

Genus-level review of pocket gophers in the family Geomyidae

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Pocket gophers (Geomyidae) comprise a well-studied family at the species level but need an updated revision at the generic level because studies of each genus have applied different data sets and different criteria for recognizing distinct taxa. Pocket gophers thrive from temperate Canada south to Panama and Colombia, where they inhabit various habitats, including temperate forests, prairies, steppes, hot and cold deserts, and subtropical and tropical areas. The taxonomy at the genus and species levels underwent many changes in the early twenty-first century due to use of different sequencing methodologies. This article builds upon those analyses to review genus-level relationships within the Geomyidae. Specifically, we analyzed the sequences available in Genbank for members of the family Geomyidae (Cytb for 47 species and COI for 33 species). We conducted different phylogenetic analyses; in all cases, genera were classified into monophyletic groups associated with the tribes Geomyini and Thomomyini. In the Thomomyini, the genus *Thomomys* was recognized with two genera, *Megascapheus* and *Thomomys*, which are more genetically distinct than many other genera. In the Geomyini, each genus and subgenus are distinct monophyletic groups with very strong support and large *p*-distances. The Mississippi River appears to function as an important geographic barrier within *Geomys*, with marked genetic differentiation between populations on the eastern and western sides of the river. Collectively, our analyses based on mtDNA sequences suggest that a more detailed revision employing multiple data sets is needed for the genera within the Geomyidae.

Las tuzas (Geomyidae) comprenden una familia bien estudiada a nivel de especies, pero necesitan una revisión actualizada a nivel de género, debido a que los estudios de cada género han utilizado diferentes conjuntos de datos y criterios para reconocer los distintos taxa. Las tuzas se distribuyen desde Canadá hasta Panamá y Colombia, en diversos hábitats, incluyendo bosques templados, praderas, estepas, desiertos fríos y calientes, así como áreas subtropicales y tropicales. La taxonomía a nivel de género y especie tuvo muchos cambios a principios del siglo veinte y uno debido al uso de diferentes metodologías de secuenciación. Este artículo se basa en esos análisis para revisar las relaciones a nivel de género dentro de los Geomyidae. Específicamente, analizamos las secuencias disponibles en Genbank para especies de la familia Geomyidae (Cytb para 47 especies y COI para 33 especies). Realizamos diferentes análisis filogenéticos; en todos los casos, los géneros fueron clasificados en grupos monofiléticos asociados con las tribus Geomyini y Thomomyini. En los Thomomyini, el género *Thomomys* fue reconocido con dos géneros, *Megascapheus* y *Thomomys*, que son genéticamente más distintos que muchos otros géneros. En los Geomyini, cada género y subgénero son grupos monofiléticos distintos con un fuerte apoyo y grandes distancias *p*. El río Misisipi parece funcionar como una importante barrera geográfica dentro de *Geomys*, con una diferenciación genética notable entre las poblaciones en los lados este y oeste del río. Colectivamente, nuestros análisis basados en secuencias de mtDNA sugieren que se necesita una revisión más detallada utilizando múltiples conjuntos de datos para los géneros dentro de los Geomyidae.

Keywords: *Geomys*; *Heterogeomys*; *Megascapheus*; genus; taxonomy; *Thomomys*.

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Introduction

The family Geomyidae is endemic to the Americas, being distributed from temperate Canada south to Panama and Colombia. Collectively, geomyids occupy a wide range of habitats, from temperate forests, prairies, steppes, hot and cold deserts, and subtropical and tropical areas (Hafner 2017). Over most of their distributions, the different genera of Geomyidae have allopatric distributions (Hall 1981; Hafner 2017). The only areas where two genera are sympatric are in the highlands of central and northern México, where different species of *Thomomys* and *Cratogeomys* or *Cratogeomys* and *Zygogeomys* co-occur (Russell 1968a; Hall 1981; Patton 2005). The genus- and species-level taxonomy of the Geomyidae underwent multiple changes in the early twenty-first century based on analyses of mitochondrial

DNA (mtDNA) and karyotype differences. For example, *Cratogeomys* and *Pappogeomys*, both previously considered subgenera of *Cratogeomys*, were elevated to generic status. Similarly, *Heterogeomys* and *Orthogeomys*, both previously considered subgenera of *Orthogeomys*, were elevated to generic status (Russell 1968a; Hall 1981; Demastes *et al.* 2002; Spradling *et al.* 2016).

While the taxonomy and systematics of the Geomyidae have been studied by multiple authors over the past few decades (*e. g.*, Elliot 1903; Russell 1968a; Honeycutt and Williams 1982; DeWalt *et al.* 1993; Patton 2005; Álvarez-Castañeda 2010; Spradling *et al.* 2016), many of these studies have focused on a specific genus or group of species within this family. For this reason, there are no consistent criteria that can be used to resolve taxonomic issues for all mem-

bers of this family. Pocket gophers are a relatively well-studied group at the species level, but a comprehensive revision is needed at the genus level and this may require reconsideration of the criteria used to distinguish between different genera.

Currently, the family Geomyidae is represented by two tribes ([Russell 1968a](#)). The tribe Thomomyini includes only the genus *Thomomys*, with two recognized subgenera, *Megascapheus* and *Thomomys* ([Elliot 1903](#)). In contrast, the tribe Geomyini ([Russell 1968a](#)) includes six genera – *Cratogeomys*, *Geomys*, *Heterogeomys*, *Orthogeomys*, *Pappogeomys*, and *Zygogeomys*. Of these, only *Heterogeomys* contains subgenera, namely *Heterogeomys* and *Macrogeomys* ([Russell 1968a](#)). Multiple taxonomic assessments have been completed for each of the currently recognized genera, as exemplified by the following: *Cratogeomys* ([Russell 1968b](#); [DeWalt et al. 1993](#); [Hafner et al. 2004, 2005, 2008](#)), *Geomys* ([Merriam 1895](#); [Hall and Kelson 1959](#); [Russell 1968a](#); [Tucker and Schmidly 1981](#); [Heaney and Timm 1983](#); [Baker et al. 1989](#); [Block and Zimmerman 1991](#); [Jolley et al. 2000](#); [Sudman et al. 2006](#); [Chambers et al. 2009](#)), *Heterogeomys* ([Nelson and Goldman 1929](#); [Russell 1968a](#); [Hall 1981](#); [Patton 2005](#); [Spradling et al. 2016](#)), *Orthogeomys* ([Nelson and Goldman 1929](#); [Russell 1968a](#); [Hall 1981](#); [Patton 2005](#); [Spradling et al. 2016](#)), *Pappogeomys* ([Nelson and Goldman 1934](#); [Russell 1968b](#); [Honeycutt and Williams 1982](#); [Demastes et al. 2002](#)), *Thomomys* ([Hall and Kelson 1959](#); [Anderson 1966, 1972](#); [Patton and Dingmen 1968](#); [Russell 1968a](#); [Thaeler 1968a, b, 1972, 1977, 1980](#); [Hoffmeister 1969, 1986](#); [Patton 1973, 1993, 2005](#); [Thaeler and Hinesley 1979](#); [Patton and Smith 1981, 1990](#); [Hall 1981](#); [Patton et al. 1984](#); [Álvarez-Castañeda 2010](#); [Hafner et al. 2011](#); [Trujano-Álvarez and Álvarez-Castañeda 2013](#); [Mathis et al. 2013a, 2013b, 2014](#); [Álvarez-Castañeda et al. 2017](#); [Bradley et al. 2023](#)), and *Zygogeomys* ([Merriam 1895](#); [Russell 1968a](#); [Hall 1981](#)).

