomic determination can be made. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops jucundus* **(=** ***C. castanops castanops*****) [=** ***C. castanops jucundus*****]**

Taxonomic history.—Described as a subspecies of *C. castanops* (Russell and Baker 1955); later recognized as a subspecies of *P. castanops* (Russell 1968b); returned to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008). *C. c. jucundus* is treated as morphologically indistinct from *C. c. castanops* by Hafner et al. (2008).

Type locality.—Hermanas, 1,205 ft, Coahuila, Mexico. No topotype sample included in this study; however, a sample from Santa Teresa de Sofia, Coahuila, located approximately 123 km SW of type locality (Locality 10), was available.

Morphologic synopsis.—This taxon is characterized by a larger body than *subsimus*, *bullatus*, and *ustulatus,* and a smaller skull than *subsimus*.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *jucundus* as a member of a clade containing *clarkii, lacrimalis*, and *parviceps*. Our study of the mtDNA *Cyt*b gene depicts *jucundus* as sister to a poorly supported clade containing *angusticeps, bullatus*, *castanops, clarkii*, *dalquesti, lacrimalis, parviceps*, *perplanus, pratensis*, *simulans, tamaulipensis,* and *torridus*. Genetically, *jucundus* differs substantially from other taxa with genetic distances ranging from 3.5 to 7.1%.

Taxonomic remarks.—Although Hafner et al (2008) recommended that *jucundus* be treated as a synonym of *C. c consitus*, given the large degree of genetic divergence from other taxa, we propose retaining it as a separate subspecies until further data become available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops lacrimalis **(=** ***C. castanops castanops*****) [=** ***C. castanops lacrimalis*****]**

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in synonymy with *perplanus* (Russell 1968b; Hall 1981); returned to *C. castanops* (Honeycutt and Williams 1982); returned to subspecific status as *C. c. lacrimalis* (Hollander 1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Roswell, 3,500 ft, Chaves Co., New Mexico. Topotype sample included in this study (Locality 11).

Morphologic synopsis.—Compared to *perplanus*, *lacrimalis* is smaller in most cranial dimensions and has larger lacrimals.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *lacrimalis* as a member of a clade containing *clarkii, jucundus*, and *parviceps*. Our study of the mtDNA *Cyt*b gene depicts *lacrimalis* is closely related to *clarkii, parviceps, pratensis*, and *torridus*. Furthermore, there is little genetic divergence between *lacrimalis* and these other subspecies (0.61%); however, this group differs genetically (2.50–6.44%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—At this time, although we are tempted to agree with Hafner et al. (2008) that *lacrimalis* should be placed in synonymy with *clarkii, parviceps, pratensis*, and *torridus* (*clarkii* has priority), the findings of Hollander (1990) should be given consideration. Consequently, we retain *lacrimalis* as a valid subspecies until additional data become available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops perplanus (= *C. castanops castanops*) [= *C. castanops perplanus*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Tascosa, 3,000 ft, Oldham Co., Texas. Topotype sample included in this study (Locality 14).

Morphologic synopsis.—*C. c. perplanus* is the largest subspecies in the U.S., with a smaller lacrimal bone than most other subspecies.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *perplanus* as sister to *lacrimalis* and *simulans*. Our study of the mtDNA *Cyt*b gene indicates that *perplanus* is closely related to *castanops, dalquesti*, and *simulans*. The sequence data indicate little genetic divergence between *perplanus* and these other subspecies (0.96%); however, this group differs genetically (2.80–6.33%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.— At this time, although we are tempted to agree with Hafner et al. (2008) that *perplanus* should be synonymized with *castanops, dalquesti*, and *simulans* (*castanops* has priority), the findings of Hollander (1990) should be given consideration. Consequently, we retain *perplanus* as a valid subspecies until additional data become available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops sordidulus** (= *C. castanops consitus*) [= *C. castanops consitus*]

Taxonomic history.—Described as a subspecies of *C. castanops* (Russell and Baker 1955); placed in *P. castanops sordidulus* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008).

Type locality.—1.5 mi NW Ocampo, 3,300 ft, Coahuila. Topotype sample included in this study (Locality 17).

Morphologic synopsis.—This is a large-sized subspecies that most closely resembles *clarkii*. It is characterized by a relatively short tail, narrow skull, and short maxillary toothrow.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted some populations of *sordidulus* as sister to *consitus*, whereas other populations were members of a clade containing *consitus*, *convexus, excelsus*, *subsimus*, and *surculus*. Our study of the mtDNA *Cyt*b gene depicts *sordidulus* as paraphyletic with individuals possessing membership of at three clades containing *consitus*, *excelsus*, *subsimus,* and *surculus*. Samples of *sordidulus* were placed as either.—1) sister to a clade containing a sample of *consitus*; 2) sister to a clade containing samples of *excelsus, subsimus*, and *surculus*; or 3) basal to all other samples of *C. castanops*. mtDNA sequence data indicated a low level of genetic divergence (2.37%) among *consitus*, *excelsus*, *sordidulus, subsimus*, and *surculus*. Further, the *consitus* group substantially differs from the other clade of *Cratogeomys* by a genetic level (6.11%) approaching a magnitude that is seen between some species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.— We concur with Hafner et al. (2008) and propose synonymizing the taxa listed above into *consitus*, which has priority. We also agree with Hafner et al. (2008) that *consitus* should be recognized as a separate subspecies within *C. castanops*. Clearly, a more thorough study is needed to discern distributions and taxonomic assignment of populations in order to sort out the phylogenetic affinities and taxonomy of *consitus*, *excelsus*, *sordidulus*, *subsimus*, and *surculus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Cratogeomys castanops subsimus **(=** ***C. castanops consitus*****) [=** ***C. castanops consitus*****]**

Taxonomic history.—Described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008).

Type locality.—Jaral (= San Antonio de Jaral), Coahuila, Mexico. Topotype sample included in this study (Locality 18).

Morphologic synopsis.—*C. c. subsimus* is closely aligned with *excelsus*, but it has a smaller body, darker color, and a skull that is somewhat smaller and relatively broader. It is similar to *tamaulipensis,* but its pelage is longer and denser; its skull is more massive, broader, flatter, and less wedge-shaped.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available but a study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *subsimus* as a member of a clade containing *consitus* and *convexus*. In our study of the mtDNA *Cyt*b gene, *subsimus* is depicted as sister to some individuals of *consitus* in a clade that contains a sample of *excelsus* and sample of *surculus* from their respective type localities. There is little genetic divergence (0.61%) between *subsimus* and the other two taxa.

Taxonomic remarks.—Given the low level of genetic divergence (2.37%) among *consitus*, *excelsus*, *sordidulus, subsimus*, and *surculus*, we concur with Hafner et al. (2008) and propose synonymizing them into *consitus*, which has priority. Further, the *consitus* group substantially differs from the other clade of *Cratogeomys* by a genetic level (6.11%) approaching a magnitude that is seen between some species of *Geomys* (Sudman et al. 2006). Consequently, we also concur with Hafner et al. (2008) that *consitus* should be recognized as a separate subspecies within *C. castanops*. Clearly, there is a need to acquire genetic samples from additional populations of *subsimus* in order to sort out the phylogenetic affinities and taxonomy of this taxon. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops surculus** (= *C. castanops consitus*) [= *C. castanops consitus*]

Taxonomic history.—Described as a subspecies of *P. castanops* (Russell 1968b); recognized as a subspecies of *P. castanops* (Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008).

Type locality.—La Zarca, Durango, Mexico. Samples collected close to topotype sample included in this study (Locality 19).

Morphologic synopsis.—*C. c. surculus* is characterized by a long and deep skull, widespread zygomata, long nasals, relatively short tail, and long hind foot; a smaller body size than *rubellus*, *goldmani*, *excelsus*, *consitus*, but not *subnubilus*; a tail and hind foot shorter, paler pelage, and skull relatively shorter and narrower than *rubellus*, *goldmani*, *excelsus*, and *consitus*.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. A taxon limited mtDNA study (Demastes et al. 2002) depicted *surculus* as a member of a clade containing samples of *parviceps* and *tamaulipensis*. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *surculus* as a member of a clade containing *consitus* and *excelsus*. Our study of the mtDNA *Cyt*b gene depicts *surculus* is a member of a clade containing samples of *excelsus, subsimus* and *surculus* as well as some individuals of *consitus* and *excelsus*. There is little genetic divergence (0.61%) between *surculus* and the other two taxa.

Taxonomic remarks.—Given the low level of genetic divergence (2.37%) among *consitus*, *excelsus*, *sordidulus, subsimus*, and *surculus*, we concur with Hafner et al. (2008) and propose synonymizing them into *consitus*, which has priority. Further, the *consitus* group substantially differs from the other clade of *Cratogeomys* by a genetic level (6.11%) approaching a magnitude that is seen between some species of *Geomys* (Sudman et al. 2006); consequently, we also concur with Hafner et al. (2008) that *consitus* should be recognized as a separate subspecies within *C. castanops*. Clearly, there is a need to acquire genetic samples from additional populations of *surculus* in order to sort out the phylogenetic affinities and taxonomy of this taxon. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Cratogeomys castanops tamaulipensis** (= *C. castanops castanops*) [= *C. castanops tamaulipensis*]

Taxonomic history.—described as a subspecies of *C. castanops* (Nelson and Goldman 1934); placed in *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Matamoros, Tamaulipas, Mexico. Topotype sample included in this study (Locality 20).

Morphologic synopsis.—*C. c. tamaulipensis* is smaller in size than most other subspecies and has dark postauricular patches.

Genetic synopsis.—No karyological or allozymic data are available. A taxon limited mtDNA study (Demastes et al. 2002) depicted *tamaulipensis* as a member of a clade containing samples of *parviceps* and *surculus*. Our study of the mtDNA *Cyt*b gene depicts *tamaulipensis* as sister to a clade containing 11 subspecies of *C. castanops* primarily north of Mexico (*angusticeps, bullatus*, *castanops, clarkii*, *dalquesti, lacrimalis, parviceps*, *perplanus, pratensis*, *simulans,* and *torridus*). Genetically, *tamaulipensis* differs substantially from other taxa with genetic distances ranging from 6.3 to 7.1%.

Taxonomic remarks.— Given the morphometric distinction identified by Hollander (1990) and the relatively large genetic distance from other taxa, we have retained *tamaulipensis* as a subspecies of *C. castanops*, although it may prove to be worthy of species recognition. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

***Cratogeomys castanops ustulatus** (= *C. castanops castanops*) [= *C. castanops ustulatus*]**

Taxonomic history.— Described as a subspecies of *C. castanops* (Russell and Baker 1955); placed in *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Don Martín, 800 ft, Coahuila, Mexico. No topotype or other sample available for this study Locality 22).

Morphologic synopsis.—This is a large-sized gopher with a relatively larger skull exceeded in size only by *subsimus*; no other morphometric data are available.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic or DNA data are available.

Taxonomic remarks.—Given that we were unable to obtain genetic material for this taxon, we cannot provide any additional taxonomic remarks beyond those presented in Hafner et al. (2008), who placed *ustulatus* in synonymy with *castanops*. Given its geographic separation from *C. c. castanops*, we propose retaining *ustulatus* as a subspecies of *C. castanops* until genetic samples are available from the type locality so that a thorough taxonomic revision can be undertaken. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

***Geomys clarkii** (= *C. castanops castanops*) [= *C. castanops pratensis*]**

Taxonomic history.—Described as *Geomys* (Baird 1855); recognized as a subspecies of *C. castanops* (Nelson and Goldman 1934); later recognized as a subspecies of *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Presidio del Norte, [at or near the present town of Ojinaga], on the Rio Grande, Chihuahua, Mexico. Near topotype (5 km E of type locality) included in this study (Locality 4a). However, the actual type locality recently has been restricted to the Upper Rio Grande Crossing, near the mouth of Cuervo Creek (also known as San Antonio Creek), about 7 kilometers southeast of El Indio, Maverick County, Texas (see Schmidly et al. 2023).

Morphologic synopsis.—*C. c. clarkii* has a relatively short, wide skull with extremely variable pelage color. It is larger in all cranial dimensions than *parviceps* and *angusticeps*, but smaller than *lacrimalis*.

Genetic synopsis.—No karyological or allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *clarkii* as sister to *parviceps*. Our study of the mtDNA *Cyt*b gene depicts *clarkii* as a member of a clade containing *lacrimalis*, *parviceps*, *pratensis*, and *torridus*.

Taxonomic remarks.—The type locality had been incorrectly referenced until the study by Schmidly et al. (2023). Specimens most likely referable to *pratensis* show a close relationship with *lacrimalis, parviceps*, *pratensis*, and *torridus*. Therefore, we propose reassigning specimens formerly referred to *clarkii* to *C. c. pratensis* until additional data are available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Geomys clarkii** (= *C. castanops castanops*) [= *C. castanops* spp.]

Taxonomic history.—Described as *Geomys* (Baird 1855); recognized as a subspecies of *C. castanops* (Nelson and Goldman 1934); later recognized as a subspecies of *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—Presidio del Norte, [at or near the present town of Ojinaga], on the Rio Grande, Chihuahua, Mexico. Near topotype (5 km E of type locality) included in this study (Locality 4a). However, the location of the type locality recently has been restricted to the Upper Rio Grande Crossing, near the mouth of Cuervo Creek (also known as San Antonio Creek), about 7 kilometers southeast of El Indio, Maverick County, Texas (Schmidly et al. 2023).

Morphologic synopsis.—No morphometric study has been conducted that would have included specimens from the revised type locality.

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene indicates that samples of *angusticeps* from Eagle Pass (approximately 30 km NW of El Indio) are genetically different from the samples historically assigned to *clarkii*.

Taxonomic remarks.—Given the close genetic association of samples from near El Indio, and those representing the type locality of *angusticeps* at Eagle Pass, samples from the new type locality will either represent a new taxon (*C. castanops* spp.), if different from *angusticeps*, or will replace *angusticeps* as an available taxon, as *clarkii* has priority over *angusticeps*. Efforts should be made to acquire genetic samples from the revised type locality of *clarkii* so that a thorough taxonomic revision can be undertaken. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Pappogeomys castanops parviceps** (= *C. castanops castanops*) [= *C. castanops parviceps*]

Taxonomic history.—Described as a subspecies of *Pappogeomys castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed as a subspecies of *C. castanops* (Hollander 1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—18 mi SW Alamogordo, 4,400 ft, Otero Co., New Mexico. Topotype sample included in this study (Locality 12).

Morphologic synopsis.—*C. c. parviceps* is smaller and darker than most other subspecies, and it has a short, narrow skull.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. A taxon limited mtDNA study (Demastes et al. 2002) depicted *parviceps* as a member of a clade containing samples of *surculus* and *tamaulipensis*. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *parviceps* as sister to *clarkii*. Our study of the mtDNA *Cyt*b gene depicts *parviceps* as a member of a clade containing *clarkii*, *lacramalis*, *pratensis*, and *torridus*. There is little genetic divergence between *parviceps* and these other subspecies (0.61%); however, this group differs genetically (2.50–6.44%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.— Although we considered Hafner's et al. (2008) interpretation that *parviceps* should be placed in synonymy with *clarkii, lacrimalis, pratensis*, and *torridus* (*clarkii* has priority), we have followed

Hollander (1990) in retaining *parviceps* as a valid subspecies of *C. castanops* until additional data are available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Pappogeomys castanops perexiguus** (= *C. castanops consitus*) [= *C. castanops consitus*]

Taxonomic history.—Described as a subspecies of *Pappogeomys castanops* (Russell 1968b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. consitus* (Hafner et al. 2008).

Type locality.—6 mi E Jaco, Chihuahua, 4,500 ft. No topotype or other sample available for this study (Locality 13).

Morphologic synopsis.—This taxon most closely resembles *consitus*. It has a smaller body than *consitus*, *surculus*, *excelsus*, *sordidulus*, *jucundus*, and *subsimus*, and compared to other subspecices of *C. castanops*, it has a shorter and broader cranium, a relatively longer tail, a longer hind foot, and is paler in coloration.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic or DNA data are available.

Taxonomic remarks.—Given that we were unable to obtain genetic material for this taxon, we cannot provide any additional taxonomic remarks beyond those presented in Hafner et al. (2008), who placed *perexiguus* in synonymy with *C. castanops consitus*. Efforts should be made to acquire genetic samples from the type locality of *perexiguus* so that a thorough taxonomic revision can be undertaken. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Pappogeomys castanops pratensis (= *C. castanops castanops*) [= *C. castanops pratensis*]

Taxonomic history.—Described as a subspecies of *P. castanops* (Russell 1968b); recognized as a subspecies of *P. castanops* (Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. castanops clarkii* (Hollander 1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—8 mi W, 3 mi S Alpine, 5,100 ft, Brewster Co., Texas. Near topotype samples included in this study (Locality 15).

Morphologic synopsis.—Medium-sized for species, braincase narrow, rostrum narrow and short; smaller in size, hind foot and tail shorter, and skull relatively smaller and shorter than *perplanus* and *clarkii* but not *angusticeps*.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *pratensis* as a member of a clade containing *clarkii*, *lacrimalis*, *parviceps*, and *torridus*, with little genetic divergence between *pratensis* and these other subspecies (0.61%); however, this group differs genetically (2.50–6.44%) from all other subspecies by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—We do not agree with Hafner et al. (2008) that *pratensis* should be placed in synonymy with *castanops* because, according to Hollander (1990), *pratensis* is more closely aligned with *clarkii, lacrimalis, parviceps*, and *torridus*, which caused him to synonymize *pratensis* with *clarkii*. However, *clarkii* as envisioned by Hollander (1990) is probably not a valid taxon (see account of *Geomys clarkii*). Consequently, we have retained *pratensis* as a valid subspecies of *C. castanops* until additional data become available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Pappogeomys castanops simulans (= *C. castanops castanops*) [= *C. castanops perplanus*]

Taxonomic history.—Described as a subspecies of *P. castanops* (Russell 1968b); placed in synonymy with *C. c. perplanus* (Dowler and Genoways 1979); returned to *P. castanops simulans* (Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—17 mi SE Washburn, Armstrong Co., Texas. No topotype included in this study; however, a sample from Lubbock, Texas, located approximately 155 km SW of type locality was included (Locality 16).