The systematics of the Geomyidae were first established during the late nineteenth to mid-twentieth centuries based on morphology ([Merriam 1895](#); [Russell 1968a, b](#)), before the advent of DNA sequencing technologies. Indeed, many of the studies that have contributed to the current taxonomy of the family (see above) pre-date the use of genetic information. Subsequent revisions within each genus or species complex that have employed genetic data have tended to be conducted by multiple groups of researchers employing different criteria to identify genetically distinct taxonomic units. As a result, a comprehensive review of the family that applies consistent sequenced-based criteria to distinguish taxonomic units is lacking. Although mtDNA, nDNA, and karyotypes have all been used to explore geomyid taxonomy (for example, [Hafner et al. 2004, 2005, 2008, 2009](#); [Spradling et al. 2016](#); [Sudman et al. 2006](#); [Chambers et al. 2009](#)), the most widely employed genetic marker is the mitochondrial cytochrome b (Cytb) locus. Accordingly, the primary objective of this study was to use Cytb data to evaluate genus-level taxonomic and systematic relationships with

the Geomyidae. Delineating generic boundaries requires a well-resolved phylogeny that includes as many species as possible to *i*) generate a comprehensive overview of current generic names and their type species and *ii*) clarify generic boundaries and the species that they contain. This article uses Cytb data to create the taxonomic and systematic background required for a rigorous revision generic-level classifications of pocket gophers.

Materials and methods

Sampling and sequencing. Previous studies have generated cytochrome b (Cytb) sequences for nearly all species of geomyids ($n = 47$ species) as well as cytochrome oxidase subunit 1 (COI) sequences for a somewhat smaller subset of species ($n = 33$ species); all of these sequences are available in GenBank (Supplementary Material 1). All sequences available for geomyids were aligned using the MEGA 11 software package ([Tamura et al. 2021](#)). Sequences containing intermediate stop codons were discarded. Analyses were performed using the sequences obtained from both genes. To optimize computational time, we analyzed a subset of five specimens from each monophyletic group, which was average number of samples per species the (Supplementary Material 2); preference was given to sequences that have been used in published taxonomic revisions. Fewer than five sequences were available for some species (Supplementary Material 2); we were unable to locate sequences for *Thomomys idahoensis* and *T. clusius*.

Phylogenetic analyses. Analyses were conducted based on a 1,141-bp fragment of Cytb ($n = 169$ sequences) and a 1,544-bp fragment of COI ($n = 88$ sequences; Supplementary Material 1). Because sequence from both Cytb and COI were not available for all species, data from each locus were analyzed separately. Our first analysis assessed the monophyly of each species based on up to five sequences per species. Since sympatry has not been reported for species in the same genus, the source of each sequence was reviewed in detail to avoid confusion between species or potential misidentifications. When multiple sequences were available, preference was given to sequences from localities located farthest from the distribution limits of other species in the same genus; in all cases, efforts were made to select sequences that clearly represented the known geographic distribution of the species in question. Some species are represented by outdated names in GenBank; in some cases, we changed the name of the species following [Álvarez-Castañeda \(2024\)](#) and [Bradley et al. \(2023\)](#); see Supplementary Material 1). Once the monophyly of each species was demonstrated, one sequence per species was selected to construct a representative tree for the family.

Sequence alignments were performed using the MUSCLE software package with default parameters ([Edgar 2004](#)). The most suitable evolutionary model for our data set was identified using the model comparison software MrModeltest ver. 2 ([Nylander 2004](#)) under the Akaike Information Criterion (AIC). Phylogenetic relationships

were assessed for each locus using neighbor-joining (NJ), unweighted pair group method with arithmetic mean (UPGMA), maximum-parsimony (MP), maximum-likelihood (ML), and Bayesian inference (BI) optimality criteria. Phylogenetic reconstructions were conducted in PhyML (Guindon *et al.* 2010), MEGA version 11 (Tamura *et al.* 2021), and PAUP* version 4.0b (Swofford and Sullivan 2003). A bootstrap consensus tree was inferred from replicates based on uniform rates of the General Time Reversible (GTR) substitution model. Values for percent sequence divergence within and between species were estimated using the uncorrected *p*-distance parameter model in PAUP. Nodal support was assessed with bootstrap analyses, including a fast heuristic procedure with 1,000 pseudo-replicates (Felsenstein 1985). A Bayesian inference analysis coupled with Markov Chain Monte Carlo (BMCMC) inference was performed in MrBayes v3.2.2 (Ronquist and Huelsenbeck 2003). We carried out two independent BMCMC analyses, each consisting of four chains. Each Markov chain was started from a random tree and run for 10 million generations using the default flat priors, sampling trees every 1,000 generations. Sequence evolution model parameters were treated as unknown variables with uniform default priors and were estimated as part of the analysis. The first 40 % of generations were conservatively deleted as burn-in. Sequences for *Chaetodipus californicus*, *Dipodomys agilis*, *Heteromys nelsoni*, *Liomys pictus*, *Microdipodops pallidus*, and *Perognathus flavescens* were used as outgroups. The outgroup specimens were selected partly following the study of Alexander and Riddle (2005); Genbank accession numbers for outgroup sequences are provided in the supplementary material.

Time calibration. Divergence times between taxa were estimated using BEAST2 v2.6.7 (Bouckaert *et al.* 2019). For each locus, we implemented three separate Markov Chain Monte Carlo (MCMC) chains to generate a gene tree, with each chain running for 10 million generations. Samples were collected every 1,000 generations to assess the posterior distribution. We set specific priors, including the processed Yule speciation model to account for branching rates, a strict molecular clock to enforce constant rates of evolution across lineages, and a random starting tree to avoid biasing the results (Gernhard *et al.* 2008). No deep data for the family Geomyidae were found as calibration points. However, because Heteromyidae is the sibling family and a Bayesian divergence dating analysis exists using combined 3-gene data (12S, 16S, and COI), we used 15.9–12.5 mya for Dipodomysinae, 22–20 mya for Perognathinae and 15.2 mya for Heteromyinae (Hafner *et al.* 2007). To achieve phylogenetic analyses as similar as possible to those reported by Hafner *et al.* (2007), we used the same specimens in our analyses. After running the chains, we used TreeAnnotator version 10.5.0 to summarize the results and construct a consensus tree. Notably, we applied a burn-in period of 1,000 states to remove any initial inconsistencies in chain convergence and to focus on the most stable estimates of the phylogenetic relationships.