Morphologic synopsis.—*C. c. perplanus* closely resembles *castanops* except *simulans* has a relatively longer tail, shorter hind foot, and slightly shorter palate. It is allied with *pratensis* except *simulans* is larger, especially in the skull, and it is larger than *angusticeps* in all skull measurements except for breadth and length of rostrum.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). There are no allozymic data available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *simulans* as sister to *lacrimalis* and *perplanus*. Our study of the mtDNA *Cyt*b gene depicts *simulans* as a member of a clade containing *castanops*, *dalquesti*, and *perplanus*, with little genetic divergence between *simulans* and these other subspecies (0.96%); however, this group differs genetically (2.80–6.33%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—Although we considered Hafner's et al. (2008) interpretation that *simulans* should be placed in synonymy with *castanops, dalquesti*, and *perplanus* (*castanops* has priority), given the findings of Hollander (1990) we continue to treat *simulans* as a synonym of *C. castanops perplanus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Pappogeomys castanops torridus (= *C. castanops castanops*) [= *C. castanops pratensis*]

Taxonomic history.—Described as a subspecies of *P. castanops* (Russell 1968b; Hall 1981); revised to *C. castanops torridus* (Honeycutt and Williams 1982); placed in synonymy with *C. c. clarkii* (Hollander 1990); placed in synonymy with *C. c. castanops* (Hafner et al. 2008).

Type locality.—3 mi E Sierra Blanca, about 4,000 ft, Hudspeth Co., Texas. Topotype sample included in this study (Locality 21).

Morphologic synopsis.—This gopher is smaller in size and lighter and paler than *hirtus* and *pratensis*.

Genetic synopsis.—The karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *torridus* as a member of a clade containing *clarkii*, *lacrimalis*, *parviceps*, and *pratensis*, with little genetic divergence between *torridus* and these other subspecies (0.61%); however, this group differs genetically (2.50–6.44%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—We disagree with Hafner et al. (2008) that *torridus* should be placed in synonymy with *castanops* because, according to Hollander (1990), *torridus* is more closely aligned with *clarkii, lacrimalis, parviceps*, and *pratensis*, which caused him to synonymize *torridus* with *clarkii*. However, *clarkii* as envisioned by Hollander (1990) is quite probably not a valid taxon (see account of *Geomys clarkii*). Consequently, we treat *torridus* as a synonym of *C. c. pratensis* (which has priority) until additional data are available. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

*Pseudostoma castanops** (= *C. castanops castanops*) [= *C. castanops castanops*]

Taxonomic history.—described as *Pseudostoma castanops* (Baird 1852); placed in *P. castanops* (Russell 1968a, b; Hall 1981); revised to *C. castanops* (Honeycutt and Williams 1982); retained as a morphologically distinct subspecies by Hollander (1990); regarded as a senior synonym of *C. c. castanops* (Hafner et al. 2008).

Type locality.—Prairie road to Bents Fort, near Las Animas, Colorado. No topotype included in this study; however, a sample from La Junta, Colorado, located approximately 30 km ENE of type locality, was included (Locality 3).

Morphologic synopsis.—Characterized by medium sized, darker color, shorter tail, larger hindfeet, and a skull that is relatively long and narrow.

Genetic synopsis.—Karyotype reported as 2n = 46, FN = 86 (Berry and Baker 1971). No allozymic data are available. A study that incorporated mtDNA and nuclear markers (Hafner et al. 2008) depicted *castanops* as sister to *perplanus*; however, our study of the mtDNA *Cyt*b gene depicts *simulans* as a member of a clade containing *dalquesti*, *perplanus,* and *simulans*, with little genetic divergence between *castanops* and these other subspecies (0.96%); however, this group differs genetically (2.80–6.33%) from all other subspecies and by a level approaching that seen between subspecies and possibly species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.— *C. c. castanops* is closely related to *dalquesti*, *perplanus,* and *simulans*, and Hafner et al. (2008) suggested they should be placed in synonymy with *C. c. castanops*; however, the findings of Hollander (1990), who treated *dalquesti* and *perplanus* as distinct subspecies, cause us to regard *castanops* as separate from *dalquesti* and *perplanus*. See Figs. 1a, 2, 5 and 8; Tables 1 and 2.

Names Applied to *Geomys*

The systematics of pocket gophers of the genus *Geomys* have changed dramatically over the course of the 20th and 21st centuries, primarily the result of the application of cytogenetic and molecular genetic techniques that have resulted in the discovery of multiple cryptic species in the state of Texas. Bailey (1905) recognized nine taxa of *Geomys* in Texas, including five species and four subspecies, all on the basis of morphological distinctness. As the biological species concept slowly began to take hold in the 20th century, all but two of the taxa recognized by Bailey (*G. personatus* and *G. arenarius*) were lumped into one wide-ranging species, *G. bursarius*, which was distributed over most of the Great Plains and south-central United States, including almost all of Texas (Hall and Kelson 1959; Hall 1981). Recent studies by specialists trained in cytological and molecular taxonomy have revealed the existence of six species of these pocket gophers over what was formerly the range of *G. bursarius*. These species (*G. bursarius, G. attwateri, G. breviceps, G. knoxjonesi, G. texensis,* and *G. jugossicularis*) are considered cryptic species meaning they cannot be easily differentiated on the basis of morphological characteristics, although they are genetically distinct and reproductively isolated (Schmidly et al. 2022). Our study of the mtDNA *Cyt*b gene confirms these conclusions except for *G. breviceps brazensis*, which according to our data should be elevated to species status. The various species and subspecies are presented below.

Geomys arenarius (= *G. arenarius arenarius*) [= *G. arenarius arenarius*]

Taxonomic history.—Described as a species (Merriam 1895); *G. a. arenarius* was constructed when *G. a. brevirostris* was described (Hall 1932a).

Type locality.—El Paso, El Paso Co., Texas. Topotype sample included in this study (Locality 1).

Morphologic synopsis.—*G. arenarius* has a distinct zygomatic arch compared to all other *Geomys* spp., and it is generally paler with a longer tail and narrower skull than most other species of *Geomys*. Mauk et al. (1999) reported that *arenarius arenarius* was distinguishable from *breviceps brazensis*, *breviceps sagittalis*, and *streckeri* but indistinguishable from *attwateri*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 102 (Davis et al. 1971). No allozymic data are available. A taxon limited study of the 12S mtDNA gene depicted *G. a. arenarius* as basal to clade containing members of *knoxjonesi*, *bursarius*, *lutescens*, *G. texensis*, *G. personatus*, *G. streckeri*, and *G. tropicalis* (Jolley et al. 2000), but a more in-depth study of the mtDNA *Cyt*b gene (Sudman et al. 2006) depicted *arenarius* as sister to *knoxjonesi,* and the *arenarius-knoxjonesi* clade was then basal to a clade containing members of the *bursarius* group (*bursarius*, *jugossicularis*, *lutescens*, and *texensis*). A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *arenarius* as sister to *knoxjonesi.* This clade was then basal to a clade containing members of the *bursarius* group (*bursarius*, *jugossicularis*, *lutescens*, and *texensis*). Our study of the mtDNA *Cyt*b gene depicts *arenarius* as sister to *brevirostris* and in a clade sister to *knoxjonesi*. It differs from its sister taxon *brevirostris* by a genetic distance of 6.74%, a level approaching that seen between species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—We are retaining *G. a. arenarius* as a subspecies of *G. arenarius* until additional data are available to determine if *arenarius* and *brevirostris* should be treated as distinct species. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

*Geomys arenarius brevirostris** (= *G. arenarius brevirostris*) [= *G. arenarius brevirostris*]

Taxonomic history.—Described as a subspecies of *G. a. arenarius* (Hall 1932a).

Type locality.—9 mi W Tularosa, Hot Springs Rd., Otero Co., New Mexico. Topotype sample included in this study (Locality 2).

Morphologic synopsis.—*G. brevirostris* is darker, smaller in size, and has a shorter tail compared to *G. arenarius*.

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *brevirostris* as sister to *arenarius*, and in turn this clade is sister to *knoxjonesi*. *G. brevirostris* is genetically divergent, differing from its sister taxon *arenarius* by a genetic distance of 6.74%, a level approaching that seen between species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—We are retaining *brevirostris* as a subspecies of *G. arenarius* until additional data are available to determine if *brevirostris* and *arenarius* should be treated as distinct species. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

*Geomys breviceps** (= *G. breviceps breviceps*) [= *G. breviceps breviceps*]

Taxonomic history.—Described as a species (Baird 1855); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in *G. breviceps* (Bohlin and Zimmerman 1982).

Type locality.—Prairie Mer Rouge, Morehouse Parish, Louisiana. Topotype sample included in this study (Locality 4).

Morphologic synopsis.—This taxon is grayish or blackish brown with a distinct tendency to melanism. It has a rostrum that is slenderer and longer than in *G. breviceps brazensis*, as well as a longer prepalatal length and large auditory bullae.

Genetic synopsis.—Karyotype reported as 2n = 74, FN = 70 (Honeycutt and Schmidly 1979). No allozymic data are available. A taxon limited study using the 12S gene mtDNA (Jolley et al. 2000) showed *breviceps* to be basal to all other species of *Geomys* from Texas and surrounding areas. A more in-depth study by Sudman et al. (2006) depicted *breviceps* as sister to *sagittalis* and that clade was then basal to all other species of *Geomys* from Texas and surrounding areas. Our study of the mtDNA *Cyt*b gene depicts *breviceps* as part of a clade containing representatives of *dutcheri* and *sagittalis* which in turn formed a sister relationship with a clade containing representatives of *brazensis, pratincola*, and *sagittalis*. The magnitude of genetic divergence between *brazensis* and *pratincola/sagittalis* (3.45% and 7.27%, respectively) is high enough to reflect taxonomic distinctions.

Taxonomic remarks.—Samples of *G. b. breviceps* are paraphyletic with representatives of *dutcheri* and *sagittalis* (in part), which argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial in resolving the paraphyletic nature of these three subspecies. At this time, we suggest *breviceps, dutcheri* and *sagittalis* (in part) should be considered a species separate from *brazensis, pratincola* and *sagittalis* (in part). Under this scenario, *breviceps* has priority for the species relative to *breviceps, dutcheri*, and *sagittalis* (in part). See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys breviceps ammophilus (= *G. attwateri*) [= *G. attwateri*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Davis 1940a); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. attwateri* (Tucker and Schmidly 1981).

Type locality.—Cuero, DeWitt Co., Texas. Topotype sample included in this study (Locality 6).

Morphologic synopsis.—*G. b. ammophilus* is similar but smaller to *attwateri* in general appearance and skull characters.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 70 or 72 (Hart 1978; Honeycutt and Schmidly 1979). No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *ammophilus* as part of a clade containing representatives of *attwateri,* which in turn formed an unresolved trichotomy with a clade containing representatives of *personatus* and *tropicalis* and a clade containing *streckeri*.

Taxonomic remarks.—Samples of *ammophilus* are embedded within a clade containing all samples of *attwateri* with little genetic divergence (2.22%) being identified among samples. For this reason, we follow Tucker and Schmidly (1981) in synonymizing *ammophilus* under *G. attwateri*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys breviceps attwateri (= *G. attwateri*) [= *G. attwateri*]

Taxonomic history.—Originally described as a subspecies of *G. breviceps* (Merriam 1895); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); elevated to species status (Tucker and Schmidly 1981).

Type locality.—Rockport, Aransas Co., Texas. Topotype sample included in this study (Locality 3).

Morphologic synopsis.—*G. attwateri* is generally larger than most other *Geomys*. Mauk et al. (1999) reported that it was distinguishable from *breviceps brazensis*, *breviceps sagittalis*, and *streckeri*, but not from *arenarius arenarius*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 72-74 (Honeycutt and Schmidly 1979; Dowler 1989; Hart 1978). A taxon limited allozymic study by Block and Zimmerman (1991) showed *attwateri* to be sister to *personatus maritimus*. A taxon limited 12S rDNA study by Davis (1986) and a 12S mtDNA study by Jolley et al. (2000) depicted *attwateri* as sister to a clade containing *fallax*, *maritimus*, *megapotamus*, and *personatus*, *streckeri*, and *tropicalis*. A more in-depth study by Sudman et al. (2006) depicted *attwateri* as basal to a clade containing four subspecies of *personatus* (*davisi, megapotamus, maritimus,* and *personatus,*), *streckeri*, and *tropicalis*. Our study of the mtDNA *Cyt*b gene depicts samples of *attwateri* and *ammophilus* as forming a clade which in turn formed an unresolved trichotomy with a clade containing representatives of *personatus* and *tropicalis* and a clade containing *streckeri*.

Taxonomic remarks.—*G. attwateri* is a monophyletic species that includes samples formerly referred to *G. b. ammophilus,* and is unresolved relative to *G. personatus*, *streckeri,* and *tropicalis*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

***Geomys breviceps brazensis* (= *G. breviceps sagittalis*) [= *G. brazensis brazensis*]**

Taxonomic history.—Described as a subspecies of *G. breviceps* (Davis 1938); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. bursarius sagittalis* (Honeycutt and Schmidly 1979); placed in *G. breviceps sagittalis* (Bohlin and Zimmerman 1982).

Type locality.—5 mi E Kurten, Grimes Co., Texas. Topotype sample included in this study (Locality 7).

Morphologic synopsis.—*G. brazensis* is weakly differentiated from *pratincola*, differing mainly in having a smaller auditory bullae and relatively broader rostrum. Mauk et al. (1999) reported that *breviceps brazensis* was distinguishable from *streckeri* but indistinguishable from *arenarius arenarius*, *attwateri*, *breviceps sagittalis*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicted *brazensis* as part of a clade containing representatives of *sagittalis* and *pratincola,* which in turn formed a sister relationship with a clade containing representatives of *breviceps* and *dutcheri*. The magnitude of genetic divergence among these taxa are relatively high (4.04% and 2.64%) and suggestive of taxonomic difference. In addition, the two clades (*brazensis, pratincola* and *sagittalis* (in part) vs *breviceps, dutcheri* and *sagittalis* (in part)) differ (8.81%) by a level approaching that seen between species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—The magnitude of genetic divergence among *brazensis*, *pratincola*, and *sagittalis* argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial in resolving the paraphyletic nature of these three subspecies. Furthemore, the high level of genetic distinction between the clade that includes *brazensis, pratincola*, and *sagittalis* (in part) as compared to the clade with *breviceps, dutcheri*, and *sagittalis* (in part) suggest they represent distinct species. Further, we suggest retaining *brazensis* and *pratincola* as distinct subspecies and synonymizing the specimens formerly assigned to *G. b. sagittalis* within *G. brazensis*. Given that *brazensis* has priority over *pratincola*, *G. brazensis brazensis* would be the appropriate name for this taxon with *G. brazensis pratincola* available for the other subspecies. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

*Geomys breviceps dutcheri** (= *G. breviceps sagittalis*) [= *G. breviceps dutcheri*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Davis 1940a); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. breviceps sagittalis* (Honeycutt and Schmidly 1979).

Type locality.—Fort Gibson, Oklahoma. Topotype sample included in this study (Locality 8).

Morphologic synopsis.—*G. b. dutcheri* is darker brown with a generally smaller skull compared to *breviceps* and has a longer hind foot and longer and narrower rostrum compared to *brazensis*.

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts *G. b. dutcheri* as part of a clade containing representatives of *breviceps* and *sagittalis,* which in turn formed a sister relationship with a clade containing representatives of *brazensis*, *pratincola*, and *sagittalis*. The magnitude of genetic divergence between the two clades (8.81%) is relatively high. The magnitude of genetic divergence among members of the two clades (*dutcheri* vs *breviceps* and *sagittalis*, 3.45% and 7.96%, respectively) and (*breviceps* vs *dutcheri*, and *sagittalis*, 7.27% and 7.96%, respectively) also are relatively high. All of these differences are indicative of taxonomic distinctions (see below).

Taxonomic remarks.—Based on the molecular sequence data from our study of the mtDNA *Cyt*b gene, we suggest that *dutcheri*, *breviceps,* and *sagittalis* (in part) be considered a species separate from *brazensis, pratincola*, and *sagittalis* (in part). The genetic distinction between these two clades is at a level approaching that seen between species of *Geomys* (Sudman et al. 2006). Under this scenario, *breviceps* has priority for the species among *breviceps, dutcheri*, and *sagittalis* (in part) and *dutcheri* should be recognized as *G. breviceps dutcheri*. Further, the magnitude of genetic divergence seen among members of each clade suggest that three subspecies should be recognized. One subspecies would be *G. breviceps novum* (formerly *sagittalis* in part) because specimens from the type locality of *sagittalis* was synonymized within the *G. brazensis* clade, thereby requiring a new name for the material from eastern Texas, Louisiana, and Arkansas. *G. b. dutcheri* is embedded within a clade containing samples of *breviceps* and *sagittalis* (in part), and the magnitude of genetic divergence among these three subspecies also argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial to resolving the taxonomy and phylogenetic relationships of these taxa. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys breviceps llanensis (= *G. texensis texensis*) [= *G. texensis llanensis*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Bailey 1905); placed as a subspecies of *G. bursarius* (Villa-R. and Hall 1947); placed as a subspecies of *G. lutescens* (Davis 1940a); placed as a subspecies of *G. texensis* (Block and Zimmermann 1991); placed in synonymy with *G. t. texensis* (McAliley and Sudman 2005).

Type locality.—Llano, Llano Co., Texas. Topotype sample included in this study (Locality 23).

Morphologic synopsis.—*G. t. llanensis* is similar to *texensis* but differs genetically.

Genetic synopsis.—Karyotype reported as 2n =70, FN = 68 (Kim 1972; Honeycutt and Schmidly 1979). A taxon limited allozymic study by Block and Zimmerman (1991) depicted *texensis llanensis* as sister to *texensis tex*ensis. mtDNA showed *llanensis* and *texensis* to be synonymous and sister to *bakeri* (McAliley and Sudman 2005). Another taxon limited study using mtDNA (Davis 1986) depicted *llanensis* as part of a clade containing several taxa formerly placed in *bursarius* (*lutescens*, *major,* and *texensis*). A taxon limited data from a study examining the 12S mtDNA gene (Jolley al. 2000) and a more in-depth study by Sudman et al. (2006) depicted *llanensis* as sister to *texensis* followed by the addition of *bakeri*. Our study of the mtDNA *Cyt*b gene depicted *llanensis* as part of a paraphyletic clade containing representatives of *bakeri* and *texensis,* which in turn formed a sister relationship with a clade containing representatives of *arenarius* and *knoxjonesi*.

Taxonomic remarks.—Samples of *G. t. llanensis* were paraphyletic with representatives of *bakeri* and *texensis*; however, the magnitude of genetic divergence among these three subspecies (3.83% and 2.13%, respectively) argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial in resolving the paraphyletic nature of these three subspecies. Although McAliley and Sudman (2005) recommended synonymizing *llanensis* with *texensis*, we have retained *G. t. llanensis* as a valid taxon until a detailed geographic study determining the subspecific boundaries becomes available. It may be that we have applied incorrect names to specimens collected at various geographic locations. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

Geomys breviceps ludemani (= *G. breviceps sagittalis*) [= *G. breviceps sagittalis*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Davis 1940a); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. bursarius sagittalis* (Honeycutt and Schmidly 1979); placed in *G. breviceps sagittalis* (Bohlin and Zimmerman 1982).

Type locality.—7 mi W Fannett, Jefferson Co., Texas. No topotype or other sample available for this study (Locality 9).

Morphologic synopsis.—*G. b. ludemani* generally has a larger skull, resembles *terricolus* but with wider zygomatic arches. It resembles *pratincola* in coloration and size.

Genetic synopsis.—No karyological, allozymic, or DNA data are available.

Taxonomic remarks.—No samples were available for analysis in this study (this taxon may be extinct); therefore, we follow Bohlin and Zimmerman (1982) in synonymizing *ludemani* with *G. breviceps sagittalis*. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys breviceps pratincolus (= *G. breviceps sagittalis*) [= *G. brazensis pratincola*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (as *pratincolus*, Davis 1940a); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. bursarius sagittalis* (Honeycutt and Schmidly 1979); placed in *G. breviceps sagittalis* (Bohlin and Zimmerman 1982).

Type locality.—2 mi E Liberty, Liberty Co., Texas. Topotype sample included in this study (Locality 11).

Morphologic synopsis.—*G. b. pratincola* is weakly differentiated from *brazensis*, with a more inflated auditory bullae and lesser width of rostrum.

Genetic synopsis.—No karyological or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicted *pratincola* as part of a clade containing representatives of *brazensis* and *sagittalis,* which in turn formed a sister relationship with a clade containing representatives of *breviceps*, *dutcheri*, and *sagittalis*. The two clades show a level of genetic distinction (8.81%) indicative of that seen between other species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—The magnitude of genetic divergence between *G. b. pratincola* and *brazensis* and *sagittalis* (in part) argues against synonymizing them into a single subspecies. Given the magnitude of genetic difference between the two clades, we suggest that *brazensis, pratincola*, and *sagittalis* (in part) be considered a species separate from *breviceps, dutcheri*, and *sagittalis* (in part) with *sagittalis* (in part). Further, we suggest retaining *brazensis* and *pratincola* as distinct subspecies and synonymizing the specimens formerly assigned to *G. b. sagittalis* within *G. brazensis pratincola*. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial to resolving the paraphyletic nature of these three subspecies. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys breviceps sagittalis (= *G. breviceps sagittalis*) [= *G. breviceps sagittalis* in part and *G. species novum* in part]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Merriam 1895); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in *G. breviceps* (Bohlin and Zimmerman 1982).

Type locality.—Clear Creek, Galveston Co., Texas. No topotype or other sample available for this study (Locality 5).

Morphologic synopsis.—*G. b. sagittalis* is generally smaller, lighter brown with a distinct dark dorsal stripe, and has larger auditory bullae. Mauk et al. (1999) reported that *breviceps sagittalis* was distinguishable from *streckeri* but indistinguishable from *arenarius arenarius*, *attwateri*, *breviceps brazensis*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 74, FN = 72 (Honeycutt and Schmidly 1979; Dowler 1989; Hart 1978). A taxon limited allozymic study by (Block and Zimmerman 1991) revealed that *breviceps sagittalis* is sister to a clade containing *attwateri* and *personatus maritimus*. Similarly, a taxon limited study using the mtDNA 12S gene (Jolley et al. 2000) showed *G. breviceps* to be basal to all other species of *Geomys* (*arenarius*, *attwateri*, *bursarius*, *knoxjonesi, jugossicularis*, *personatus*, *streckeri*, *texensis*, and *tropicalis*) from Texas and surrounding areas. A more in-depth study by Sudman et al. (2006) depicted *G. b. sagittalis* as sister to *G. b. breviceps*, and this clade was then basal to all other species of *Geomys* from Texas and surrounding areas. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *sagittalis* as basal to a clade containing to all other species of *Geomys* from Texas and surrounding areas. Our study using the mtDNA *Cyt*b gene depicts *sagittalis* as members of two separate clades, which contain representatives of *brazensis*, *breviceps*, *dutcheri*, *pratincola*, and *sagittalis*. Samples of *G. b. sagittalis* are paraphyletic with representatives being included in a clade containing samples of *breviceps* and *dutcheri* and with representatives included in a separate clade that contains samples of *brazensis* and *pratincola.* These two clades differ genetically (8.81%) at a level approaching that seen between species of *Geomys* (Sudman et al. 2006).

Taxonomic remarks.—Based on our molecular genetic data, we suggest that *dutcheri*, *breviceps,* and *sagittalis* (in part) be considered a species separate from *brazensis, pratincola*, and *sagittalis* (in part). Given that samples of *G. b. sagittalis* (in part) from Texas differ from *G. brazensis* by a genetic distance of 2.64%, we suggest that they be subsumed into *G. brazensis*. Further, given the genetic divergence seen among members of the second clade where samples of *sagittalis* (in part) from eastern Texas, Arkansas, and Louisiana differed from samples of *breviceps* and *dutcheri* by 7.27% and 7.96%, respectively, it may be that three subspecies should be recognized. If so, one subspecies would be *G. breviceps novum* (formerly *sagittalis* in part) because specimens from the type locality of *sagittalis* were synonymized within the *G. brazensis* clade, thereby requiring a new name for the material from eastern Texas, Louisiana, and Arkansas. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial in resolving the taxonomy and phylogenetic relationships of these subspecies. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys breviceps terricolus (= *G. breviceps sagittalis*) [= *G. breviceps sagittalis*]

Taxonomic history.—Described as a subspecies of *G. breviceps* (Davis 1940a); placed as a subspecies of *G. bursarius* (Baker and Glass 1951); placed in synonymy with *G. bursarius sagittalis* (Honeycutt and Schmidly 1979); placed in *G. breviceps sagittalis* (Bohlin and Zimmerman 1982).

Type locality.—1 mi N Texas City, Galveston Co., Texas. No topotype or other sample available for this study (Locality 12).

Morphologic synopsis.—*G. b. terricolus* generally is larger and darker with a wider rostrum and zygomatic arches and relatively smaller auditory bullae compared to other subspecies.

Genetic synopsis.—No karyological, allozymic, or DNA data are available.

Taxonomic remarks.—No samples were available for analysis in this study (this taxon may be extinct); therefore, we follow Bohlin and Zimmerman (1982) in synonymizing *terricolus* with *G. breviceps sagittalis*. See Figs. 1b, 3a, 3b, 6a, 6b, and 9; Tables 1, 3, and 4.

Geomys bursarius knoxjonesi (= *G. knoxjonesi*) [= *G. knoxjonesi*]

Taxonomic history.—Described as a subspecies of *G. bursarius* (Baker and Genoways 1975); elevated to species (Baker et al. 1989).

Type locality.—4.1 mi N, 5.1 E Kermit, Winkler Co., Texas. Topotype sample included in this study (Locality 13).

Morphologic synopsis.—*G. knoxjonesi* is smaller but nearly indistinguishable from other species. Mauk et al. (1999) reported that cranial measurements of *knoxjonesi* were distinguishable from *breviceps brazensis*, *breviceps sagittalis*, and *streckeri* but indistinguishable from *arenarius arenarius*, *attwateri*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 68-70 (Hart 1978; Baker and Genoways 1975). A taxon limited allozymic study by (Block and Zimmerman 1991) placed *knoxjonesi* as sister to a clade containing *bursarius major*, *texensis llanensis* and *texensis tex*ensis. A taxon limited mtDNA study (Davis 1986) depicted *G. knoxjonesi* as sister to a clade containing several taxa formerly placed in *G. bursarius* (*llanensis*, *lutescens, major*, and *texensis*). A taxon limited data from a study examining the 12S mtDNA gene depicted *G. knoxjonesi* as basal to clade containing members of *bursarius*, *lutescens*, *texensis*, *personatus*, *streckeri*, and *tropicalis* (Jolley al. 2000), and a more in-depth study by Sudman et al. (2006) depicted *G. knoxjonesi* as sister to *G. a. arenarius*; this clade, in turn, was basal to a clade containing members of the *bursarius* group (*bursarius*, *jugossicularis*, *lutescens*, and *texensis*). A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *knoxjonesi* as sister to *G. arenarius*, and this clade was then basal to a clade containing members of the *bursarius* group (*bursarius*, *jugossicularis*, *lutescens*, and *texensis*). Our study of the mtDNA *Cyt*b gene depicts *G. knoxjonesi* as sister to a clade containing *G. a. arenarius* and *G. a. brevirostris*, with significant genetic divergence (10.37%) between *knoxjonesi* and *arenarius*.

Taxonomic remarks.—Given the large magnitude of genetic divergence between *G. knoxjonesi* and *G. arenarius*, we disagree with Hafner and Geluso (1983) who suggested that *knoxjonesi* was a subspecies of *G. arenarius*; consequently, we follow Baker et al. (1989) and Sudman et al. (2006) in retaining *knoxjonesi* as a separate species. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

*Geomys lutescens jugossicularis** (= *G. jugossicularis*) [= *G. jugossicularis jugossicularis*]

Taxonomic history.—Described as a subspecies of *G. lutescens* (Hooper 1940); placed as a subspecies of *G. bursarius* (Villa-R. and Hall 1947); elevated to species (Sudman et al. 2006).

Type locality.—Lamar, Prowers Co., Colorado. No topotype included in this study; however, a sample approximately 350 km SW of type locality was included (Locality 2).

Morphologic synopsis.—*G. jugossicularis* generally is smaller, yellowish cinnamon in coloration, and has a shorter jugal bone, deeper zygomatic plate of maxilla, and a slight mastoid process on the mastoid bulla.

Genetic synopsis.—Karyotype reported as 2n = 72, FN = 72 (Hart 1978). No allozymic data are available. A more in-depth study by Sudman et al. (2006) depicted *jugossicularis* as sister to *halli*; this clade was then sister to a clade containing subspecies of *bursarius*, *lutescens*, and *texensis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *jugossicularis* as sister to *halli*; this clade was then sister to a clade containing subspecies of *bursarius*, *lutescens*, and *texensis*. A chromosomal and DNA sequence study (Genoways et al. 2008) of multiple hybrid zones in Nebraska and surrounding regions depicted *jugossicularis* as sister to but distinct from *halli*. Our study of the mtDNA *Cyt*b gene depicted *jugossicularis* as sister to *halli*, and this clade was then sister to a clade containing representatives of *bursarius* and *lutescens*.

Taxonomic remarks.—Given the magnitude of genetic divergence (2.46%) between the two subspecies of *jugossicularis* (*halli* and *jugossicularis*), we retain *jugossicularis* as a species and follow Genoways et al. (2008) in suggesting that *halli* and *jugossicularis* be treated as valid subspecies with *G. jugossicularis jugossicularis* being the appropriate name applied to populations occurring in Texas. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

Geomys lutescens major (= *G. bursarius major*) [= *G. bursarius major*]

Taxonomic history.—Described as a subspecies of *G. lutescens* (Davis 1940a); placed as a subspecies of *G. bursarius* (Villa-R. and Hall 1947).

Type locality.—8 mi W Clarendon, Donley Co., Texas. Topotype sample included in this study (Locality 10).

Morphologic synopsis.—*G. b. major* generally is larger and has larger auditory bullae and a nearly flat dorsal profile of the cranium. Mauk et al. (1999) reported that in its cranial measurements *bursarius major* was distinguishable from *breviceps brazensis*, *breviceps sagittalis*, and *streckeri* but indistinguishable from *arenarius arenarius*, *attwateri*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 70–72, FN = 70–72 (Hart 1978; Baker et al. 1973). A taxon limited allozymic study by (Block and Zimmerman 1991) placed *bursarius major* as sister to a clade containing *texensis llanensis* and *texensis texensis*. A taxon limited mtDNA study (Davis 1986) depicted *major* as part of a clade containing several taxa formerly placed in *bursarius* (*llanensis*, *lutescens*, and *texensis*). A taxon limited study of the 12S mtDNA gene depicted *major* as sister to a clade containing the three subspecies of *texensis* (Jolley et al. 2000), and a more in-depth study by Sudman et al. (2006) depicted *major* as a member of a clade containing the seven subspecies of *bursarius*. This clade, in turn, was sister to *lutescens*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *major* as sister to *majusculus*, and this clade was then sister to a clade containing *jugossicularis*, *lutescens*, and *texensis*. Our study of the mtDNA *Cyt*b gene depicted *G. b. major* as a member of a clade containing several subspecies of *G. bursarius* (*bursarius*, *il-*

linoensis, *industrius*, *majusculus*, *missouriensis*, and *ozarkensis*), and this clade was then sister to *G. lutescens*. The magnitude of genetic divergence among the seven subspecies of *bursarius* ranged from 4.73 to 5.31%.

Taxonomic remarks.—Given the magnitude of genetic divergence among the seven subspecies of *bursarius* examined, we have retained *G. bursarius major* as a subspecies until a detailed geographic study determining the subspecific boundaries is available. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

Geomys personatus (= *G. personatus personatus*) [= *G. personatus personatus*]

Taxonomic history.—Described as a species (True 1889); placed as a subspecies of *G. personatus* (Strecker 1926).

Type locality.—Padre Island, Cameron Co., Texas. No topotype included in this study; however, a sample approximately 160 km N of type locality was included (Locality 20).

Morphologic synopsis.—*G. p. personatus* is the largest of the *personatus* subspecies. Henke et al. (2014) reported that *personatus* appeared to be indistinguishable from *maritimus* and *megapotamus.*

Genetic synopsis.—Karyotype reported as 2n = 68–70, FN = 72 (Davis et al. 1971; Smolen and Bickham 1995). No allozymic data are available. mtDNA data showed *G. p. personatus* in a clade containing samples of *davisi*, *maritimus*, *megapotamus*, and *tropicalis* (Henke et al. 2014). A taxon limited study examining the 12S rRNA gene depicted *G. p. personatus* as sister to *megapotamus*. A taxon limited mtDNA (Davis 1986) as well as a study of the 12S mtDNA (Jolley et al. 2000) depicted *personatus* as sister to *megapotamus*, with *tropicalis* and *streckeri* then joining in a step-wise fashion. A more in-depth study by Sudman et al. (2006) depicted *personatus* as sister to *megapotamus*, with this clade part of a larger clade containing subspecies of *personatus*, *streckeri*, and *tropicalis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *personatus* as sister to *megapotamus*, and this clade, in turn, was part of a larger clade containing subspecies of *personatus* and *tropicalis*. Our study of the mtDNA *Cyt*b gene) depicts *personatus* as an unresolved member of a clade containing samples of *megapotamus*, and this clade is part of a larger one containing the remaining subspecies of *personatus* and *tropicalis*.

Taxonomic remarks.—Given the low level of genetic divergence between *G. p. personatus* and *G. p. megapotamus* (1.97%), it may be prudent to synonymize these two taxa; however, we have followed Williams and Genoways (1981) in retaining *G. p. personatus* as a subspecies until additional genetic data are available about the subspecific boundaries of all subspecies of *G. personatus*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys personatus davisi (= *G. personatus davisi*) [= *G. personatus davisi*]

Taxonomic history.—Described as a subspecies of *G. personatus* distinct from the other named subspecies (Williams and Genoways 1981).

Type locality.—3 mi N, 2.8 W Zapata, Zapata Co., Texas. Topotype sample included in this study (Locality 15).

Morphologic synopsis.—This is a smaller subspecies similar to *fallax* in size; smaller in size than *megapotamus*; skull smaller than *maritimus* and *personatus*; paler in pelage when compared to *fallax*.

Genetic synopsis.—Karyotype reported as 2n = 68-70, FN = 72 (Smolen and Bickham 1995). No allozymic data are available. A mtDNA study by Henke et al. (2014) showed *davisi* in a clade containing samples of *maritimus*, *megapotamus*, *personatus*, and *tropicalis*, but a more in-depth study by Sudman et al. (2006) depicted *davisi* as sister to *tropicalis*, and this clade, in turn, was part of a larger clade containing subspecies of *personatus* and *streckeri*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *davisi* as sister to *tropicalis* and part of a larger clade containing subspecies of *personatus*. Our study of the mtDNA *Cyt*b gene showed that *davisi* formed a monophyletic clade that was unresolved to clades containing the other subspecies of *G. personatus* (*megapotamus*, *personatus*, and *maritimus*) and *G. tropicalis*.

Taxonomic remarks.—Given the relatively high level of genetic divergence between *davisi* and the other subspecies of *G. personatus* (4.33%–6.34%), we suggest retaining *G. p. davisi* as a subspecies until additional genetic data are available for all of the subspecies of *G. personatus*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

***Geomys personatus fallax* (= *G. personatus fallax*) [= *G. personatus fallax*]**

Taxonomic history.—Described as a subspecies of *G. personatus* (Merriam 1895); determined to be morphometrically distinct from the other subspecies of *G. personatus* (Williams and Genoways 1981).

Type locality.—South side Nueces Bay, Nueces Co., Texas. No topotype or other sample available for this study (Locality 16).

Morphologic synopsis.—*G. p. fallax* is the darkest colored (blackish or grayish brown) subspecies besides *fuscus* and generally smaller in size than the other subspecies.

Genetic synopsis.—Karyotype reported as 2n = 68 or 70, FN = 70 (Davis et al. 1971; Smolen and Bickham 1995). No allozymic data are available. A taxon limited mtDNA study (Davis 1986) depicted *fallax* as sister to *G. p. megapotamus*, and part of a larger clade that was sister to a clade containing *megapotamus* and *personatus* with *tropicalis* and *streckeri* joining in a step-wise fashion.

Taxonomic remarks.—No samples were available for analysis in this study; however, given the difference in karyotypes between *fallax* and other subspecies of *G. personatus*, we are retaining *G. p. fallax* as a subspecies as recommended by Williams and Genoways (1981). See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

***Geomys personatus fuscus* (= *G. personatus fuscus*) [= *G. personatus fuscus*]**

Taxonomic history.—Described as a subspecies of *G. personatus* (Davis 1940a); determined to be morphometrically distinct from the other subspecies of *G. personatus* (Williams and Genoways 1981).

Type locality.—Fort Clark, Kinney Co., Texas. No topotype or other sample available for this study (Locality 17).

Morphologic synopsis.—*G. p. fuscus* is the darkest colored (toward reddish brown) subspecies, and is generally smaller in size, with relatively longer nasals and shorter and narrower claw on the fifth digit of the manus.

Genetic synopsis.—No karyological, allozymic, or DNA data are available.