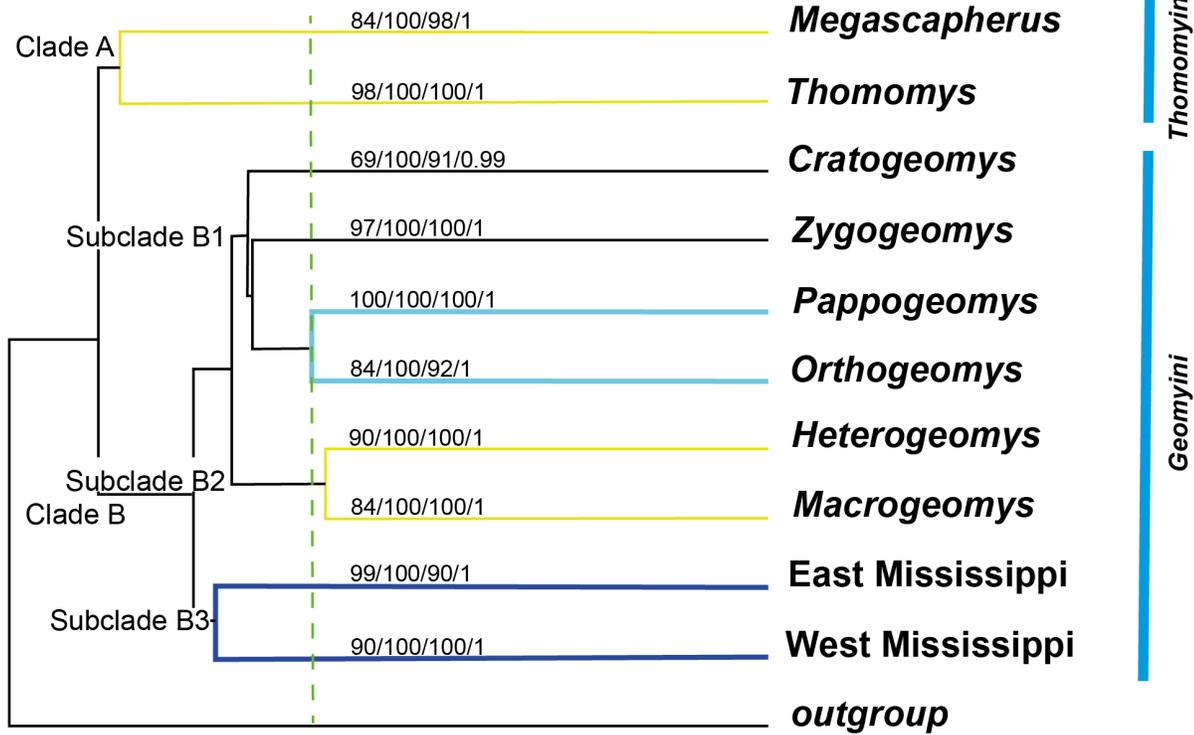
Results

Phylogenetic analyses. The most appropriate evolutionary model for our phylogeny reconstruction was the GTR+I+G model. The model parameters were $I = 0.3872$ and $G = 0.7090$, $\ln L = 28961.9492$, $k = 10$, $AIC = 57943.8984$. The base frequencies were $A = 0.3689$, $C = 0.3012$, $G = 0.0502$, $T = 0.2796$, and the relative substitution rates were $A-C = 0.4558$, $A-G = 9.6062$, $A-T = 0.4878$, $C-G = 0.4080$, $C-T = 5.7622$, and $G-T = 1.0000$. All phylogenetic reconstructions for Cytb and COI indicated that Geomyidae is a monophyletic family containing ten monophyletic subgroups, each of which is markedly divergent from the others and is strongly supported by bootstrap values (Figure 1; Supplementary Material 3). The neighbor-joining (NJ), unweighted pair group method with arithmetic mean (UPGMA), maximum-parsimony (MP), maximum-likelihood (ML), and Bayesian inference (BI; Supplementary Material 3) analyses all produced trees with similar topologies. The same primarily clades were recovered for both the Cytb and COI analyses (Figure 1).

Analyses of both loci revealed that all genera were sorted into two monophyletic groups, each associated with a recognized tribe within the family, namely the Thomomyini (Clade A) and the Geomyini (Clade B), as proposed by Russell (1968a). The tribe Thomomyini includes the single genus *Thomomys*, which consists of two previously recognized subgenera: *Megascapheus* and *Thomomys*. Each subgenus, in turn, contains multiple reciprocally monophyletic groups that are differentiated at the same level and characterized by a high degree of dissimilarity (Tables 1 and 2). Many groups have distinctive morphological characteristics that can be used to differentiate them (see appendix 1). The tribe Geomyini (Clade B) includes three subclades. Subclade B1 consists of four monophyletic groups: *Cratogeomys*, *Pappogeomys*, *Orthogeomys*, and *Zygogeomys*. This was the only subclade to display differences in tree topology between the Cytb and COI sequences. Subclade B2 is monophyletic and contains the subgenera *Heterogeomys* and *Macrogeomys*. The final subclade (B3), which includes all species of *Geomys*, is split into two monophyletic groups that are distributed on the eastern versus western sides of the Mississippi River (Figure 1).