Taxonomic remarks.—No samples were available for analysis in this study (this taxon may be extinct); therefore, given the paucity of data available, we follow Williams and Genoways (1981) in recognizing *G. p. fuscus* as a valid subspecies. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys personatus maritimus (= *G. personatus maritimus*) [= *G. personatus maritimus*]

Taxonomic history.—Described as a subspecies of *G. personatus* (Davis 1940a).

Type locality.—Flour Bluff, 11 mi SE Corpus Christi, Nueces Co., Texas. Topotype sample included in this study (Locality 18).

Morphologic synopsis.—The subspecies *maritimus* is similar to *G. p. personatus* except slightly smaller. Henke et al. (2014) reported that *maritimus* appeared to be indistinguishable from *megapotamus* and *personatus*.

Genetic synopsis.—Karyotype reported as 2n = 68 or 70, FN = 70 (Davis et al. 1971; Smolen and Bickham 1995). A taxon limited allozymic study by (Block and Zimmerman 1991) revealed that *maritimus* was sister to *attwateri*. A mtDNA study showed *G. p. maritimus* in a clade containing samples of *davisi*, *megapotamus*, *personatus*, and *tropicalis* (Henke et al. 2014). A taxon limited study mtDNA (Davis 1986) depicted *G. p. maritimus* as sister to *fallax* and part of this clade that was sister to a clade containing *megapotamus* and *personatus* with *tropicalis* and *streckeri* joining in a step-wise fashion. A more in-depth study by Sudman et al. (2006) depicted *maritimus* as sister to a clade containing subspecies of *personatus*, *streckeri*, and *tropicalis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *maritimus* as sister to a clade containing subspecies of *davisi* and *tropicalis*. Our study of the mtDNA *Cyt*b gene depicts that *maritimus* forms a monophyletic clade that is unresolved to clades containing the other subspecies of *G. personatus* (*davisi*, *megapotamus*, and *personatus*) and *G. tropicalis*.

Taxonomic remarks.—Given the relatively high level of genetic divergence between *maritimus* and the other subspecies of *G. personatus* (5.25%–6.34%), we suggest retaining *G. p. maritimus* as a subspecies as recommended by Williams and Genoways (1981). See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys personatus megapotamus (= *G. personatus megapotamus*) [= *G. personatus megapotamus*]

Taxonomic history.—Described as a subspecies of *G. personatus* (Davis 1940a).

Type locality.—4 mi SE Oilton, Webb Co., Texas. Topotype sample included in this study (Locality 19).

Morphologic synopsis.—*Geomys p. megapotamus* is smaller in size than *personatus* and *maritimus*, but larger than other *personatus* subspecies. Henke et al. (2014) reported that *megapotamus* appeared to be indistinguishable from *maritimus* and *personatus*.

Genetic synopsis.—Karyotype reported as 2n = 68-70, FN = 72 (Davis et al. 1971; Smolen and Bickham 1995). No allozymic data are available. The mtDNA study by Henke et al. (2014) showed *megapotamus* in a clade containing samples of *G. p. davisi*, *G. p. maritimus*, *personatus*, and *tropicalis*. A taxon limited study (Davis 1986) examining the 12S rRNA gene depicted *megapotamus* as sister to *personatus* and part of a clade that was sister to a clade containing *maritimus* and *fallax* with *tropicalis* and *streckeri* joining in a step-wise fashion. The 12S mtDNA study of Jolley et al. (2000) depicted *megapotamus* as sister to *personatus* with *tropicalis* and *streckeri* then joining in a step-wise fashion. A more in-depth study by Sudman et al. (2006) depicted *megapotamus* as sister to *personatus* in a clade that was part of a larger clade containing subspecies of *personatus*, *streckeri*, and *tropicalis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *megapotamus* as sister to *personatus* in a clade that was part of a larger one containing subspecies of *personatus* and *G. tropicalis*. Our study of the mtDNA *Cyt*b gene depicts *megapotamus* as sister to *personatus* in a clade that is part of a larger clade containing the remaining subspecies of *personatus* and *tropicalis*.

Taxonomic remarks.—Given the low level of genetic divergence between *G. p. megapotamus* and *G. p. personatus* (1.97%), it may be prudent to synonymize these two taxa; however, until additional data are available, we follow Williams and Genoways (1981) in retaining *G. p. megapotamus* as a subspecies. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys personatus streckeri **(=** ***G. streckeri*****) [=** ***G. streckeri*****]**

Taxonomic history.—Described as a subspecies of *G. p. minor* (Davis 1940a); reassigned as *G. p. streckeri* (Davis 1943); determined by Williams and Genoways (1981) to be morphometrically distinct from other subspecies of *G. personatus*; elevated to a distinct species (Jolley et al. 2000; Sudman et al. 2006).

Type locality.—Carrizo Springs, Dimmit Co., Texas. Topotype sample included in this study (Locality 21).

Morphologic synopsis.—*G. streckeri* is generally smaller and lighter in coloration compared to the subspecies of *personatus*. It differs from *fallax* in nasals that are acute posteriorly, and in having a mastoidal bullae that is more swollen and projects farther posteriorly. It differs from *fuscus* in having grayish coloration and larger auditory bullae. Mauk et al. (1999) reported that cranial measurements of *streckeri* were distinguishable from *breviceps brazensis* and *breviceps sagittalis* but indistinguishable from *arenarius arenarius*, *attwateri*, *bursarius major*, *knoxjonesi*, and *texensis texensis*.

Genetic synopsis.—Karyotype reported as 2n = 72, FN = 72 (Davis et al. 1971; Smolen and Bickham 1995). No allozymic data are available. A taxon limited mtDNA study (Davis 1986) depicted *G. streckeri* as sister to a clade containing *fallax*, *maritimus*, *megapotamus*, *personatus*, and *tropicalis*. The 12S mtDNA study of Jolley et al. (2000) depicted *streckeri* as basal to a clade containing *G. tropicalis* and the two subspecies of *personatus* (*megapotamus* and *personatus*). A more in-depth study by Sudman et al. (2006) depicted *streckeri* as basal to a clade containing subspecies of *personatus* and *tropicalis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *G. streckeri* as sister (statistically unsupported, however) to *G. attwateri*. Our study of the mtDNA *Cyt*b gene depicts *G. streckeri* as forming an unresolved trichotomy with a clade containing representatives of *G. personatus* and *G. tropicalis* and a clade containing *G. attwateri*.

Taxonomic remarks.—*G. streckeri* is a monophyletic species that is unresolved relative to *G. attwateri*, *personatus*, and *tropicalis*. Given its genetic divergence (12.25%) from the other subspecies of *G. personatus*, it is best to treat *streckeri* as a species separate from *G. personatus*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys personatus tropicalis *** (=** ***G. tropicalis*****) [=** ***G. tropicalis*****]**

Taxonomic history.—Described as a subspecies of *G. personatus* (Goldman 1915); elevated to a distinct species (Alvarez 1963).

Type locality.—Altamira, Tamaulipas, Mexico. Topotype sample included in this study (Locality 25).

Morphologic synopsis.—*G. tropicalis* is similar in color to typical *personatus* and *fallax*. In size, it is similar to *fallax* and much smaller than typical *personatus*. It has a smaller and narrower skull than typical *personatus*, and the mastoid and auditory bullae are not as rounded as in *fallax*. Williams and Genoways (1977) determined there was no appreciable morphometric variation within samples of *tropicalis*.

Genetic synopsis.—Karyotype reported as 2n = 38, FN = 72 (Davis et al. 1971). No allozymic data are available. A mtDNA study showed *G. p. tropicalis* in a clade containing samples of *G. p. davisi*, *G. p. maritimus*, *G. p. megapotamus*, and *G. p. personatus* (Henke et al. 2014). A taxon limited mtDNA study (Davis 1986) depicted *G. tropicalis* as sister to a clade containing *G. p. fallax*, *G. p. maritimus*, *G. p. megapotamus*, and *G. p. personatus* with *G. streckeri* being basal to this larger clade. The 12S mtDNA study of Jolley et al. (2000) depicted *G. tropicalis* as sister to a clade containing the two subspecies of *G. personatus* (*megapotamus* and *personatus*), but a more in-depth study by Sudman et al. (2006) depicted *G. tropicalis* as sister to *G. p. davisi*, as part of a larger clade containing subspecies of *G. personatus* and *G. streckeri*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *G. tropicalis* as sister to *G. p. davisi* and part of a larger clade containing subspecies of *G. personatus*. Our study of the mtDNA *Cyt*b gene depicted *G. tropicalis* as forming an unresolved trichotomy with a clade containing representatives of *G. personatus* (*davisi*, *maritimus*, *megapotamus*, and *personatus*) and part of a larger clade containing *G. streckeri* and a clade containing *G. attwateri*.

Taxonomic remarks.—Despite the moderate level of genetic divergence between *tropicalis* and the other subspecies of *G. personatus* (4.48%–5.81%), the radically reorganized karyotype of *tropicalis* (Davis et al. 1971) strongly supports its recognition as a species separate from *G. personatus*. See Figs. 1b, 3a, 3c, 6a, 6c, and 9; Tables 1, 3, and 5.

Geomys texensis bakeri (= *G. texensis bakeri*) [= *G. texensis bakeri*]

Taxonomic history.—Described as a subspecies of *G. texensis* (Smolen et al. 1993).

Type locality.—1 mi E D'Hanis, Medina Co., Texas. Topotype sample included in this study (Locality 22).

Morphologic synopsis.—*Geomys t. bakeri* is similar to *attwateri* in external and cranial measurements, but generally smaller in size, less pale in coloration, has relatively smaller cranial measurements and a shorter and narrower skull. Smolen et al. (1993) determined that *bakeri* was morphologically distinct from other subspecies of G. *texensis*.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 68 (Smolen et al. 1993). The limited allozymic data available depicted no fixed differences between *G. t. bakeri* and *G. t. texensis* (Smolen et al. 1993). A mtDNA study showed *G. t. bakeri* as sister to a clade containing samples of both *G. t. llanensis* and *G. t. texensis* (McAliley and Sudman 2005). Limited data from a study examining the 12S rRNA gene (Davis 1986) and 12S mtDNA (Jolley et al. 2000) depicted *G. t. bakeri* as sister to a clade containing *G. t. llanensis* and *G. t. texensis*. A more in-depth study by Sudman et al. (2006) depicted *G. t. bakeri* as sister to a clade containing *G. t. llanensis* and *G. t. texensis*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *G. t. bakeri* as sister to a clade containing *G. t. texensis*, and that clade, in turn, was sister to a clade containing *G. bursarius, G. jugossicularis,* and *G. lutescens*. Our study of the mtDNA *Cyt*b gene depicts *G. t. bakeri* as part of a clade containing representatives of *G. t. llanensis* and *G. t. texensis* which in turn forms a sister relationship with a clade containing representatives of *G. arenarius* and *G. knoxjonesi*.

Taxonomic remarks.—The magnitude of genetic divergence between *bakeri* and *lllanensis*/*texensis* (3.83% and 2.13%, respectively) argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial to resolving the paraphyletic nature of these three subspecies. Therefore, we are retaining *G. t. bakeri* as a valid taxon until a detailed study determining subspecific boundaries is available. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

Geomys texensis (= *G. texensis texensis*) [= *G. texensis texensis*]

Taxonomic history.—Described as a species (Merriam 1895); placed as a subspecies of *G. breviceps* (Davis 1938); placed as a subspecies of *G. bursarius* (Baker 1950); elevated to species (Block and Zimmermann 1991). The subspecies *G. texensis* was constructed when *G. t. bakeri* was described (Smolen et al. 1993).

Type locality.—Mason, Mason Co., Texas. Topotype sample included in this study (Locality 24).

Morphologic synopsis.—*G. t. texensis* is the smallest subspecies of the species, with a tail short that is nearly naked at the tip. Its color is white-bellied with a back chestnut-brown or liver brown dorsum like *bursarius*. It has a smaller skull with a shorter and more pointed nasal bone, shorter jugal, a more flattened zygomatic arch, and a smaller mastoid and auditory bullae compared to *breviceps*. Mauk et al. (1999) reported that *texensis texensis* was distinguishable in cranial measurements from *breviceps brazensis*, *breviceps sagittalis*, and *streckeri* but indistinguishable from *arenarius arenarius*, *attwateri*, *bursarius major*, and *knoxjonesi*.

Genetic synopsis.—Karyotype reported as 2n = 70, FN = 68 (Hart 1978; Smolen et al. 1993). A taxon limited allozymic study by (Block and Zimmerman 1991) revealed that *texensis tex*ensis was sister to *texensis llanensis*. A mtDNA study showed *G. t. texensis* and *G. t. llanensis* to be synonymous and sister to *G. t. bakeri* (McAliley and Sudman 2005). A limited allozymic study depicted no fixed differences between *G. t. texensis* and *G. t. bakeri* (Smolen et al. 1993). A taxon limited study of the 12S rDNA gene (Davis 1986) depicted *G. b. texensis* as part of a clade containing several taxa formerly placed in *G. bursarius* (*llanensis*, *lutescens*, and *major*). Similarly, a taxon limited study of the 12S mtDNA gene (Jolley et al. 2000) depicted *G. t. texensis* as sister to *G. t. llanensis* followed by the addition of *G. t. bakeri*. A more in-depth study by Sudman et al. (2006) depicted *G. t. texensis* as sister to *G. t. llanensis* followed by the addition of *G. t. bakeri*. A taxon limited study that incorporated a multi-gene approach (Chambers et al. 2008) depicted *G. t. texensis* as sister to a clade containing *G. t. bakeri*, and this clade was then sister to a clade containing *G. bursarius, G. jugossicularis,* and *G. lutescens*. Our study of the mtDNA *Cyt*b gene depicts *G. t. texensis* as part of a clade containing representatives of *G. t. bakeri* and *G. t. llanensis* (genetic divergence among these are 3.62% and 2.13%, respectively), which in turn forms a sister relationship with a clade containing representatives of *G. arenarius* and *G. knoxjonesi*.

Taxonomic remarks.—The magnitude of genetic divergence among *texensis, bakeri*, and *llanensis* argues against synonymizing them into a single subspecies. A detailed investigation of subspecific boundaries and corresponding assignment of specimens to the appropriate taxon is crucial in resolving the paraphyletic nature of these three subspecies. Although McAliley and Sudman (2005) recommended synonymizing *llanensis* with *G. t. texensis*, we are retaining *G. t. texensis* as a separate subspecies from *G. t. llanensis* until a detailed study determining the subspecific boundaries is available. See Figs. 1b, 3a, 3d, 6a, 6d, and 9; Tables 1, 3, and 6.

Names that have been applied to *Thomomys*

Historically, the pocket gophers of the genus *Thomomys* from the study area were referred to as a single species, *T. bottae*, a widespread taxon distributed across northern Mexico and the western U.S. from California to western and central Texas (Schmidly and Bradley 2016). Álvarez-Castañeda (2010), on the basis of molecular data, identified three genetic clades within this complex and placed all of the nominal taxa pertinent to this study (type localities in Texas, eastern New Mexico, and northern Mexico) in a "southwestern clade" that was genetically distinct from the two other clades at a level suggesting separate species status. The molecular data reported herein support their conclusion, as well as the recognition of four distinct species (*T. baileyi, T. connectens, T. ruidosae,* and *T. fulvus*) within the "southwestern clade." As presented below, the name *T. baileyi* has priority over the previously used name *T. bottae* and applies to populations of these gophers with a widespread distribution and numerous subspecies recognized; the other 3 species have restricted geographic ranges and are monotypic.

Thomomys aureus lachuguilla **(=** ***T. bottae lachuguilla*****) [=** ***T. baileyi lachuguilla*****]**

Taxonomic history.—Described as a subspecies of *T. aureus* (Bailey 1902); elevated to species by Strecker (1926); moved to a subspecies of *T. bottae* (Goldman 1938); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies but expanded to include *T. b. limitaris* and *T. b. pervarius* (Beauchamp et al. 2019)

Type locality.—Arid foothills near El Paso, El Paso Co., Texas. Topotype sample included in this study (Locality 9).

Morphologic synopsis.—*T. b. lachuguilla* is smaller, buffy-yellow in coloration, with larger auditory bullae, a narrower basioccipital, and two pair of pectoral mammae.

Genetic synopsis.—A taxon limited karyotypic study by Thaeler (1980) depicted *lachuguilla* as having a 2n = 76. No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts that *lachuguilla* belongs to a genetic clade that contains 18 subspecies that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *lachuguilla* being sister to some samples of *actuosus*. This interpretation is complicated by some samples of *actuosus* possessing a mtDNA haplotype similar to *ruidosae*, which presumably is a result of ancient hybridization (see Ruedi et al. 1997). However, *lachuguilla* is moderately different from *actuosus*, differing by a genetic distance of 3.15%. The level of genetic differentiation (11.10% and 7.22%) between the clade containing *lachuguilla* (and the other 23 previously recognized subspecies) and the other two major clades identified herein, represents a major genetic subdivision that warrants taxonomic recognition.

Taxonomic remarks.—Based on the lack of morphological distinction, Beauchamp et al. (2019) suggested that the subspecies *limitaris* and *pervarius* should be synonymized into *lachuguilla*. Although a taxon distributed along the Rio Grande Flood Plains makes sense geographically, given the fact that the DNA sequence data shows no support for a *lachuguilla*, *limitaris*, and *pervarius* relationship presents an incongruent interpretation. Further, those same data reflect a genetic relationship of *lachuguilla* and *actuosus* that cannot be explained by a geographical connection. Therefore, until additional data are available, we are recognizing *lachuguilla* as a subspecies of *T. baileyi* separate from *limitaris* and *pervarius*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys baileyi **(=** ***T. bottae baileyi*****) [=** ***T. baileyi baileyi*****]**

Taxonomic history.—Described as a species (Merriam 1901); recognized as a subspecies of *T. baileyi* (Hall 1932b); placed as a subspecies of *T. bottae* (Anderson 1966) placed as a subspecies of *T. umbrinus* (Hall 1981); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies of *T. bottae* but expanded to include part of *T. b. lachuguilla* (Beauchamp et al. 2019).

Type locality.—Sierra Blanca, Hudspeth Co., Texas. No topotype or other sample available for this study (Locality 3).

Morphologic synopsis.—*T. b. baileyi* is similar to *lachuguilla* but has a shorter and wider skull, and a dull ochraceous tawny to cinnamon coloration.

Genetic synopsis.—No karyotypic, allozymic, or DNA data are available.