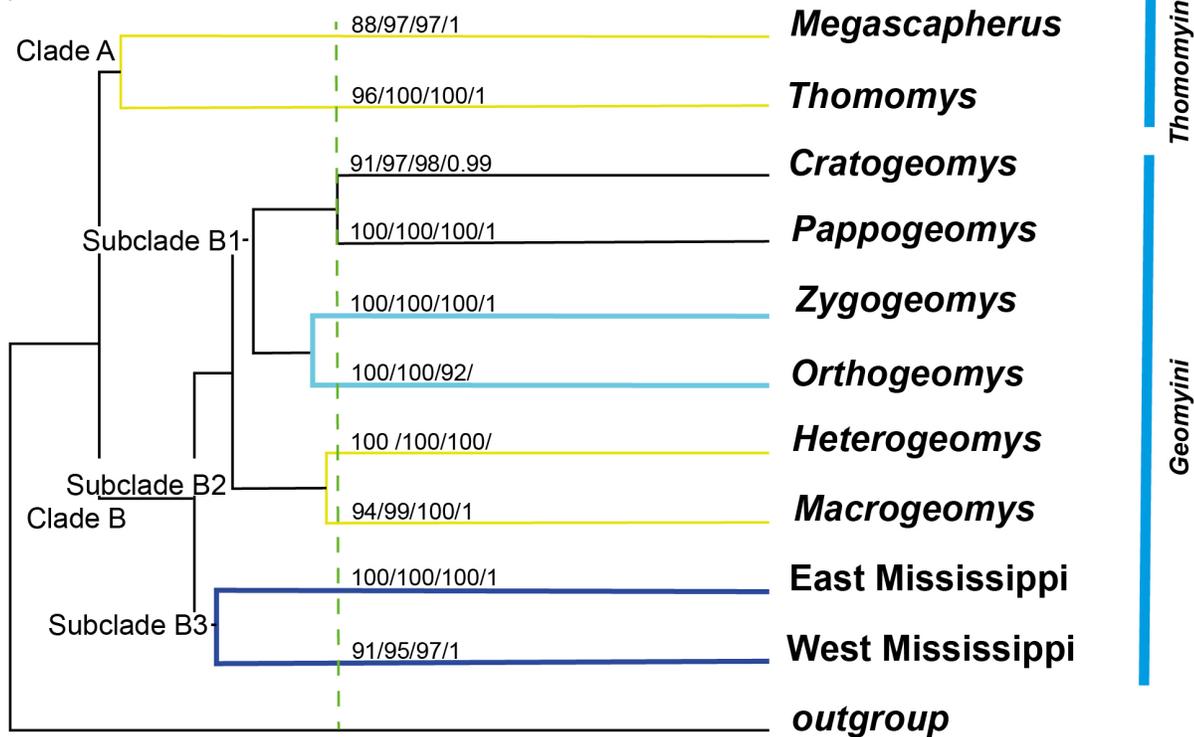
Percentage of uncorrected *p*-distance. Percent sequence divergences between species for Cytb and COI sequences analyses are shown in Tables 1 and 2, respectively; percent divergences within species are shown in Table 3. The least divergence between species was found in *Cratogeomys*, with *p*-distances ranging from 2.35 % between *C. tylosinus* and *C. fumosus* to 5.00% between *C. perotensis* and *C. merriami*. When all ten monophyletic subgroups of geomyids were considered, percent sequence divergence for Cytb ranged from $p = 11.09$ % to $p = 21.64$ % (Table 1); for COI sequences, these values were $p = 4.48$ % and $p = 18.62$ % (Table 2). In Clade A, the difference between the two subgenera was 19.92 % (Table 1). In Clade B, sub-clade B1 contains four monophyletic units, each consisting of a single

A) Cytb



Maximum-parsimony / neighbor-joining bootstrap / maximum-likelihoods bootstrap support values / Bayesian posterior probabilities

B) COI



Maximum-parsimony / neighbor-joining bootstrap / maximum-likelihoods bootstrap support values / Bayesian posterior probabilities

Figure 1. Phylogenetic analysis based on 46 specimens (1,141 bp) using cytochrome b gene sequences. The sequences represent individuals of different species belonging to the family Geomyidae. This tree supports the monophyly of ten clades within the Geomyidae. Each clade represents one genus.

Table 1. Pairwise percentage of genetic differences based on cytochrome b (Cytb) across genera and subgenera in the family Geomyidae.

	1	2	3	4	5	6	7	8	9	10
1 <i>Cratogeomys</i>										
2 <i>Pappogeomys</i>	15.70%									
	14.04-16.77									
3 <i>Zygogeomys</i>	15.99%	15.50%								
	13.74-18.42	14.73-15.95								
4 <i>Orthogeomys</i>	15.97%	13.03%	15.94%							
	13.27-18.42	6.76-15.48	15.24-16.23							
5 <i>Heterogeomys</i>	16.47%	16.51%	16.45%	14.81%						
(subgenus)	13.10-18.70	14.86-18.19	15.87-17.11	2.64-17.67						
6 <i>Macrogeomys</i>	16.36%	16.54%	15.38%	15.36%	11.09%					
(subgenus)	14.65-17.72	15.96-17.01	14.88-15.79	14.43-16.32	9.11-11.67					
7 <i>Geomys</i>	17.95%	16.34%	16.65%	16.66%	18.23%	17.09%				
(west Mississippi)	16.23-20.32	15.28-17.37	14.56-18.49	12.65-19.34	16.27-19.74	15.92-18.21				
8 <i>Geomys</i>	17.55%	16.56%	16.31%	14.94%	17.62%	16.85%	16.76%			
(east Mississippi)	16.32-18.74	16.36-16.83	16.19-16.41	12.74-16.80	15.96-18.60	16.23-18.07	15.48-17.83			
9 <i>Megascapheus</i>	20.71%	19.85%	20.27%	21.64%	20.59%	18.96%	20.15%	19.72%		
(subgenus)	18.77-22.98	18.49-21.71	18.74-22.15	18.95-25.40	17.60-22.09	17.47-21.48	17.98-22.65	17.33-21.75		
10 <i>Thomomys</i>	20.74%	21.15%	19.61%	21.63%	20.31%	19.18%	20.91%	20.02%	19.92%	
(subgenus)	19.47-21.99	20.59-21.75	18.78-21.40	20.44-23.89	17.52-22.55	16.97-21.23	19.65-22.46	19.38-20.53	18.16-21.23	
0 outgroup	23.31%	22.92%	22.80%	23.82%	22.61%	21.66%	23.15%	23.01%	23.36%	24.01%
	20.88-25.50	21.23-25.73	20.58-24.73	21.30-27.79	19.35-24.50	19.48-24.06	11.34-25.81	11.34-25.81	21.63-25.81	22.72-25.36

recognized genus. Percent sequence divergences within these genera are as follows: *Cratogeomys* ($p = 15.70\%$ Cytb, $p = 13.09\%$ COI), *Pappogeomys* ($p = 13.03\%$ Cytb, $p = 13.99\%$ COI), *Orthogeomys* ($p = 13.03\%$ Cytb, $p = 14.46\%$ COI), and *Zygogeomys* ($p = 15.38\%$ Cytb, $p = 14.46\%$ COI). Subclades B2 and B3 contain only two groups each, with $p = 11.09\%$ Cytb and $p = 10.44\%$ COI for Subclade B2 and $p = 16.76\%$ Cytb and $p = 14.40\%$ COI for Subclade B3.

The Geomyidae underwent adaptive radiation during the Cenozoic, resulting in all of the current genera (Álvarez-Castañeda 2024). Our estimates of mitochondrial sequence divergence are consistent with this time frame (Figure 2, 3). Overall, our estimates revealed that the divergence between Heteromyidae and Geomyidae taxa occurred ~ 25.0 mya, placing the crown age for these taxa in the Early Miocene. Within the Geomyidae, estimated divergence times are ~ 14.84 mya for the tribe Thomomyini (Clade A) and ~ 10.82 mya for the Geomyini (Clade B), both of which fall between the Hemingfordian and Barstovian stages of the North American Land Mammal Ages (NALMA) scheme (Wood et al. 1941). Generic-level divergence times range from the Middle Miocene (~ 14 mya) to the Early-Pliocene (~ 4 mya), while most species-level divergence times fall within the Late Pliocene and Pleistocene (3.0 – 0.8 mya). Within *Thomomys*, divergence of the two subgenera occurred at ~ 7.29 mya for *Megascapheus* and ~ 7.23 mya for *Thomomys*. Diversification within the Geomyini began during the Late Miocene (~ 9.0 mya) and continued until the early Pliocene (~ 3.7 mya; Figure 2, 3).