Taxonomic remarks.—Although no genetic data were available for study, the geographic distribution for this taxon clearly places *baileyi* within the "southwestern clade" of Álvarez-Castañeda (2010), as well as within the clade containing the 24 nominal subspecies of *T. baileyi* reported herein. Beauchamp et al. (2019) reported that morphologically *baileyi* was similar to *lachuguilla* (in part) but recommended retention as a separate subspecies; consequently, we recognize *baileyi* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys baileyi spatiosus* (= *T. bottae spatiosus*) [= *T. baileyi spatiosus*]**

Taxonomic history.—Described as a subspecies of *T. baileyi* (Goldman 1938); placed as a subspecies of *T. bottae* (Anderson 1966); placed as a subspecies of *T. umbrinus* (Hall 1981); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies of *T. bottae* by Beauchamp et al. (2019).

Type locality.—Alpine, 4,500 ft, Brewster Co., Texas. No topotype included in this study; however, a sample approximately 37 km S of type locality was included (Locality 19).

Morphologic synopsis.—*T. b. spatiosus* is generally darker with a broader, heavier, and longer rostrum compared to other subspecies of *T. baileyi*.

Genetic synopsis.—No karyotypic or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts that *spatiosus* belongs to a strongly supported clade, with little divergence among taxa, that contains *actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limitaris*, *limpiae*, *pectoralis*, *pervagus, pervarius*, *robertbakeri, scotophilus*, *sturgisi, texensis*, and *tularosae*. These 18 subspecies differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with the two samples of *spatiosus* unresolved relative to each other and to the other taxa examined herein. The two samples of *spatiosus* examined differed from each other by a genetic distance of 0.97% and from the other taxa by genetic distances ranging from 1.06 to 4.29%.

Taxonomic remarks.—The DNA sequence data agree with the morphological findings of Beauchamp et al. (2019) in treating *spatiosus* as a distinct subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys baileyi tularosae** (= *T. bottae tularosae*) [= *T. baileyi tularosae*]**

Taxonomic history.—Described as a subspecies of *T. baileyi* (Hall 1932b); placed as a subspecies of *T. bottae* (Anderson 1966); placed as a subspecies of *T. umbrinus* by Hall (1981); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004); treated as a subspecies of *T. bottae* by Beauchamp et al. (2019).

Type locality.—0.5 mi W Tularosa, Otero Co., New Mexico. No topotype included in this study; however, a sample approximately 65 km SE of type locality was included (Locality 23).

Morphologic synopsis.—*T. b. tularosae* is larger size and has a more robust skull than other subspecies of *T. baileyi*.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *tularosae* as having a 2n = 76 and FN = 110 or 112. No allozymic data are available. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *tularosae*, *analogus*, *confinalis*, *fulvus*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, and *texensis* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *tularosae* was a member of a clade containing *boregoensis, confinalis*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, and *texensis*. Our study of the mtDNA *Cyt*b gene depicts that *tularosae* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%). The two samples of *tularosae* formed a clade with samples of *boregoensis* and *scotophilus*; differing by average genetic distances of 0.92% and 0.44%, respectively.

Taxonomic remarks.—The DNA sequence data agree with the morphological findings of Beauchamp et al. (2019) in separating *tularosae* from other pocket gophers in New Mexico and Texas; thus, we recognize *tularosae* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae actuosus** (= *T. bottae actuosus*) [= *T. baileyi actuosus*]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Kelson 1951); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies by Beauchamp et al. (2019).

Type locality.—Corona, Lincoln Co., New Mexico. Topotype sample included in this study (Locality 1).

Morphologic synopsis.—*T. b. actuosus* is larger than *texensis* but smaller than *tularosae*.

Genetic synopsis.—A taxon limited karyotypic study by Patton and Sherwood (1982) depicted *actuosus* as having a 2n = 76 and FN = 116. A taxon limited allozymic study by Patton and Smith (1990) depicted *actuosus* as part of a clade containing *analogus*, *cultellus*, *guadalupensis*, and *limpiae* and a separate allozyme study by Reudi et al. (1997) showed *actuosus* as paraphyletic with *cultellus* and *pervagus*. A taxon limited mtDNA study by Reudi et al. (1997) showed *actuosus* as a member of a strongly supported clade containing *analogus*, *cultellus*, *fulvus*, *guadalupensis*, *opulentus*, and *pervagus*; a comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *actuosus* was sister to *ruidosae*. Our study of the mtDNA *Cyt*b gene depicts *actuosus* as part of a genetic clade that contains 18 subspecies that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *actuosus* being sister to some samples of *lachuguilla.* This relationship is complicated by some samples of *actuosus* that possess a mtDNA haplotype similar to *ruidosae*, presumably as a result of ancient hybridization (see Ruedi et al. 1997). *T. b. actuosus* is moderately different from *lachuguilla*, differing by a genetic distance of 3.15%.

Taxonomic remarks.—Beauchamp et al. (2019) treated *actuosus* as a subspecies separate from other pocket gophers in New Mexico and Texas; therefore, until additional data are available, we have retained *actuosus* as a separate subspecies of *T. baileyi*. Further studies are needed to determine whether samples of *actuosus* that presumably hybridize with *ruidosae* should be assigned to the new species, *T. ruidosae* (see below). See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae analogus** (= *T. bottae analogus*) [= *T. baileyi analogus*]**

Taxonomic history.—Described as a subspecies of *T. umbrinus* (Goldman 1938); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—12 mi S General Cepeda, Coahuila, Mexico. No topotype included in this study; however, a sample approximately 70 km NE of type locality was included (Locality 2).

Morphologic synopsis.—This subspecies is pinkish buff in coloration and slightly darker than *perditus*. It has broad and distinctive nasals and a skull similar in size to *potosinus*. The skull is more elongated and broader, with less rounded and inflated auditory bullae comparted to *perditus*. The nasals are broader; the auditory bullae are larger and less flattened, and the incisors are broader than in *goldmani*.

Genetic synopsis.—No karyotypic data are available. A taxon limited allozymic study by Patton and Smith (1990) depicted *analogus* as part of a clade containing *actuosus*, *cultellus*, *guadalupensis*, and *limpiae* and a separate allozyme study by Reudi et al. (1997) showed *analogus* as basal to a clade containing *actuosus*, *cultellus*, *guadalupensis*, and *pervagus*. A taxon limited mtDNA study by Reudi et al. (1997) showed *analogus* as a member of a strongly supported clade containing *actuosus*, *cultellus*, *furvus*, *guadalupensis*, *opulentus*, and *pervagus*. A taxon limited mtDNA by Wickliffe et al. (2005) showed *analogus*, *confinalis*, *fulvus*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *analogus* was a member of a large unresolved clade containing 28 subspecies of *T. bottae*. Our study of the mtDNA *Cyt*b gene depicts *analogus* as a member of a strongly supported clade containing 18 subspecies (*actuosus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limitaris*, *limpiae*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri, scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%). The two samples of *analogus* examined differed from each other by a genetic distance of 0.00% and from the other taxa by genetic distances ranging from 1.95 to 5.15%.

Taxonomic remarks.—Until additional data are available, we recognize *analogus* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae connectens **(=** ***T. bottae connectens*****) [=** ***T. connectens*****]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Hall 1936); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Clawson Dairy, 5 mi N Albuquerque, 4,943 ft, Bernalillo Co., New Mexico. A topotype was included in this study (Locality 5).

Morphologic synopsis.—*T. connectens* is most similar to *aureus* from which it differs in having a larger body size, larger and heavier skull, and darker color. It has a larger body, is less reddish in color, and has a larger and heavier skull than *opulentus*. It is lighter in color, with longer hind feet and a larger skull than *toltecus.*

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *connectens* as having a 2n = 76 and FN = 148. An allozyme study by Reudi et al. (1997) showed *ruidosae* as basal to a clade containing *actuosus*, *analogus*, *cultellus*, *guadalupensis*, *fulvus*, *opulentus*, *pervagus,* and *ruidosae*. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *connectens* and *ruidosae* to be sister taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *connectens* was sister to a clade containing *actuosus* and *ruidosae*. Our study of the mtDNA *Cyt*b gene depicts that *connectens* is sister to a clade containing *actuosus* and *ruidosae*. Furthermore, the level of genetic differentiation (11.10%) between the clade containing *connectens* and the other major clades identified herein, are indicative of major taxonomic distinctions.

Taxonomic remarks.—Given the magnitude of genetic distinction, it may be appropriate to assign all recognized subspecies contained in this group to *T. ruidosae* (which has priority over *connectens*). However, *connectens* differs from the clade containing *ruidosae* by 7.70%, and given that relatively large magnitude of genetic divergence, we recognize *connectens* as a separate species until additional data aver available. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae cultellus** (= *T. bottae cultellus*) [= *T. baileyi cultellus*]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Kelson 1951); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Hall's Peak, Mora Co., New Mexico. No topotype included in this study; however, a sample approximately 125 km NE of type locality was included (Locality 6).

Morphologic synopsis.—*T. b. cultellus* is darker in color than *fulvus*, *internatus*, *pervagus*, and *connectens*; less rufescent in color than *fulvus* and *internatus*; smaller in body and skull measurements than *internatus*, *pervagus*, and *connectens*; and in most cranial features generally smaller and narrower than *fulvus*, *internatus*, *pervagus*, and *connectens*.

Genetic synopsis.—No karyotypic data are available. A taxon limited allozymic study by Patton and Smith (1990) depicted *cultellus* as part of a clade containing *actuosus*, *analogus*, *guadalupensis*, and *limpiae*, and a separate allozyme study by Reudi et al. (1997) showed *cultellus* as paraphyletic with *actuosus* and *pervagus*. A taxon limited mtDNA study by Reudi et al. (1997) showed *cultellus* as a member of a strongly supported clade containing *actuosus*, *analogus*, *fulvus*, *guadalupensis*, *opulentus*, and *pervagus*. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *cultellus* was sister to *guadalupensis*. Our study of the mtDNA *Cyt*b gene depicts that *cultellus* is a member of a strongly supported clade that contains 18 subspecies (*actuosus*, *analogus*, *boregoensis, confinalis, guadalupensis, lachuguilla, limitaris*, *limpiae*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri, scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *cultellus* being unresolved relative to the other taxa examined. The sample of *cultellus* differed from the other taxa by genetic distances ranging from 1.58 to 4.68%.

Taxonomic remarks.—Until additional data are available, we recognize *cultellus* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae guadalupensis* (= *T. bottae texensis*) [= *T. baileyi guadalupensis*]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Goldman 1936); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); subsumed into *T. b. texensis* (Beauchamp-Martin et al. 2019).

Type locality.—McKittrick Canyon, 7,800 ft, Guadalupe Mts. Texas. Topotype sample included in this study (Locality 7).

Morphologic synopsis.—*T. b. guadalupensis* is similar to *texensis*, but it is paler and has a more massive skull.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *guadalupensis* as having a 2n = 76 and FN = 120. A taxon limited allozymic study by Patton and Smith (1990) depicted *guadalupensis* as part of a clade containing *actuosus*, *analogus*, *cultellus*, and *limpiae* and an allozyme study by Reudi et al. (1997) showed *guadalupensis* as basal to a clade containing *actuosus*, *cultellus*, and *pervagus*. A taxon limited mtDNA study by Reudi et al. (1997) showed *guadalupensis* as a member of a strongly supported clade containing *actuosus*, *analogus*, *cultellus*, *fulvus*, *opulentus*, and *pervagus*. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *guadalupensis* was sister to *cultellus*. Our study of the mtDNA *Cyt*b gene depicts *guadalupensis* as a member of a strongly supported clade that contains 18 subspecices (*actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, lachuguilla, limitaris*, *limpiae*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri,* *scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with the two samples of *guadalupensis* examined being unresolved relative to each other and to the other taxa examined herein. The two samples of *guadalupensis* examined differed from each other by a genetic distance of 0.99% and from the other taxa by genetic distances ranging from 0.93 to 4.15%.

Taxonomic remarks.—Although Beauchamp et al. (2019) suggested that *guadalupensis* be synonymized (along with *pectoralis* and *ruidosae*) into *texensis*, the DNA sequence data suggest that *guadalupensis* represents a distinct taxon and until additional data are available, we suggest that it be recognized as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

*Thomomys bottae humilis** (= *T. bottae texensis*) [= *T. baileyi humilis*]

Taxonomic history.—Described as a subspecies of *T. bottae* (Baker 1953); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—3 mi W Hacienda San Miguel, 2,200 ft, Coahuila, Mexico. No topotype or other sample available for this study (Locality 8).

Morphologic synopsis.—*T. b. humilis* is similar to *limitaris* and *retractus*, but paler and with a smaller skull.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *humilis* as having a 2n = 76 and FN = 122. No allozymic or DNA data are available.

Taxonomic remarks.—Although no genetic data were available for study, the geographic distribution for this taxon clearly place *humilis* within the "southwestern clade" as hypothesized by Álvarez-Castañeda (2010). Based on the data presented in Berry and Baker (1971), it appears that the karyotype of *humilis* differs from taxa located immediately north of the Rio Grande; however, little is known about taxa adjacent to *humilis* south of the of the Rio Grande. Until additional data are available, we suggest that *humilis* be recognized as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae limpiae (= *T. bottae limpiae*) [= *T. baileyi limpiae*]

Taxonomic history.—Described as a subspecies of *T. bottae* (Blair 1939); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies by Beauchamp et al. (2019).

Type locality.—Limpia Canyon, 1 mi N Fort Davis, 4,700 ft, Jeff Davis Co., Texas. Topotype sample included in this study (Locality 11).

Morphologic synopsis.—This subspecies is similar in color to *texensis* but has two instead of four pectoral mammae and a larger skull; it is noticeably darker than *guadalupensis*.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *limpiae* as having a 2n = 76 and FN = 116. A taxon limited allozymic study by Patton and Smith (1990) depicted *limpiae* as part of a clade containing *actuosus*, *analogus*, *cultellus*, and *guadalupensis*. A taxon limited mtDNA by Wickliffe et al. (2005) showed *limpiae*, *analogus*, *confinalis*, *fulvus*, *limitaris*, *pervarius*, *scotophilus*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *limpiae* was a member of a clade containing *boregoensis, confinalis*, *limitaris*, *pervarius*, *scotophilus*, *texensis*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts that *limpiae* is a member of a strongly supported clade that contains 18 subspecies (*actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limitaris*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri, scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *limpiae* being unresolved relative to the other taxa examined herein. The two samples of *limpiae* differed from each other by a genetic distance of 0.97% and from the other taxa by genetic distances ranging from 1.20 to 4.04%.

Taxonomic remarks.—The morphological findings of Beauchamp et al. (2019) regard *limpiae* as a separate subspecies from other pocket gophers in New Mexico and Texas; until additional genetic data are available, we continue this arrangement and place it as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae opulentus* **(=** ***T. bottae opulentus*****) [=** ***T. baileyi opulentus*****]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Goldman 1935); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Las Palomas on the Rio Grande, Sierra Co., New Mexico. No topotype included in this study; however, a sample approximately 120 km SW of type locality was included (Locality 12).

Morphologic synopsis.—This is a large subspecies most similar to *toltecus* and in body size to *fulvus*. It is distinguished by a rich, light tawny coloration, although some darker specimens resemble *fulvus* and *ruidosae*. Compared to the latter, *opulentus* is larger in body size with a richer more rufescent coloration.

Genetic synopsis.—A taxon limited karyotypic study by Thaeler (1980) depicted *opulentus* as having a 2n = 74–76. A taxon limited allozymic study by Patton and Smith (1990) depicted *opulentus* as part of a clade containing *fulvus* and *morulus,* and a separate allozyme study by Reudi et al. (1997) showed *opulentus* and *fulvus* as sister taxa. A taxon limited mtDNA study by Reudi et al. (1997) showed *opulentus* and *fulvus* as sister taxa within a strongly supported clade containing *actuosus*, *analogus*, *cultellus*, *guadalupensis*, and *pervagus*. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *opulentus* was a member of a clade containing *divergens* and *grahamensis*. Our study of the mtDNA *Cyt*b gene depicts that *opulentus* belongs to a genetic clade that contains 6 subspecies differing from each other by an average genetic distance of 1.99% (range 0.00–5.29%), with *opulentus* being unresolved relative to *fulvus* and *grahamensis*.

Taxonomic remarks.—Until additional data are available, we recognize *opulentus* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae pervarius **(=** ***T. bottae lachuguilla*****) [=** ***T. baileyi pervarius*****]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Goldman 1938); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004), subsumed into *T. b. lachuguilla* (Beauchamp-Martin et al. 2019).

Type locality.—Lloyd Ranch, 35 mi S Marfa, 4,200 ft, Presidio Co., Texas. No topotype included in this study; however, a sample approximately 30 km W of type locality was included (Locality 14).

Morphologic synopsis.—*T. b. pervarius* is similar to *limitaris* but larger in size. It is similar in color to *lachuguilla*, but paler than *texensis*.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *pervarius* as having a 2n = 76 and FN = 110. No allozymic data are available. A taxon limited mtDNA by Wickliffe et al. (2005) showed *pervarius*, *analogus*, *confinalis*, *fulvus*, *limitaris*, *limpiae*, *scotophilus*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *pervarius* was a member of a clade containing *boregoensis, confinalis*, *limitaris*, *limpiae*, *scotophilus*, *texensis*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts that *pervarius* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *pervarius* being sister to *sturgisi*, and these taxa being unresolved relative to the other taxa. The two samples of *pervarius* differed from each other by a genetic distance of 0.62% and from the other taxa by genetic distances ranging from 2.00 to 5.05%.

Taxonomic remarks.—Although Beauchamp et al. (2019) synonymized *pervarius* (along with *limitaris*) into *lachuguilla*, the DNA sequence data suggest that *pervarius* represents a distinct taxon; therefore, until additional data are available, we recognize it as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae retractus** (= *T. bottae retractus*) [= *T. baileyi retractus*]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Baker 1953); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Fortin, 3,300 ft, 20 mi N, 2 mi E San Geronimo, Coahuila, Mexico. No topotype or other sample available for this study (Locality 15).

Morphologic synopsis.—*T. b. retractus* is generally larger than other subspecies of *T. baileyi*.

Genetic synopsis.—No karyotypic, allozymic, or DNA data are available.

Taxonomic remarks.—Although no genetic data were available for study, the geographic distribution of this taxon would place it within the "southwestern clade" as hypothesized by Álvarez-Castañeda (2010). Until additional data are available, we recognize *retractus* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae robertbakeri* (= *T. bottae robertbakeri*) [= *T. baileyi robertbakeri*]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Beauchamp-Martin et al. 2019) who reallocated specimens of *T. baileyi limitaris* and *T. baileyi lachuguilla* to this new taxon.