Discussion

The use of different date sets – notably the use of different genetic markers – to examine the taxonomy and systematics of the Geomyidae has made it challenging to develop a comprehensive understanding of diversification within this family. For example, reviews of the different genera of geomyids have tended to employ different combinations of mitochondrial and nuclear genetic markers (Demastes et al. 2002, 2003; Hafner et al. 2009; Mathis et al. 2013a, 2013b; Spradling et al. 2016; Bradley et al. 2023), with the result that data cannot easily be compared across studies. The marker that has been most commonly used across analyses is the mitochondrial Cytb locus and for this reason we have focused our analyses on this gene. Although Cytb tends to reveal relatively low levels of differentiation (*i. e.*, small p-distances) between species, many of these distinctions are supported by data from other genes that serve to validate the separation of species. Here, monophyly was used to establish the degree of differentiation between distinct phylogenetic units; the resulting values for differentiation at the Cytb locus were then used to set boundaries between genera and subgenera, to provide a quantitative basis for distinguishing between taxonomic units at these levels. When possible, these criteria were supplemented by other data sets with potential diagnostic value, including a) time since divergence (estimated ages of clades), b) strength of support (*e. g.*, bootstrap values) for different units, c) genetic distances among other, established taxonomic units within the Geomyidae, and e) morphological

Table 2. Pairwise percentage of genetic differences based on cytochrome oxidase subunit 1 (COI) across genera and subgenera in the family Geomyidae.

	1	2	3	4	5	6	7	8	9	10
1 <i>Cratogeomys</i>										
2 <i>Pappogeomys</i>	13.99%									
	12.95-15.14									
3 <i>Zygozemys</i>	14.73%	14.46%								
	13.65-16.02	14.27-14.64								
4 <i>Orthogeomys</i>	14.59%	15.51%	14.56%							
	13.71-16.10	15.35-15.67	14.04-15.09							
5 <i>Heterogeomys</i>	15.09%	13.56%	16.05%	14.46%						
(subgenus)	14.25-16.34	12.82-14.18	15.55-16.37	14.05-14.89						
6 <i>Macrogeomys</i>	15.98%	14.78%	15.18%	15.24%	10.44%					
(subgenus)	15.04-17.10	14.18-15.59	14.21-16.12	13.99-16.06	10.04-10.96					
7 <i>Geomys</i>	16.23%	15.69%	15.89%	15.72%	17.41%	17.41%				
(west Mississippi)	15.23-17.74	15.03-16.32	15.29-16.43	15.22-16.32	16.32-18.41	16.32-18.41				
8 <i>Geomys</i>	16.31%	14.70%	15.43%	15.48%	15.47%	15.47%	14.66%			
(east Mississippi)	15.29-16.71	14.31-15.09	15.35-15.51	15.41-15.54	14.96-15.87	14.96-15.87	13.67-15.93			
9 <i>Megascapheus</i>	18.32%	18.28%	14.57%	18.20%	18.62%	18.62%	18.25%	18.43%		
(subgenus)	16.97-19.86	17.36-19.17	12.24-16.43	17.49-19.44	17.86-19.66	17.86-19.66	16.72-19.43	17.75-19.32		
10 <i>Thomomys</i>	18.21%	17.73%	18.05%	17.86%	18.17%	18.17%	17.52%	17.42%	15.46%	
(subgenus)	16.91-19.11	17.16-18.33	17.51-18.78	17.29-18.34	17.25-18.91	17.25-18.91	16.66-18.54	16.58-17.88	8.34-19.49	
11 outgroup	20.00%	20.41%	19.50%	20.22%	20.07%	20.07%	20.34%	20.04%	20.11%	19.97%
	17.62-21.76	19.17-21.83	17.97-20.40	18.58-21.32	18.58-21.88	18.58-21.88	18.33-22.41	18.85-21.31	18.13-21.78	17.80-22.41

differences reported in the literature. Based on these analyses, we suggest that a formal revision of generic-level differentiation within this family is warranted.

Evidence for monophyly. Our phylogenetic analyses provided clear evidence of the monophyly of the ten terminal taxa depicted in Figure 1. With the exception of the distinct eastern and western clades of *Geomys* depicted in this figure, all other groups have been recognized previously at the generic or sub-generic levels (Demastes *et al.* 2002; Hafner *et al.* 2004, 2005, 2008; Sudman *et al.* 2006; Chambers *et al.* 2009; Mathis *et al.* 2013a, 2013b, 2014; Spradling *et al.* 2016; Álvarez-Castañeda *et al.* 2017; Bradley *et al.* 2023). In our analyses, both CytB and COI sequence data provided strong support for these monophyletic units, with 100% support being provided by one or more of the following metrics: neighbor-joining (NJ), unweighted pair group method with arithmetic mean (UPGMA), maximum-parsimony (MP), maximum-likelihood (ML), and Bayesian inference (BI; Figure 1). Monophyly within the genus *Geomys* has also been documented through the use of three combined genetic regions: the nuclear gene Rbp3, ribosomal RNA (12S rRNA), and mitochondrial DNA (Chambers *et al.* 2009). These findings align with our analysis, which includes all genera in the family and incorporates the Heteromyidae as an external group. Thus, both our data and those from previous studies indicate that the taxonomic units in Figure 1 are monophyletic. In the case of *Thomomys*, it had previously been reported based on nuclear genes (seven non-coding nuclear sequence loci) that the monophyly of the species within this genus was not wholly resolved since three of the four named species within

the subgenus *Thomomys* were found to be monophyletic (Belfiore *et al.* 2008). Our analysis of mitochondrial genes supports the findings of the previously mentioned study regarding the two clades, *Megascapheus* and *Thomomys*. Belfiore *et al.* (2008) proposed that these subgenera originated approximately 5 million years ago (Ma). However, our analysis estimates the origin of these clades to be around 7 Ma. Our estimate aligns with the fossil record for Thomomyines, which date to the middle Hemphillian period (NALMA), also approximately 7 Ma, according to Shotwell (1967) and Tedford *et al.* (2004).

Genetic differentiation between taxa. At the species level, the least genetic differentiation (*i. e.*, smallest p-distance) evident in our data occurred between *Cratogeomys tylosinus* and *C. fumosus*, which were separated by an average p-distance of 2.35%. Despite their limited divergence, these taxa have been recognized as distinct species based on mtDNA and nDNA analyses (Hafner *et al.* 2004). Within *Geomys*, Sudman *et al.* (2006) and Bradley *et al.* (2023) employed an estimated percent divergence of ~ 6 % to distinguish between species; this same level of divergence has been applied to Cytb data from other genera of Geomyidae that also included analyses of nuclear markers, karyotypes, and morphology (*e. g.*, *Pappogeomys*: Demastes *et al.* 2003; Hafner *et al.* 2009; *Orthogeomys* and *Heterogeomys*: Spradling *et al.* 2016; *Thomomys*: Álvarez-Castañeda 2010; Trujano-Álvarez and Álvarez-Castañeda 2013; Mathis *et al.* 2013a). Our analyses are generally consistent with this 6 % criterion, although several exceptions are evident. One is the small p-distance between *C. tylosinus* and *C. fumosus* noted

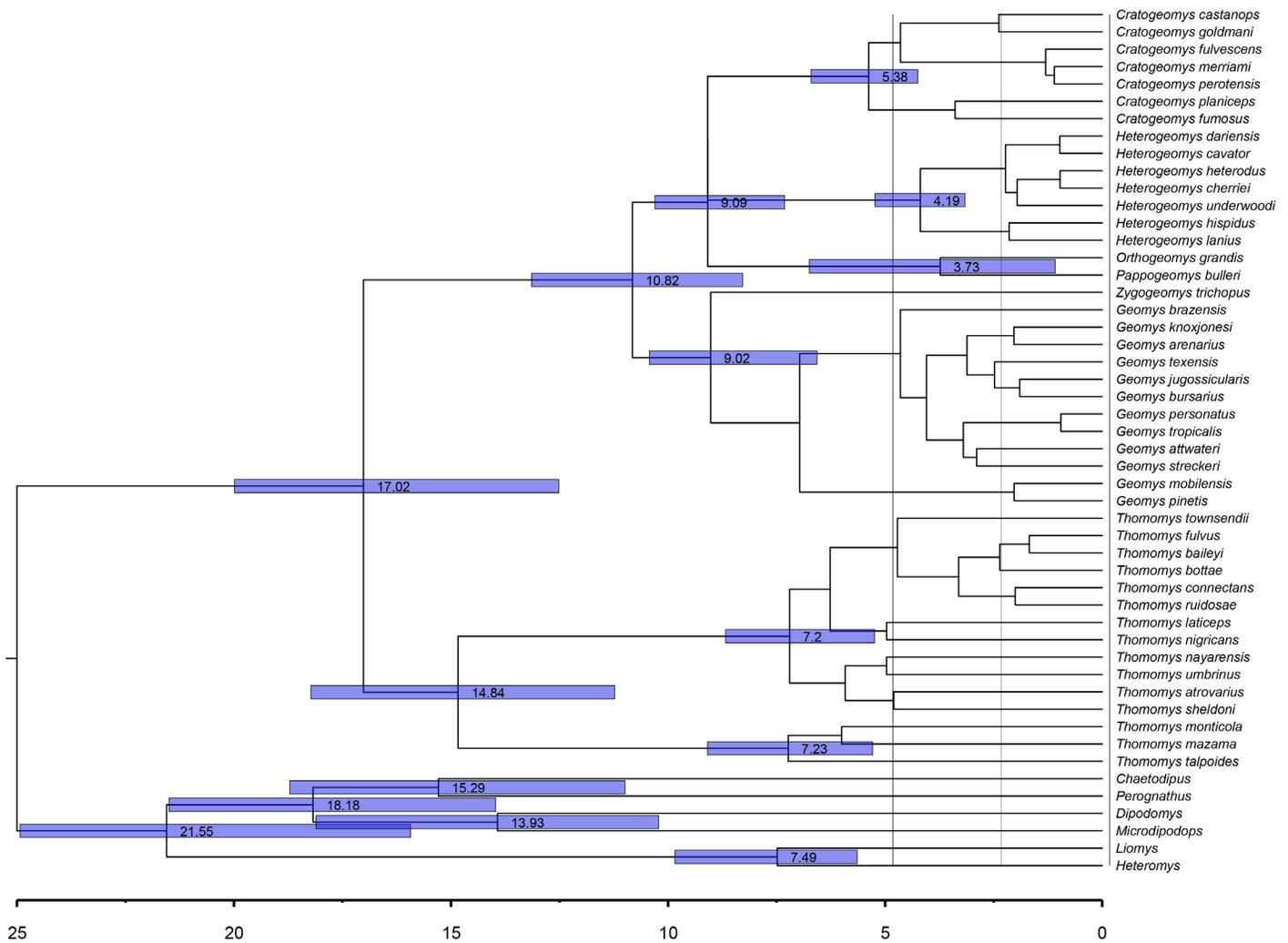


Figure 2. Calibrated maximum clade credibility tree of the Geomyidae and Heteromyidae using Cytb. Node labels include divergence time estimates in millions of years. Horizontal bars show the 95 % highest posterior density intervals surrounding each estimate. Calibration points were obtained from a Bayesian divergence dating analysis for the Heteromyidae using multigenes data (Hafner et al. 2007).

above. At the other extreme, differentiation with *Thomomys townsendii* ($p = 9.62\%$) and *T. talpoides* ($p = 14.61\%$) is greater than average values reported for all other species. Although use of p -distances alone to distinguish species is somewhat controversial, revisions based primarily on this metric have been conducted for geomyids, with minimal morphological information used to diagnose species of *Geomys* (Baker et al. 1989; Block and Zimmerman 1991; Jolley et al. 2000; Sudman et al. 2006; Chambers et al. 2009; Bradley et al. 2023) and *Thomomys* (Álvarez-Castañeda 2010; Trujano-Álvarez and Álvarez-Castañeda 2013; Álvarez-Castañeda et al. 2017; Bradley et al. 2023). While Patton 2005Beauchamp-Martin et al. (2019) do not recognize *Thomomys fulvus* as a valid species based on p -distance values, Bradley et al. (2023) not only accept this species but use similar criteria to recognize three other species of *Thomomys* (*T. baileyi*, *T. connectans*, and *T. ruidosae*). Regardless of whether p -distances alone are considered sufficient for distinguishing species, the range of values for this metric between currently recognized species of geomyids suggests that a species-level revision of these animals is warranted.