Type locality.—2.5 mi E McCamey, Upton Co., Texas. Topotype sample included in this study (Locality 16).

Morphologic synopsis.—*T. b. robertbakeri* is a medium-sized gopher that is larger than *confinalis* but smaller than *lachuguilla*.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depict populations of *robertbakeri* with a 2n = 76 or 78 and FN = 116 or 118. No allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts that *robertbakeri* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *robertbakeri* being paraphyletic to each other and sister to *confinalis*. The eight samples of *robertbakeri* differed from each other by an average genetic distance of 0.77% and from the other taxa by genetic distances ranging from 0.96 to 4.27%.

Taxonomic remarks.—A finer scale geographic study of *robertbakeri* and *confinalis* is needed to determine a more precise distribution and better understanding of their taxonomic status; until additional data are available, we recognize *robertbakeri* as a subspecies of *T. bailey*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae ruidosae* **(=** ***T. bottae texensis*****) [=** ***T. ruidosae*****]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Hall 1932a); placed as a subspecies of *T. bottae* (Anderson 1966); placed as a subspecies of *T. umbrinus* (Hall 1981); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); subsumed into *T. b. texensis* (Beauchamp-Martin et al. 2019).

Type locality.—Ruidoso, Lincoln Co., New Mexico. Topotype sample included in this study (Locality 17).

Morphologic synopsis.—*T. ruidosae* is most similar to *fulvus*. Its color is fuscous to fuscous-black above with underparts having a strong wash of ochraceous-tawny; its tail is black except for the distal third which is white; its feet and ankles are white; its skull is relatively broad and generally moderate in size.

Genetic synopsis.—Taxon-limited karyotypic studies by Berry and Baker (1971) and Patton and Sherwood (1982) depicted *ruidosae* as having a 2n = 76 and FN = 146 and 2n = 76 and FN = 148, respectively. A taxon limited allozymic study by Patton and Smith (1990) depicted *ruidosae* as basal to a clade containing 20 other subspecies of *bottae* and a separate allozyme study by Reudi et al. (1997) showed *ruidosae* as basal to a clade containing *actuosus*, *analogus*, *cultellus*, *guadalupensis*, *fulvus*, *opulentus*, and *pervagus*. A taxon limited mtDNA study by Reudi et al. (1997) showed *ruidosae* as basal to a strongly supported clade containing *actuosus*, *analogus*, *cultellus*, *fulvus*, *guadalupensis*, *opulentus*, and *pervagus*. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *ruidosae* and *connectens* to be sister taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *ruidosae* was sister to *actuosus*. Our study of the mtDNA *Cyt*b gene depicts *ruidosae* as a sister taxon to *actuosus* (in part). The 12 samples of *ruidosae* differed from each other by a genetic distance of 1.92%. The clade containing samples of *ruidosae* also included samples from the type locality of *actuosus* that possessed a mtDNA haplotype similar to *ruidosae* (presumably as a result of ancient hybridization, see Ruedi et al. 1997).

Taxonomic remarks.—Given the level of genetic differentiation (11.10%) between the clade containing *ruidosae* and the other major clades and the fact that *ruidosae* differs from the clade containing *connectens* by 7.70%, we have assigned all recognized subspecies contained in this group to *T. ruidosae* (which has priority over *connectens*). Although Beauchamp et al. (2019) synonymized *ruidosae* (along with *guadalupensis*, *pectoralis*, and *scotophilus*) into *texensis*, the DNA sequence data suggest that *ruidosae* represents a distinct species. Further studies are needed to determine whether samples of *actuosus* that presumably hybridize with *ruidosae* should be assigned to this new species. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys bottae scotophilus **(=** ***T. bottae texensis*****) [=** ***T. baileyi scotophilus*****]**

Taxonomic history.—Described as a subspecies of *T. bottae* (Davis 1940b); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); subsumed into *T. b. texensis* (Beauchamp-Martin et al. 2019).

Type locality.—1.5 mi W Bat Cave, Sierra Diablo, Hudspeth Co., Texas. Topotype sample included in this study (Locality 18).

Morphologic synopsis.—*T. b. scotophilus* is similar in color to *baileyi* but with a smaller hindfoot and skull. It is lighter in coloration compared to *guadalupensis* and *texensis*.

Genetic synopsis.—No karyotypic or allozymic data are available. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *scotophilus*, *analogus*, *confinalis*, *fulvus*, *limitaris*, *limpiae*, *pervarius*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *scotophilus* was a member of a clade containing *boregoensis, confinalis*, *limitaris*, *limpiae*, *pervarius*, *texensis*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts that *scotophilus* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *scotophilus* either being sister to *boregoensis* and *tularosae* or unresolved relative to the other taxa examined herein. The four samples of *scotophilus* differed from each other by a genetic distance of 0.50% and from the other taxa by genetic distances ranging from 0.44 to 4.10%; however, the samples of *scotophilus, boregoensis*, and *tularosae* differ genetically by 0.94% indicating that they may be consubspecific. If so, *tularosae* would have priority over *boregoensis* and *tularosae*.

Taxonomic remarks.—Given the allopatric geographic distribution of *scotophilus, boregoensis*, and *tularosae* it is unlikely that the three are consubspecific. Based on morphologic data, Beauchamp et al. (2019) synonymized *scotophilus* (along with *guadalupensis*, *pectoralis*, and *ruidosae*) into *texensis*; however, the DNA sequence data suggest that *scotophilus* likely represents a distinct taxon. Therefore, until additional data are available, we recognize *scotophilus* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

***Thomomys bottae toltecus** (= *T. bottae toltecus*) [= *T. fulvus toltecus*]**

Taxonomic history.—Described as a species (Allen 1893); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Colonia Juarez, 4,500 ft, Casas Grande River, Chihuahua, Mexico. No topotype included in this study; however, a sample approximately 175 km SW of type locality was included (Locality 22).

Morphologic synopsis.—The subspecies *toltecus* exceeds *fulvus* greatly in size; it differs from other subspecies by having a peculiar pale grayish brown on the upperparts, lighter in color on the sides, and nearly black along the median line of the back; the interparietal is relatively smaller.

Genetic synopsis.—No karyotypic or allozymic data are available. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *toltecus* was sister to *catalinae*. Our study of the mtDNA *Cyt*b gene depicts that *toltecus* is a member of a clade containing 11 subspecies that differ from each other by an average genetic distance of 5.07% (range 0.00–5.29%), with samples of *toltecus* being sister to *catalinae*.

Taxonomic remarks.—Given the level of genetic differentiation (11.10% and 7.22%) between the clade containing *toltecus* (and the other 10 previously recognized subspecies) and the other two major clades, we have assigned all subspecies in this group to *T. fulvus* (which has priority). See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

*Thomomys bottae villai** (= *T. bottae villai*) [= *T. baileyi villai*]

Taxonomic history.—Described as a subspecies of *T. bottae* (Baker 1953); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—7 mi S, 2 mi E Boquillas, 1,800 ft, Coahuila, Mexico. No topotype or other sample available for this study (Locality 24).

Morphologic synopsis.—*T. b. villai* is generally paler in coloration compared to other subspecies from Mexico.

Genetic synopsis.—No karyotypic, allozymic, or DNA data are available.

Taxonomic remarks.—Although no genetic data were available for study, the geographic distribution for this taxon clearly place *villai* within the "southwestern clade" as hypothesized by Álvarez-Castañeda (2010). Until additional data are available, we assign *villai* to a subspecific rank within *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys fulvus texensis (= *T. bottae texensis*) [= *T. baileyi texensis*]

Taxonomic history.—Described as a subspecies of *T. fulvus* (Bailey 1902); placed as a subspecies of *T. bottae* (Goldman 1935); placed as a subspecies of *T. umbrinus* (Blair 1939; Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies but expanded to include *T. b. guadalupensis*, *T. b. pectoralis*, *T. b. ruidosae*, and *T. b. scotophilus* (Beauchamp et al. 2019)

Type locality.—Head of Limpia Creek, 5,500 ft, Jeff Davis Co., Texas. Topotype sample included in this study (Locality 21).

Morphologic synopsis.—*T. b. texensis* is generally smaller in size, has a smaller and rounded skull, and weak forefeet.

Genetic synopsis.—A taxon limited karyotypic study by Berry and Baker (1971) depicted *texensis* as having a 2n = 76 and FN = 114. No allozymic data are available. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *texensis*, *analogus*, *confinalis*, *fulvus*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *texensis* was a member of a clade containing *boregoensis, confinalis*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts *texensis* is a member of a strongly supported clade that contains 18 subspecies (*actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limitaris*, *limpiae*, *pectoralis*, *pervagus, pervarius*, *robertbakeri, scotophilus*, *spatiosus, sturgisi,* and *tularosae*) differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *texensis* being sister to each other but unresolved relative to the other taxa examined. The two samples of *texensis* differed from each other by a genetic distance of 0.18% and from the other taxa by genetic distances ranging from 1.20 to 4.76%.

Taxonomic remarks.—Based on morphologic data, Beauchamp et al. (2019) synonymized *guadalupensis*, *pectoralis*, *ruidosae*, and *scotophilus*) into *texensis*; however, the DNA sequence data suggest that all four taxa probably represent distinct taxa. Therefore, until additional data are available, we place *texensis* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys lachuguilla confinalis **(=** ***T. bottae confinalis*****)** **[=** ***T. baileyi confinalis*****]**

Taxonomic history.—Described as a subspecies of *T. lachuguilla* (Goldman 1936); placed as a subspecies of *T. bottae* (Goldman 1938); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); retained as a subspecies by Beauchamp et al. (2019).

Type locality.—35 mi E Rocksprings, 2,450 ft, Uvalde Co., Texas. No topotype included in this study; however, a sample approximately 70 km N of type locality was included (Locality 4).

Morphologic synopsis.—*T. b. confinalis* is similar to *limitaris*, but smaller, slenderer, and more cinnamon in coloration; it has a weakly developed and more delicate skull.

Genetic synopsis.—No allozymic data are available. A taxon limited karyotypic study by Berry and Baker (1971) depicted *confinalis* as having a 2N = 76 or 78 and FN = 122. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *confinalis*, *analogus*, *fulvus*, *limitaris*, *limpiae*, *pervarius*, *scotophilus*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *confinalis* was a member of a clade containing *boregoensis, limitaris*, *limpiae*, *pervarius*, *scotophilus*, *texensis*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts *confinalis* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *confinalis* being paraphyletic to each other, and with two groups of *confinalis* samples being sister to *robertbakeri*. The five samples of *confinalis* differed from each other by a genetic distance of 1.07% and from the other taxa by genetic distances ranging from 1.07 to 4.61%.

Taxonomic remarks.—The DNA sequence data agree with the morphological findings of Beauchamp et al. (2019) in treating *confinalis* as a subspecies separate from other pocket gophers in New Mexico and Texas. Therefore, we recognize *confinalis* as a subspecies of *T. baileyi*. A finer scale geographic study of *confinalis* and *robertbakeri* is needed to determine their precise distribution. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys lachuguilla limitaris **(=** ***T. bottae lachuguilla*****)** **[=** ***T. baileyi limitaris*****]**

Taxonomic history.—Described as a subspecies of *T. lachuguilla* (Goldman 1936); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); subsumed into *T. b. lachuguilla* (Beauchamp-Martin et al. 2019).

Type locality.—4 mi W Boquillas, Brewster Co., Texas. Topotype sample included in this study (Locality 10).

Morphologic synopsis.—*T. b. limitaris* is similar to *lachuguilla* but with smaller and more delicate cranial characteristics, a paler coloration, and two pair of pectoral mammae.

Genetic synopsis.—No karyotypic or allozymic data are available. A taxon limited mtDNA study by Wickliffe et al. (2005) showed *limitaris*, *analogus*, *confinalis*, *fulvus*, *limpiae*, *pervarius*, *scotophilus*, *texensis*, and *tularosae* as members of a strongly supported clade but with little divergence among taxa. A comprehensive mtDNA study by Álvarez-Castañeda (2010) indicated that *limitaris* was a member of a clade containing *boregoensis, confinalis*, *limpiae*, *pervarius*, *scotophilus*, *texensis*, and *tularosae*. Our study of the mtDNA *Cyt*b gene depicts that *limitaris* belongs to a genetic clade that contains 18 subspecies (*actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limpiae*, *pectoralis*, *pervagus*, *pervarius*, *robertbakeri, scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with *limitaris* being unresolved relative to the other taxa. The three samples of *limitaris* differed from each other by a genetic distance of 0.71% and from the other taxa by genetic distances ranging from 0.96 to 4.38%.

Taxonomic remarks.—Although Beauchamp et al. (2019) synonymized *limitaris* (along with *pervarius*) into *lachuguilla*, the DNA sequence data suggest that *limitaris* probably represents a distinct taxon. Therefore, until additional data are available, we recognize *limitaris* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys pectoralis **(=** ***T. bottae texensis*****) [=** ***T. baileyi pectoralis*****]**

Taxonomic history.—Described as a species (Goldman 1936); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004); subsumed into *T. b. texensis* (Beauchamp-Martin et al. 2019).

Type locality.—Carlsbad Cave, Eddy Co., New Mexico. No topotype included in this study; however, a sample approximately 20 km W of type locality was included (Locality 13).

Morphologic synopsis.—*T. b. pectoralis* resembles *lachuguilla* but is smaller, pinkish buffy in coloration, with a smaller and less massive skull, and only one pair of pectoral mammae.

Genetic synopsis.—No karyotypic or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts that *pectoralis* is a member of a strongly supported clade that contains 18 subspecies (*actuosus*, *analogus*, *boregoensis, confinalis*, *cultellus, guadalupensis, lachuguilla, limitaris*, *limpiae*, *pervagus*, *pervarius*, *robertbakeri, scotophilus*, *spatiosus*, *sturgisi, texensis*, and *tularosae*) that differ from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *pectoralis* being unresolved to each other and to the other taxa examined herein. The two samples of *pectoralis* differed from each other by a genetic distance of 1.33% and from the other taxa by genetic distances ranging from 0.91 to 4.38%.

Taxonomic remarks.—Based on morphologic data, Beauchamp et al. (2019) synonymized *pectoralis* (along with *guadalupensis*, *ruidosae*, and *scotophilus*) into *texensis*; however, the DNA sequence data suggest that *pectoralis* represents a distinct taxon. Therefore, until additional data are available, we recognize *pectoralis* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Thomomys sturgisi **(=** ***T. bottae sturgisi*****) [=** ***T. baileyi sturgisi*****]**

Taxonomic history.—Described as a species (Goldman 1938); placed as a subspecies of *T. umbrinus* (Hall and Kelson 1959); returned to *T. bottae* (Anderson 1966; Patton and Smith 1990; Jones and Baxter 2004).

Type locality.—Sierra del Carmen 6,000 ft, Coahuila, Mexico. No topotype included in this study; however, a sample approximately 30 km S of type locality was included (Locality 20).

Morphologic synopsis.—*T. b. sturgisi* is smaller in size, has a smaller skull, shorter tail, and slenderer rostrum, and is darker in coloration compared to *limitaris*.

Genetic synopsis.—No karyotypic or allozymic data are available. Our study of the mtDNA *Cyt*b gene depicts that *sturgisi* belongs to a genetic clade that contains 18 subspecies differing from each other by an average genetic distance of 2.33% (range 0.00–5.29%), with samples of *sturgisi* being paraphyletic (one sample was sister to *pervarius*) and unresolved relative to the other taxa. The two samples of *sturgisi* differed substantially from each other by a genetic distance of 4.43% and from the other taxa by genetic distances ranging from 1.93 to 5.73%.

Taxonomic remarks .— Until additional data are available, we recognize *sturgisi* as a subspecies of *T. baileyi*. See Figs. 1c, 4, 7, and 10; Tables 1 and 7.

Appendix III. Synonymies

List of names and selected authorities documenting the various scientific names that have been associated with gophers residing in Texas and adjacent areas. Emphasis was on listing authorities that: 1) either recommended name changes or served as the primary information source during revisionary efforts and 2) synonymies are restricted to taxa recognized in the current study. An equal sign enclosed in brackets [=] indicates the classification-based data generated in this current study.

Cratogeomys castanops angusticeps

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.
1934. *Cratogeomys castanops angusticeps* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:139.
1968. *Pappogeomys castanops angusticeps* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:630.
1981. *Pappogeomys castanops angusticeps* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 518.
1982. *Cratogeomys castanops angusticeps* Honeycutt and Williams, J. Mamm. 63:212.
1990. *Cratogeomys castanops angusticeps* Hollander, Spec. Publ. Mus., Texas Tech Univ. 33:36.
2008. *Cratogeomys castanops castanops* Hafner et al., J. Mamm. 89:202.
2016. *Cratogeomys castanops angusticeps* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.
2023. *Cratogeomys castanops angusticeps* Schmidly et al., Spec. Publ., Mus. Texas Tech Univ. 77:63.

Cratogeomys castanops bullatus [= *C. castanops angusticeps*]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1968. *Pappogeomys castanops bullatus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:632.
1981. *Pappogeomys castanops bullatus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 518.
1982. *Cratogeomys castanops bullatus* Honeycutt and Williams, J. Mamm. 63:212.

2008. C*ratogeomys castanops castanops* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops angusticeps* This study.

Cratogeomys castanops consitus

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1934. *Cratogeomys castanops consitus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:140.
1968. *Pappogeomys castanops consitus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:669.
1981. *Pappogeomys castanops consitus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.
1982. *Cratogeomys castanops consitus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2008. *Cratogeomys castanops excelsus* Hafner et al. 2008 89:203.
2008. *Cratogeomys castanops sordidulus* Hafner et al. 2008 89:203.
2008. *Cratogeomys castanops subsimus* Hafner et al. 2008 89:203.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops consitus* This study.

Cratogeomys castanops convexus [= *C. castanops* spp.]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.
1934. *Cratogeomys castanops convexus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:142.
1968. *Pappogeomys castanops clarkii* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:638.
1981. *Pappogeomys castanops clarkii* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.
1982. *Cratogeomys castanops clarkii* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops* spp. This study.

Cratogeomys castanops dalquesti

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1990. *Cratogeomys castanops dalquesti* Hollander, Spec. Publ., Mus. Texas Tech Univ., 33:162.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2016. *Cratogeomys castanops dalquesti* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.

2023. *Cratogeomys castanops dalquesti* Schmidly et al., Spec. Publ., Mus. Texas Tech Univ. 77:63.

2023. *Cratogeomys castanops dalquesti* This study.

***Cratogeomys castanops excelsus* [= *C. castanops consitus*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1934. *Cratogeomys castanops excelsus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:143.

1968. *Pappogeomys castanops excelsus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:641.

1981. *Pappogeomys castanops excelsus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.

1982. *Cratogeomys castanops excelsus* Honeycutt and Williams, J. Mamm. 63:212.

2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.

2023. *Cratogeomys castanops consitus* This study.

Cratogeomys castanops hirtus

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Cratogeomys castanops hirtus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:138.

1968. *Pappogeomys castanops hirtus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:646.

1981. *Pappogeomys castanops hirtus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.

1982. *Cratogeomys castanops hirtus* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops hirtus* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:48.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2023. *Cratogeomys castanops hirtus* This study.

Cratogeomys castanops jucundus

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1955. *Cratogeomys castanops jucundus* Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist. 7:599.
1968. *Pappogeomys castanops jucundus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:648.
1981. *Pappogeomys castanops jucundus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.
1982. *Cratogeomys castanops jucundus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops jucundus* This study.

Cratogeomys castanops lacrimalis

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.
1934. *Cratogeomys castanops lacrimalis* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:137.
1968. *Pappogeomys castanops perplanus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:650.
1981. *Pappogeomys castanops perplanus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 520.
1982. *Cratogeomys castanops perplanus* Honeycutt and Williams, J. Mamm. 63:212.
1990. *Cratogeomys castanops lacrimalis* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:50.
2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.
2016. *Cratogeomys castanops lacrimalis* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.
2023. *Cratogeomys castanops lacrimalis* This study.

Cratogeomys castanops perplanus

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.
1934. *Cratogeomys castanops perplanus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:136.
1968. *Pappogeomys castanops perplanus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:650.

1968. *Pappogeomys castanops lacrimalis* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:650.
1979. *Pappogeomys castanops simulans* Dowler and Genoways, Southwest. Nat. 24:599.
1981. *Pappogeomys castanops perplanus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 520.
1981. *Pappogeomys castanops lacrimalis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 520.
1982. *Cratogeomys castanops perplanus* Honeycutt and Williams, J. Mamm. 63:212.
1990. *Cratogeomys castanops simulans* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:52.
1990. *Cratogeomys castanops perplanus* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:52.
2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.
2016. *Cratogeomys castanops perplanus* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.
2023. *Cratogeomys castanops perplanus* Schmidly et al., Spec. Publ., Mus. Texas Tech Univ. 77:63.
2023. *Cratogeomys castanops perplanus* This study.

***Cratogeomys castanops sordidulus* [= *C. castanops consitus*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1955. *Cratogeomys castanops sordidulus* Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist. 7:600.
1968. *Pappogeomys castanops sordidulus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:658.
1981. *Pappogeomys castanops sordidulus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.
1982. *Cratogeomys castanops sordidulus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops consitus* This study.

***Cratogeomys castanops subsimus* [= *C. castanops consitus*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1934. *Cratogeomys castanops subsimus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:144.
1968. *Pappogeomys castanops subsimus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:660.
1981. *Pappogeomys castanops subsimus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 520.
1982. *Cratogeomys castanops subsimus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops consitus* This study.

Cratogeomys castanops surculus [= *C. castanops consitus*]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1968. *Pappogeomys castanops surculus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:688.
1981. *Pappogeomys castanops surculus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.
1982. *Cratogeomys castanops surculus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops consitus* This study.

Cratogeomys castanops tamaulipensis

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1934. *Cratogeomys castanops tamaulipensis* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:144.
1968. *Pappogeomys castanops tamaulipensis* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:663.
1981. *Pappogeomys castanops tamaulipensis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.
1982. *Cratogeomys castanops tamaulipensis* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops tamaulipensis* This study.

Cratogeomys castanops ustulatus [= *C. castanops ustulatus*]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1955. *Cratogeomys castanops ustulatus* Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist. 7:598.
1968. *Pappogeomys castanops ustulatus* Russell, Univ. Kansas Pub., Mus. Nat. Hist. 16:667.
1981. *Pappogeomys castanops ustulatus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.
1982. *Cratogeomys castanops ustulatus* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.
2023. *Cratogeomys castanops ustulatus* This study.

Geomys clarkii [= *C. castanops pratensis*]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1852. *Geomys castanops* Le Conte, Proc. Acad. Nat. Sci. Phil. 6:163.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1875. *Geomys castanops* Coues, Rept. Maj. J. W. Powell's Explor. Colorado River in the west and its tributaries, 1869, 1870, 1871, and 1872:233.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Cratogeomys castanops convexus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:142.

1968. *Pappogeomys castanops clarkii* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:38.

1981. *Pappogeomys castanops clarkii* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.

1982. *Cratogeomys castanops clarkii* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops pratensis* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:42.

1990. *Cratogeomys castanops torridus* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:42.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2016. *Cratogeomys castanops clarkii* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.

2023. *Cratogeomys castanops clarkii* Schmidly et al., Spec. Publ., Mus. Texas Tech Univ. 77:63.

2023. *Cratogeomys castanops pratensis* This study.

Geomys clarkii [= *C. castanops* spp.]

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Cratogeomys castanops convexus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:142.

1968. *Pappogeomys castanops convexus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:638.

1981. *Pappogeomys castanops convexus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.

1982. *Cratogeomys castanops convexus* Honeycutt and Williams, J. Mamm. 63:212.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2016. *Cratogeomys castanops clarkii* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.

2023. *Cratogeomys castanops* spp. This study.

***Pappogeomys castanops parviceps* [= *C. castanops parviceps*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1968. *Pappogeomys castanops parviceps* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:673.

1981. *Pappogeomys castanops parviceps* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 518.

1982. *Cratogeomys castanops parviceps* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops parviceps* Hollander, Spec. Publ. Mus. Texas Tech Univ. 33:51.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2016. *Cratogeomys castanops parviceps* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.

2023. *Cratogeomys castanops parviceps* This study.

***Pappogeomys castanops perexiguus* [= *C. castanops consitus*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1968. *Pappogeomys castanops perexiguus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:676.

1981. *Pappogeomys castanops perexiguus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 519.

1982. *Cratogeomys castanops perexiguus* Honeycutt and Williams, J. Mamm. 63:212.

2008. *Cratogeomys castanops consitus* Hafner et al. 2008 89:203.

2023. *Cratogeomys castanops consitus* This study.

***Pappogeomys castanops pratensis* [= *C. castanops pratensis*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Cratogeomys castanops clarkii* [of Mexican side of Big Bend section of Rio Grande Valley, in northeastern Chihuahua and northern Coahuila, Mexico] Nelson and Goldman, Proc. Biol. Soc. Wash. 47:140.

1968. *Pappogeomys castanops pratensis* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:653.

1968. *Pappogeomys castanops clarkii* [of Rio Grande Valley, vicinity of Ojinaga, Chihuahua, Mexico] Russell, Univ. Kansas Publ. Mus. Nat. Hist. 16:638.

1981. *Pappogeomys castanops pratensis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 520.

1982. *Cratogeomys castanops pratensis* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops clarkii* [of Trans-Pecos Texas] Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:42.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2023. *Cratogeomys castanops pratensis* This study.

***Pappogeomys castanops simulans* [= *C. castanops perplanus*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Cratogeomys castanops perplanus* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:136.

1968. *Pappogeomys castanops simulans* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:656.

1979. *Pappogeomys castanops perplanus* Dowler and Genoways, Southwest. Nat. 24:600.

1981. *Pappogeomys castanops simulans* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.

1982. *Cratogeomys castanops simulans* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops perplanus* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:52.

2008.*Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2016. *Cratogeomys castanops perplanus* Schmidly and Bradley, Mammals of Texas, Univ. Texas Press, p. 533.

2023. *Cratogeomys castanops perplanus* This study

***Pappogeomys castanops torridus* [= *C. castanops pratensis*]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.

1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.

1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.

1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.

1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.

1934. *Crategeomys castanops clarkii* Nelson and Goldman, Proc. Biol. Soc. Wash. 47:140.

1968. *Pappogeomys castanops torridus* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:665.

1981. *Pappogeomys castanops torridus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.

1982. *Cratogeomys castanops simulans* Honeycutt and Williams, J. Mamm. 63:212.

1990. *Cratogeomys castanops clarkii* Hollander, Spec. Publ., Mus. Texas Tech Univ. 33:42.

2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

2023. *Cratogeomys castanops pratensis* Schmidly et al., Spec. Publ., Mus. Texas Tech Univ. 77:63.
2023. *Cratogeomys castanops pratensis* This study.

Pseudostoma castanops **[=** ***C. castanops castanops*****]**

1852. *Pseudostoma castanops* Baird, Expl. Surv. Valley Great Salt Lake Utah, Appen. C, Zool., p. 313.
1855. *Geomys clarkii* Baird, Proc. Acad. Nat Sci. Phil. 7:322.
1858. *Geomys castanops* Baird, Mammals in the Re. Expl. Surv. Rept. to Pacific…, 8:384.
1895. *Cratogeomys castanops* Merriam, N. Amer. Fauna 8:159.
1926. *Cratogeomys castanops castanops* Strecker, Baylor Univ. Bull. 29:22.
1968. *Pappogeomys castanops* Russell, Univ. Kansas Publ., Mus. Nat. Hist. 16:635.
1981. *Pappogeomys castanops* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 521.
1982. *Cratogeomys castanops* Honeycutt and Williams, J. Mamm. 63:212.
2008. *Cratogeomys castanops castanops* Hafner et al. 2008 89:203.

Geomys arenarius **[=** ***G. arenarius arenarius*****]**

1895. *Geomys arenarius* Merriam, N. Amer. Fauna, 8:139.
1926. *Geomys arenarius* Strecker, Baylor Univ. Bull. 29:21.
1955. *Geomys arenarius arenarius* Miller and Kellogg, U.S. Nat. Mus. Bull. 205:338.
1981. *Geomys arenarius arenarius* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.

Geomys arenarius brevirostris **[=** ***G. arenarius brevirostris*****]**

1895. *Geomys arenarius* Merriam, N. Amer. Fauna, 8:139.
1932. *Geomys arenarius brevirostris* Hall, Proc. Biol. Soc. Wash. 45:97.
1981. *Geomys arenarius brevirostris* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.

Geomys breviceps **[=** ***G. breviceps breviceps*****]**

1855. *Geomys breviceps* Baird, Proc. Acad. Nat. Sci. Philadelphia. 7:335.
1926. *Geomys lutescens* Strecker, Baylor Univ. Bull. 29(3):21.
1951. *Geomys bursarius breviceps* Baker and Glass, Proc. Biol. Soc. Wash. 4647:57.
1940. *Geomys breviceps breviceps* Davis, Bull. Texas Agri. Exper. Stat., 590:14.
1979. *Geomys breviceps breviceps* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ., 58:42.
1981. *Geomys bursarius breviceps* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.
1982. *Geomys breviceps* Bohlin and Zimmerman, J. Mamm. 63:227.
2023. *Geomys breviceps breviceps* This study

Geomys breviceps ammophilus [= *G. attwateri*]

1895. *Geomys breviceps attwateri* Merriam, N. Amer. Fauna 8:135.
1940. *Geomys breviceps ammophilus* Davis, Bull. Texas Agri. Exper. Stat. 590:16.
1951. *Geomys bursarius ammophilus* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius attwateri* Honeycutt and Schmidly, Spec. Publ., Mus. Texas Tech Univ. 58:45.
1981. *Geomys bursarius ammophilus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 498.
1981. *Geomys attwateri* Tucker and Schmidly, J. Mamm. 62:270.

Geomys breviceps attwateri [= *G. attwateri*]

1895. *Geomys breviceps attwateri* Merriam, N. Amer. Fauna 8:135.
1951. *Geomys bursarius attwateri* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1981. *Geomys bursarius attwateri* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 498.
1981. *Geomys attwateri* Tucker and Schmidly, J. Mamm. 62:270.

Geomys breviceps brazensis [= *G. brazensis brazensis*]

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1938. *Geomys breviceps brazensis* Davis, J. Mamm. 19:489.
1951. *Geomys bursarius brazensis* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius sagittalis* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ. 58:43.
1981. *Geomys bursarius brazensis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.
1982. *Geomys breviceps sagittalis* Bohlin and Zimmerman, J. Mamm. 63:227.
2023. *Geomys brazensis brazensis* This study.

Geomys breviceps dutcheri

1926. *Geomys breviceps breviceps* Strecker, Baylor Univ. Bull. 29(3):21.
1940. *Geomys breviceps dutcheri* Davis, Bull. Texas Agri. Exper. Stat. 590:12.
1951. *Geomys bursarius dutcheri* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius sagittalis* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ. 58:43.
1981. *Geomys bursarius dutcheri* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.
2023. *Geomys breviceps dutcheri* This study.

Geomys breviceps llanensis [= *G. texensis llanensis*]

1905. *Geomys breviceps llanensis* Bailey, N. Amer. Fauna 25:129.
1940. *Geomys lutescens llanensis* Davis, Bull. Texas Agri. Exper. Sta. 590:32.

1947. *Geomys bursarius llanensis* Villa-R. and Hall, Univ. Kansas Publ., Mus. Nat. Hist. 1:234.
1981. *Geomys bursarius llanensis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 500.
1991. *Geomys texensis* Block and Zimmermann, Southwest. Nat. 36:32.
2000. *Geomys texensis llanensis* Jolley et al., J. Mamm. 87:676.
2005. *Geomys texensis texensis* McAliley and Sudman, Southwest. Nat. 50:334.
2023. *Geomys texensis llanensis* This study.

***Geomys breviceps ludemani* [= *G. breviceps sagittalis*]**

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1940. *Geomys breviceps ludemani* Davis, Bull. Texas Agri. Exper. Stat. 590:12.
1951. *Geomys bursarius ludemani* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius sagittalis* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ. 58:43.
1981. *Geomys bursarius ludemani* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 500.
1982. *Geomys breviceps sagittalis* Bohlin and Zimmerman, J. Mamm. 63:227.

***Geomys breviceps pratincolus* [= *G. brazensis pratincola*]**

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1940. *Geomys breviceps pratincolus* Davis, Bull. Texas Agri. Exper. Stat. 590:18.
1951. *Geomys bursarius pratincolus* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius sagittalis* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ. 58:43.
1981. *Geomys bursarius pratincola* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.
1982. *Geomys breviceps sagittalis* Bohlin and Zimmerman, J. Mamm. 63:227.
2023. *Geomys brazesis pratincola* This study.

***Geomys breviceps sagittalis* [= *G. breviceps sagittalis* in part and *G. species novum* in part]**

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1951. *Geomys bursarius sagittalis* R. H. Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1981. *Geomys bursarius sagittalis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.
1982. *Geomys breviceps sagittalis* Bohlin and Zimmerman, J. Mamm. 63:227.
2023. *Geomys breviceps sagittalis* in part and *G. species novum* in part This study.

***Geomys breviceps terricolus* [= *G. breviceps sagittalis*]**

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna 8:134.
1940. *Geomys breviceps terricolus* Davis, Bull. Texas Agri. Exper. Stat. 590:17.

1951. *Geomys bursarius terricolus* Baker and Glass, Proc. Biol. Soc. Wash. 64:57.
1979. *Geomys bursarius sagittalis* Honeycutt and Schmidly, Occas. Pap., Mus. Texas Tech Univ. 58:43.
1981. *Geomys bursarius terricolus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.
1982. *Geomys breviceps sagittalis* Bohlin and Zimmerman, J. Mamm. 63:227.

Geomys bursarius knoxjonesi [= *G. knoxjonesi*]

1975. *Geomys bursarius knoxjonesi* Baker and Genoways, Occas. Pap., Mus. Texas Tech Univ. 29:1.
1981. *Geomys bursarius knoxjonesi* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.
1989. *Geomys knoxjonesi* Baker et al., Evol. 43:74.

Geomys lutescens jugossicularis [= *G. jugossicularis jugossicularis*]

1926. *Geomys lutescens* Strecker, Baylor Univ. Bull. 29:21.
1940. *Geomys lutescens jugossicularis* Hooper, Occas. Pap.,. Mus. Zool., Univ. Mich. 420:1.
1947. *Geomys bursarius major* Villa-R. and Hall, Univ. Kansas Publ., Mus. Nat. Hist. 1:229.
1981. *Geomys bursarius knoxjonesi* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.
2006. *G. jugossicularis* Sudman et al., J. Mamm. 87:671.
2009. *G. jugossicularis jugossicularis* Chambers et al., J. Mamm. 89:542.

Geomys lutescens major [= *G. bursarius major*]

1940. *Geomys lutescens major* Davis, Bull. Texas Agric. Exper. Stat. 590:32.
1947. *Geomys bursarius major* Villa-R. and Hall, Univ. Kansas Publ., Mus. Nat. Hist. 1:229.
1981. *Geomys bursarius major* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 499.

Geomys personatus [= *G. personatus personatus*]

1889. *Geomys personatus* True, Proc. U.S. Nat. Mus. [1888] 11:159.
1926. *Geomys personatus personatus* Strecker, Baylor Univ. Bull. 29:22.
1981. *Geomys personatus personatus* Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:468.
1981. *Geomys personatus personatus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 503.

Geomys personatus davisi [= *G. personatus davisi*]

1981. *Geomys personatus davisi* Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:459.

Geomys personatus fallax [= *G. personatus fallax*]

1895. *Geomys personatus fallax* Merriam, N. Amer. Fauna 8:144.
1981. *Geomys personatus fallax* Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:462.
1981. *Geomys personatus fallax* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 502.

Geomys personatus fuscus [= *G. personatus fuscus*]

1940. *Geomys personatus fuscus* Davis, Texas Agri. Exper. Stat. Bull. 590:30.
1981. *Geomys personatus fuscus* Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:465.
1981. *Geomys personatus fuscus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 503.

Geomys personatus maritimus [= *G. personatus maritimus*]

1926. *Geomys personatus personatus* Strecker, Baylor Univ. Bull. 29:22.
1940. *Geomys personatus maritimus* Davis, Texas Agri. Exper. Stat. Bull. 590:26.
1981. *Geomys personatus maritimus*, Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:466.
1981. *Geomys personatus maritimus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 503.

Geomys personatus megapotamus [= *G. personatus megapotamus*]

1926. *Geomys personatus personatus* Strecker, Baylor Univ. Bull. 29:22.
1940. *Geomys personatus megapotamus* Davis, Texas Agri. Exper. Stat. Bull. 590:27.
1981. *Geomys personatus megapotamus* Williams and Genoways, Ann. Carnegie Mus. Nat. Hist. 50:467.
1981. *Geomys personatus megapotamus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 503.