At the generic level, our analyses of Cytb sequences indicate that *Pappogeomys* and *Orthogeomys* are sibling taxa. These genera, which have long been recognized as distinct based on morphological characteristics (Hall and Kelson 1959; Russell 1968a; Hall 1981; Álvarez-Castañeda 2024), have Cytb a p -distance of 13.03 %, suggesting that this degree of differentiation may provide a basis for defining distinct genera. Based on COI sequences, the most closely related genera are *Pappogeomys* and *Cratogeomys*, which are separated by a p -distance of 14 %, providing a potential baseline divergence value for this gene. Although morphological analyses were not conducted as part of this study, information obtained from the literature suggests that with the exception of the east-west split within *Geomys*, all monophyletic groups reported here (Figure 1) have been recognized previously at the generic or subgeneric levels and that each is associated with a diagnostic description that can be clearly used for identification purposes (Merriam 1895; Nelson and Goldman 1929, 1934; Hall and Kelson 1959; Anderson 1966, 1972; Russell 1968a, b; Hall 1981; Álvarez-Castañeda 2024). Thus, available information indicates that

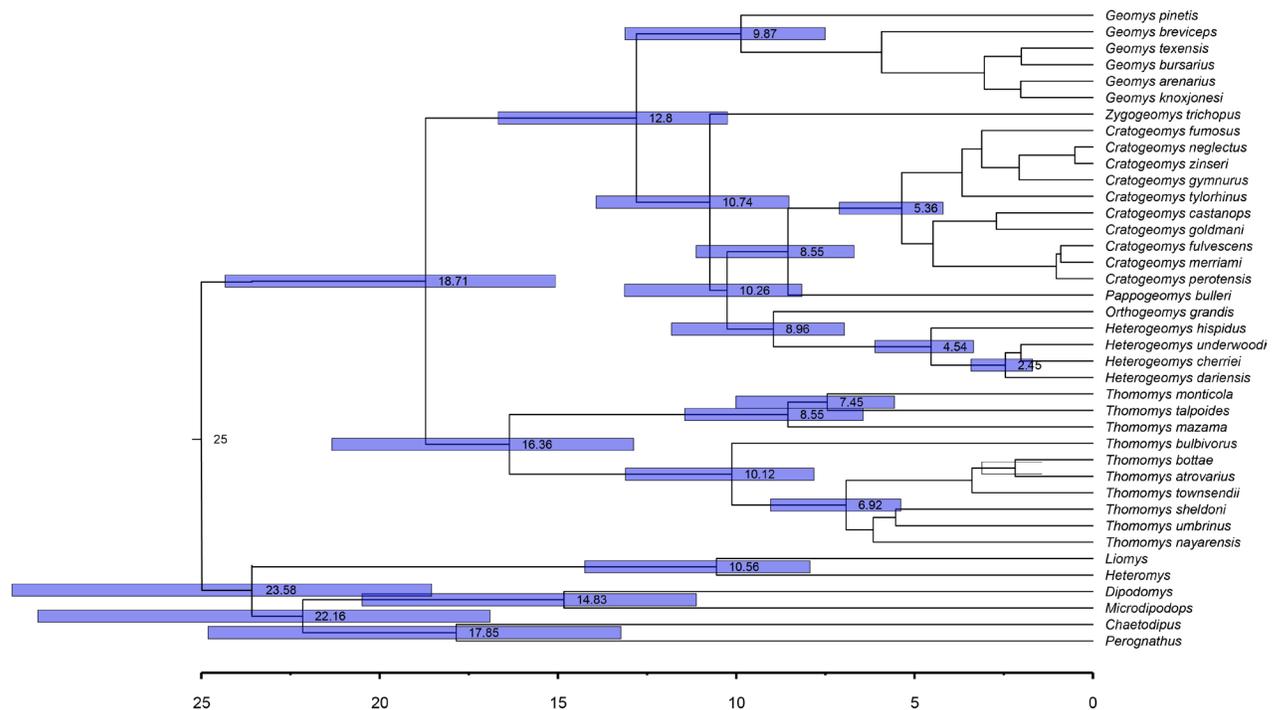


Figure 3. Calibrated maximum clade credibility tree of the Geomyidae and Heteromyidae using COI. Node labels include divergence time estimates in millions of years. Horizontal bars show the 95% highest posterior density intervals surrounding each estimate. Calibration points were obtained from a Bayesian divergence dating analysis for the Heteromyidae using multigenes data (Hafner *et al.* 2007).

the taxonomic units revealed by analyses of Cytb and COI are robust and should be recognized as distinct.

Review of geomyid taxonomy at the generic level. Our phylogenetic analyses revealed a clear separation between the two standardly recognized sub-clades of geomyids, the tribes Geomyini and Thomomyini (Russell 1968a; Appendix 1).

Tribe Thomomyini. Our analyses indicate that the tribe Thomomyini (our Clade A) is composed of two reciprocally monophyletic clades, each related to one of the subgenera of *Thomomys* proposed by Thaler (1980), namely *Megascapheus* and *Thomomys* (Patton and Smith 1981, 1989). *Megascapheus* was proposed by Elliot (1903) but was not recognized by Russell (1968a) or Hall (1981). Our data reveal a clear genetic separation between the proposed sub-genera (p -distance = 19.2% for Cytb and 15.46% for COI). Morphologically, *Megascapheus* species can be distinguished from *Thomomys* based on a variety of cranial traits (Nelson and Goldman 1934; Russell 1968a; Álvarez-Castañeda 2024); cytogenetically, the number of chromosomes also differs markedly. Thus, overall, our analyses support recognition of *Megascapheus* and *Thomomys* as distinct taxonomic units. The degree of genetic differentiation detected between these taxa suggests that they likely should be recognized as distinct genera. concern the skull and teeth, structures normally used as diagnostic attributes at the genus level.

Tribe Geomyini. The Geomyini (our Clade B) was proposed by Russell (1968a) and includes six genera: *Cratogeomys*, *Geomys*, *Heterogeomys* (subgenus *Heterogeomys* and *Macrogeomys*), *Orthogeomys*, *Pappogeomys*, and

Zygozomys. This scheme has been accepted since it was first proposed, although there have been subsequent modification at the generic and sub-generic levels (Russell 1968a, b; Hall 1981; Spradling *et al.* 2016). Our analyses indicate that the Geomyini are divided into three reciprocally monophyletic sub-clades. The first of these (our subclade B1) contains the genera *Cratogeomys*, *Pappogeomys*, *Orthogeomys*, and *Zygozomys*. *Cratogeomys* has been considered as a subgenus of *Pappogeomys* (Russell 1968a, b) but our analyses support those of Demastes *et al.* (2003) in suggesting that these are distinct genera. Our Cytb analyses suggest that *Pappogeomys* is sibling to *Orthogeomys*; this is in contrast to previous work that placed *Orthogeomys* closer to *Zygozomys* (Russell 1968a). Results from other studies indicate that *Pappogeomys* and *Orthogeomys* are clearly morphologically different (Merriam 1895; Russell 1968a; Honeycutt and Williams 1982; DeWalt *et al.* 1993; Demastes *et al.* 2002, 2003; Spradling *et al.* 2016; Nelson and Goldman 1934; Álvarez-Castañeda 2024) and thus p -distances between these taxa ($p = 13\%$ for Cytb and 14% for COI) may provide useful metrics for evaluation the degree of genetic differentiation between other putative genera of geomyids. The final genus in this sub-clade, *Zygozomys*, contains only one extant species that is endemic to Michoacán, Mexico; these animals are clearly morphological distinct from other members of the sub-clade (Merriam 1895, Russell 1968a, Álvarez-Castañeda 2024), thereby supporting recognition of *Zygozomys* as a separate genus.