Geomys personatus streckeri [= *G. streckeri*]

1940. *Geomys personatus minor* Davis, Texas Agri. Exper. Stat. Bull. 590:29.
1943. *Geomys personatus streckeri* Davis, J. Mamm. 24:508.
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1915. *Geomys personatus tropicalis* Goldman, Proc. Biol Soc., Washington, 28:134.
1963. *Geomys tropicalis* Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:426.
1981. *Geomys tropicalis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 504.

Geomys texensis bakeri [= *G. texensis bakeri*]

1993. *Geomys texensis bakeri* Smolen et al., Proc. Biol. Soc. Wash. 106:19.

Geomys texensis [= *G. texensis texensis*]

1895. *Geomys texensis* Merriam, N. Amer. Fauna 8:137.
1938. *Geomys breviceps texensis* Davis, J. Mamm. 19:488.
1950. *Geomys bursarius texensis* Baker, J. Mamm. 31:349.
1981. *Geomys bursarius texensis* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 501.
1991. *Geomys texensis* Block and Zimmerman, Southwest. Nat. 36:29.
1993. *Geomys texensis texensis* Smolen et al., Proc. Biol. Soc. Wash. 106:6.

Thomomys aureus lachuguilla [= *T. baileyi lachuguilla*]

1902. *Thomomys aureus lachuguilla* Bailey, Proc. Biol. Soc. Wash. 15:120.
1926. *Thomomys lachuguilla* Strecker, Baylor Univ. Bull. 29:21.
1936. *Thomomys lachuguilla limitaris* Goldman, J. Wash. Acad. Sci. 26:118.
1938. *Thomomys bottae lachugilla* [sic] Goldman, Proc. Biol. Soc. Wash. 51:55.
1938. *Thomomys bottae pervarius* Goldman, Proc. Biol. Soc. Wash. 51:57.
1959. *Thomomys umbrinus lachuguilla* Hall and Kelson, Mammals of North America, Ronald Press, p. 426.
1966. *Thomomys bottae lachuguilla* Anderson, Syst. Zool. 15:195.
1981. *Thomomys umbrinus lachuguilla* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 485.
1990. *Thomomys bottae lachuguilla* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae lachuguilla* Jones and Baxter, Mammalian Species. 742:3.
2019. *Thomomys bottae lachuguilla* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:530.
2023. *Thomomys baileyi lachuguilla* This study.

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1901. *Thomomys baileyi* Merriam, Proc. Biol. Soc. Wash. 14:109.
1915. *Thomomys lachuguilla* (in part) Bailey, N. Amer. Fauna 39:89.
1926. *Thomomys baileyi* Strecker, Baylor Univ. Bull. 29:21.
1932. *Thomomys baileyi baileyi* Hall, Univ. California Publ., Zool. 38:411.
1959. *Thomomys baileyi baileyi* Hall and Kelson, Mammals of North America, Ronald Press, p. 435.
1966. *Thomomys bottae baileyi* Anderson, Syst. Zool. 15:195.
1981. *Thomomys umbrinus baileyi* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 477.

1990. *Thomomys bottae baileyi* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae baileyi* Jones and Baxter, Mammalian Species. 742:2.

2019. *Thomomys bottae baileyi* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:528.

2023. *Thomomys baileyi baileyi* This study.

Thomomys baileyi spatiosus [= *T. baileyi spatiosus*]

1938. *Thomomys baileyi spatiosus* Goldman, Proc. Biol. Soc. Wash. 51:58.

1966. *Thomomys bottae spatiosus* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus spatiosus* Hall, Mammals of North America, John Wiley & Sons, Inc., p. 494.

1990. *Thomomys bottae spatiosus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae spatiosus* Jones and Baxter, Mammalian Species. 742:5.

2019. *Thomomys bottae spatiosus* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.

2023. *Thomomys baileyi spatiosus* This study.

Thomomys baileyi tularosae [= *T. baileyi tularosae*]

1932. *Thomomys baileyi tularosae* Hall Univ. California Publ. Zool., 38:411.

1966. *Thomomys bottae tularosae* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus tularosae* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 495.

1990. *Thomomys bottae tularosae* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae tularosae* Jones and Baxter, Mammalian Species. 742:5.

2019. *Thomomys bottae tularosae* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.

2023. *Thomomys baileyi tularosae* This study.

Thomomys bottae actuosus [= *T. baileyi actuosus*]

1951. *Thomomys bottae actuosus* Kelson Univ. Kansas Publ., Mus. Nat. Hist. 5:67.

1959. *Thomomys umbrinus actuosus* Hall and Kelson, Mammals of North America, Ronald Press, p. 418.

1990. *Thomomys bottae actuosus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae actuosus* Jones and Baxter, Mammalian Species. 742:2.

2019. *Thomomys bottae actuosus* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:528.

2023. *Thomomys baileyi actuosus* This study.

Thomomys bottae analogus [= *T. baileyi analogus*]

1938. *Thomomys umbrinus analogus* Goldman, Proc. Biol. Soc. Wash. 51:59.

1966. *Thomomys bottae analogus* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus analogus* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 471.

1990. *Thomomys bottae analogus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae analogus* Jones and Baxter, Mammalian Species. 742:2.

2023. *Thomomys baileyi analogus* This study.

***Thomomys bottae connectens* [= *T. connectens*]**

1936. *Thomomys bottae connectens* Hall, J. Washington Acad. Sci., 26:296.

1959. *Thomomys umbrinus connectens* Hall and Kelson, Mammals of North America, Ronald Press, p. 423.

1990. *Thomomys bottae connectens* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae connectens* Jones and Baxter, Mammalian Species. 742:3.

2023. *Thomomys connectens* This study.

***T. bottae cultellus* [= *T. baileyi cultellus*]**

1951. *Thomomys bottae cultellus* Kelson Univ. Kansas Publ., Mus. Nat. Hist. 5:64.

1959. *Thomomys umbrinus cultellus* Hall and Kelson, Mammals of North America, Ronald Press, p. 423.

1990. *Thomomys bottae cultellus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae cultellus* Jones and Baxter, Mammalian Species. 742:3.

2023. *Thomomys baileyi cultellus* This study.

***Thomomys bottae guadalupensis* [= *T. baileyi guadalupensis*]**

1852. *Geomys fulvus* Woodhouse, Proc. Acad. Nat. Sci. Phil. 6:201.

1902. *Thomomys fulvus texensis* Bailey, Proc. Biol. Soc. Wash. 15:119.

1926. *Thomomys fulvus fulvus* Strecker, Baylor Univ. Bull. 29(3):20.

1935. *Thomomys bottae texensis* Goldman, Proc. Biol. Soc. Wash. 48:157.

1936. *Thomomys bottae guadalupensis* Goldman, J. Wash Acad. Sci. 26:117.

1959. *Thomomys umbrinus guadalupensis* Hall and Kelson, Mammals of North America, Ronald Press, p. 425.

1966. *Thomomys bottae guadalupensis* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus guadalupensis* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 483.

1990. *Thomomys bottae guadalupensis* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae guadalupensis* Jones and Baxter, Mammalian Species. 742:3.

2019. *Thomomys bottae texensis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.

2023. *Thomomys baileyi guadalupensis* This study.

Thomomys bottae humilis [= *T. baileyi humilis*]

1953. *Thomomys bottae humilis* Baker Univ. Kansas Publ., Mus. Nat. Hist. 5:503.
1959. *Thomomys umbrinus humilis* Hall and Kelson, Mammals of North America, Ronald Press, p. 425.
1966. *Thomomys bottae humilis* Anderson, Syst. Zool. 15:195.
1981. *Thomomys umbrinus humilis* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 484.
1990. *Thomomys bottae humilis* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae humilis* Jones and Baxter, Mammalian Species. 742:3.
2023. *Thomomys baileyi humilis* This study.

Thomomys bottae limpiae [= *T. baileyi limpiae*]

1939. *Thomomys bottae limpiae* Blair, Occas. Pap. Mus. Zool. Univ. Mich. 403:2.
1959. *Thomomys umbrinus limpiae* Hall and Kelson, Mammals of North America, Ronald Press, p. 427.
1966. *Thomomys bottae limpiae* Anderson, Syst. Zool. 15:195.
1981. *Thomomys umbrinus limpiae* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 486.
1990. *Thomomys bottae limpiae* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae limpiae* Jones and Baxter, Mammalian Species. 742:3.
2019. *Thomomys bottae limpiae* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:532.
2023. *Thomomys baileyi limpiae* This study.

Thomomys bottae opulentus [= *T. baileyi opulentus*]

1935. *Thomomys bottae opulentus* Goldman, Proc. Biol. Soc. Wash. 48:150.
1959. *Thomomys umbrinus opulentus* Hall and Kelson, Mammals of North America, Ronald Press, p. 429.
1966. *Thomomys bottae opulentus* Anderson, Syst. Zool. 15:195.
1981. *Thomomys umbrinus opulentus* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 489.
1990. *Thomomys bottae opulentus* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae opulentus* Jones and Baxter, Mammalian Species. 742:4.
2023. *Thomomys baileyi opulentus* This study.

Thomomys bottae pervarius [= *T. baileyi pervarius*]

1902. *Thomomys aureus lachuguilla* Bailey, Proc. Biol. Soc. Wash. 15:120.
1926. *Thomomys lachuguilla* Strecker, Baylor Univ. Bull. 29:21.
1936. *Thomomys lachuguilla limitaris* Goldman, J. Wash. Acad. Sci. 26:118.
1938. *Thomomys bottae lachugilla* [sic], Goldman, Proc. Biol. Soc. Wash. 51:55.
1938. *Thomomys bottae pervarius* Goldman, Proc. Biol. Soc. Wash. 51:57.

1959. *Thomomys umbrinus pervarius* Hall and Kelson, Mammals of North America, Ronald Press, p. 430.

1966. *Thomomys bottae pervarius* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus pervarius* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 491.

1990. *Thomomys bottae pervarius* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae pervarius* Jones and Baxter, Mammalian Species. 742:4.

2019. *Thomomys bottae lachuguilla* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:531.

2023. *Thomomys baileyi pervarius* This study.

***Thomomys bottae retractus* [= *T. baileyi retractus*]**

1953. *Thomomys bottae retractus* Baker Univ. Kansas Publ., Mus. Nat. Hist. 5:507.

1959. *Thomomys umbrinus retractus* Hall and Kelson, Mammals of North America, Ronald Press, p. 432.

1966. *Thomomys bottae retractus* Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus retractus* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 492.

1990. *Thomomys bottae retractus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae retractus* Jones and Baxter, Mammalian Species. 742:4.

2023. *Thomomys baileyi retractus* This study.

***Thomomys bottae robertbakeri* [= *T. baileyi robertbakeri*]**

1901. *Thomomys perditus* Merriam, Proc. Biol. Soc. Wash. 15:120.

1902. *Thomomys aureus lachuguilla* [in part] Bailey, Proc. Biol. Soc. Wash. 15:120.

1936. *Thomomys lachuguilla limitaris* Goldman, J. Wash. Acad. Sci. 26:118.

1938. *Thomomys bottae limitaris* [in part] Goldman, Proc. Biol. Soc. Wash. 51:55.

1966. *Thomomys bottae limitaris* [in part] Anderson, Syst. Zool. 15:195.

1981. *Thomomys umbrinus limitaris* [in part] Hall, Mammals of North American, John Wiley and Sons, Inc., p. 486.

1990. *Thomomys bottae limitaris* [in part] Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae limitaris* [in part] Jones and Baxter, Mammalian Species. 742:4.

2019. *Thomomys bottae robertbakeri* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:526.

2023. *Thomomys baileyi robertbakeri* This study.

***Thomomys bottae ruidosae* [= *T. ruidosae*]**

1932. *Thomomys baileyi baileyi* Hall, Proc. Biol. Soc. Wash. 45:96.

1959. *Thomomys umbrinus retractus* Hall and Kelson, Mammals of North America, Ronald Press, p. 432.

1966. *Thomomys bottae ruidosae* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus ruidosae* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 493.

1990. *Thomomys bottae ruidosae* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae ruidosae* Jones and Baxter, Mammalian Species. 742:4.

2019. *Thomomys bottae texensis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.

2023. *Thomomys ruidosae* This study.

Thomomys bottae scotophilus [= *T. baileyi scotophilus*]

1902. *Thomomys fulvus texensis* Bailey, Proc. Biol. Soc. Wash. 15:119.

1935. *Thomomys bottae texensis* Goldman, Proc. Biol. Soc. Wash. 48:157.

1939. *Thomomys umbrinus texensis* Blair, Occas. Pap. Univ. Mich. Mus. Zool. 403:2.

1940. *Thomomys bottae scotophilus* Davis, J. Mamm. 21:204.

1959. *Thomomys umbrinus scotophilus* Hall and Kelson, Mammals of North America, Ronald Press, p. 432.

1966. *Thomomys bottae scotophilus* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus scotophilus* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 493.

1990. *Thomomys bottae scotophilus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae scotophilus* Jones and Baxter, Mammalian Species. 742:4.

2019. *Thomomys bottae texensis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:534.

2023. *Thomomys baileyi scotophilus* This study.

T. bottae toltecus [= *T. fulvus toltecus*]

1893. *Thomomys toltecus* Allen, Bull. Amer. Mus. Nat. Hist. 5:52

1990. *Thomomys bottae toltecus* Patton and Smith, Univ. California Press 123:3

1959. *Thomomys umbrinus toltecus* Hall and Kelson, Mammals of North America, Ronald Press, p. 432.

1966. *Thomomys bottae toltecus* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus toltecus* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 495.

1990. *Thomomys bottae toltecus* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae toltecus* Jones and Baxter, Mammalian Species. 742:5.

2023. *Thomomys fulvus toltecus* This study.

Thomomys bottae villai [= *T. baileyi villai*]

1953. *Thomomys bottae villai* Baker Univ. Kansas Publ., Mus. Nat. Hist. 5:505.

1959. *Thomomys umbrinus villai* Hall and Kelson, Mammals of North America, Ronald Press, p. 434.

1966. *Thomomys bottae villai* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus villai* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 496.

1990. *Thomomys bottae villai* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae villai* Jones and Baxter, Mammalian Species. 742:5.
2023. *Thomomys baileyi villai* This study.

Thomomys fulvus texensis [= *T. baileyi texensis*]

1902. *Thomomys fulvus texensis* Bailey, Proc. Biol. Soc. Wash. 15:119.
1932. *Thomomys bottae ruidosae* Hall, Proc. Biol. Soc. Wash. 45:96.
1935. *Thomomys bottae texensis* Goldman, Proc. Biol. Soc. Wash. 48:157.
1936. *Thomomys bottae guadalupensis* Goldman, J. Wash. Acad. Sci. 26:117.
1936. *Thomomys pectoralis* Goldman, J. Wash. Acad. Sci. 26:117.
1939. *Thomomys umbrinus texensis* Blair, Occas. Pap. Mus. Zool., Univ. Mich. 403:2.
1940. *Thomomys bottae scotophilus* Davis, J. Mamm. 21:204.
1959. *Thomomys umbrinus texensis* Hall and Kelson, Mammals of North America, Ronald Press, p. 432.
1966. *Thomomys bottae texensis* Anderson, Syst. Zool., 15:196.
1981. *Thomomys umbrinus texensis* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 495.
1990. *Thomomys bottae texensis* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae texensis* Jones and Baxter, Mammalian Species. 742:5.
2019. *Thomomys bottae texensis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.
2023. *Thomomys baileyi texensis* This study.

Thomomys lachuguilla confinalis [= *T. baileyi confinalis*]

1936. *Thomomys lachuguilla confinalis* Goldman, J. Wash. Acad. Sci. 26:119.
1938. *Thomomys bottae confinalis* Goldman, Proc. Biol. Soc. Wash. 51:55.
1959. *Thomomys umbrinus confinalis* Hall and Kelson, Mammals of North America, Ronald Press, p. 423.
1966. *Thomomys bottae confinalis* Anderson, Syst. Zool., 15:196.
1981. *Thomomys umbrinus confinalis* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 481.
1990. *Thomomys bottae confinalis* Patton and Smith, Univ. California Press 123:3
2004. *Thomomys bottae confinalis* Jones and Baxter, Mammalian Species. 742:3.
2019. *Thomomys bottae confinalis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:529.
2023. *Thomomys baileyi confinalis* This study.

Thomomys lachuguilla limitaris [= *T. baileyi limitaris*]

1902. *Thomomys aureus lachuguilla* Bailey, Proc. Biol. Soc. Wash. 15:120.
1936. *Thomomys lachuguilla limitaris* Goldman, J. Wash. Acad. Sci. 26:118.
1938. *Thomomys bottae lachugilla* [sic], Goldman, Proc. Biol. Soc. Wash. 51:55.

1959. *Thomomys umbrinus limitaris* Hall and Kelson, Mammals of North America, Ronald Press, p. 427.

1966. *Thomomys bottae limitaris* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus limitaris* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 486.

1990. *Thomomys bottae limitaris* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae limitaris* Jones and Baxter, Mammalian Species. 742:3.

2019. *Thomomys bottae lachuguilla* Beauchamp-Martin et al., Spec. Publ. Mus. Texas Tech Univ. 71:530.

2023. *Thomomys baileyi limitaris* This study.

***Thomomys pectoralis* [= *T. baileyi pectoralis*]**

1936. *Thomomys pectoralis* Goldman, J. Wash. Acad. Sci. 26:120.

1959. *Thomomys umbrinus pectoralis* Hall and Kelson, Mammals of North America, Ronald Press, p. 430.

1966. *Thomomys bottae pectoralis* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus pectoralis* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 490.

1990. *Thomomys bottae pectoralis* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae pectoralis* Jones and Baxter, Mammalian Species. 742:4.

2019. *Thomomys bottae texensis* Beauchamp-Martin et al., Spec. Publ., Mus. Texas Tech Univ. 71:533.

2023. *Thomomys baileyi pectoralis* This study.

***Thomomys sturgisi* [= *T. baileyi sturgisi*]**

1938. *Thomomys sturgisi* Goldman, Proc. Biol. Soc. Wash. 51:56.

1959. *Thomomys umbrinus sturgisi* Hall and Kelson, Mammals of North America, Ronald Press, p. 433.

1966. *Thomomys bottae sturgisi* Anderson, Syst. Zool., 15:196.

1981. *Thomomys umbrinus sturgisi* Hall, Mammals of North American, John Wiley and Sons, Inc., p. 494.

1990. *Thomomys bottae sturgisi* Patton and Smith, Univ. California Press 123:3

2004. *Thomomys bottae sturgisi* Jones and Baxter, Mammalian Species. 742:4.

2023. *Thomomys baileyi sturgisi* This study.