The second sub-clade of Geomyini (our sub-clade B2) includes the genus *Heterogeomys*, which consists of two

Table 3. Average and range of genetic differences based on Cytb and COI within each of the species examined in the family Geomyidae. *Only one individual was recorded.

Species	Cytb	COI
	Average (Min – Max)	Average (Min – Max)
<i>Cratogeomys castanops</i>	1.42% (0.09 - 3.07)	2.45% (0.00 - 4.07)
<i>Cratogeomys fulvescens</i>	0.39% (0.00 - 0.61)	0.48% (0.13 - 0.78)
<i>Cratogeomys fumosus</i>	1.87% (1.14 - 2.46)	*
<i>Cratogeomys goldmani</i>	2.75% (0.49 - 5.15)	0.03% (0.01 - 0.04)
<i>Cratogeomys gymnurus</i>	2.81% (0.44 - 4.04)	*
<i>Cratogeomys merriami</i>	2.58% (0.00 - 4.74)	0.99% (0.00% - 1.82)
<i>Cratogeomys neglectus</i>	0.72% (0.26 - 4.38)	*
<i>Cratogeomys perotensis</i>	1.26% (0.00 - 2.02)	0.93% (0.06 - 1.49)
<i>Cratogeomys planiceps</i>	0.94% (0.53 - 1.23)	
<i>Geomys arenarius</i>	3.34% (0.00 - 6.24)	*
<i>Geomys attwateri</i>	2.43% (1.32 - 3.84)	
<i>Geomys bursarius</i>	3.55% (0.00 - 5.61)	*
<i>Geomys jugossicularis</i>	1.83% (0.18 - 2.77)	
<i>Geomys knoxjonesi</i>	2.12% (0.09 - 2.72)	*
<i>Geomys personatus</i>	0.66% (0.00 - 0.96)	
<i>Geomys mobilensis</i>	0.31% (0.00 - 0.56)	
<i>Geomys pinetis</i>	2.02% (0.18 - 3.05)	0.04% (0.00 - 0.06)
<i>Geomys streckeri</i>	0.43% (0.00 - 0.89)	
<i>Geomys texensis</i>	1.44% (0.00 - 2.89)	0.58% (0.58 - 0.58)
<i>Geomys tropicalis</i>	1.05% (0.52 - 1.57)	
<i>Orthogeomys cavator</i>	2.89% (2.89 - 2.89)	
<i>Orthogeomys cherriei</i>	0.72% (0.26 - 1.23)	*
<i>Orthogeomys dariensis</i>	0.25% (0.00 - 0.53)	*
<i>Orthogeomys grandis</i>	*	3.98% (2.26 - 5.14)
<i>Orthogeomys heterodus</i>	0.24% (0.00 - 0.75)	
<i>Orthogeomys hispidus</i>	0.39% (0.00 - 0.79)	1.42% (0.34 - 2.74)
<i>Orthogeomys lanius</i>	*	
<i>Orthogeomys underwoodi</i>	1.34% (0.76 - 1.76)	*
<i>Pappogeomys bulleri</i>	5.83% (0.60 - 8.01)	3.89% (0.00 - 5.26)
<i>Thomomys atrovarius</i>	4.59% (0.35 - 5.88)	9.02% (2.01 - 4.88)
<i>Thomomys bottae</i>	3.14% (0.96 - 4.74)	5.65% (0.00 - 4.50)
<i>Thomomys bulbivorus</i>		*
<i>Thomomys fulvus</i>	4.58% (0.20 - 6.83)	
<i>Thomomys laticeps</i>	3.30% (2.02 - 4.24)	
<i>Thomomys mazama</i>	0.58% (0.09 - 0.88)	*
<i>Thomomys monticola</i>	0.06% (0.00 - 0.09)	*
<i>Thomomys nayarensis</i>	0.61% (0.00 - 1.23)	0.65% (0.65 - 0.65)
<i>Thomomys nigricans</i>	1.74% (0.20 - 2.61)	
<i>Thomomys sheldoni</i>	4.47% (0.79 - 6.23)	4.21% (3.44 - 5.39)
<i>Thomomys talpoides</i>	14.6% (6.32 - 16.84)	5.27% (0.00%- 9.91)
<i>Thomomys townsendii</i>	9.62% (9.62 - 9.62)	*
<i>Thomomys umbrinus</i>	3.89% (0.18 - 5.90)	*
<i>Zygogeomys trichopus</i>	*	*

recognized subgenera, *Heterogeomys* and *Macrogeomys* (Spradling et al. 2016). *Heterogeomys* was previously considered a sub-genus of *Orthogeomys* (Russell 1968a; Hall 1981; Patton 2005), but our analyses indicate that the former is clearly distinct from *Orthogeomys*. Although relationships among the species in *Heterogeomys* and *Macrogeomys* have been reviewed previously (Hafner 1991; Sudman and

Hafner 1992), it appears that no detailed analysis has been conducted at the level of these subgenera. Differentiation of *Heterogeomys* and *Macrogeomys* is strongly supported by our analyses (Figure 1). Although p-distances between these taxa (11.09 % for Cytb; 10.44 % for COI) are somewhat lower than those reported for *Pappogeomys* and *Orthogeomys*, the strong support for the monophyly of these units coupled with documented morphological differences between them (Russell 1968a; Hall 1981) lead us to support their recognition as distinct sub-genera.

The final sub-clade (our sub-clade B3) includes all species of *Geomys sensu lato*. While our analyses support the monophyly of this genus, they also reveal the presence of two distinct, reciprocally monophyletic lineages that correspond to the eastern and western sides of the Mississippi River (Figure 1). The clade occurring to the east of the Mississippi has been recognized previously as part of the *G. pinetis* species complex (Russell 1968a; Penney and Zimmerman 1976; Sudman et al. 2006). In contrast, the clade to the west of the Mississippi includes the *bursarius* and *breviceps* species groups (Davis 1940; Hall 1981; Sudman et al. 2006). The two lineages display marked variation in cranial morphology (Russell 1968a; Penney and Zimmerman 1976; Sudman et al. 2006), lending further support to the apparent differentiation of these animals. These geographically distinct lineages are characterized by genetic distances ($p = 16.72$ % for Cytb and 14.66 % for COI) that are larger than those reported here for pairs of established genera (e. g., *Pappogeomys-Orthogeomys*), suggesting that their inclusion within the single genus *Geomys* should be reconsidered and the more derived, western lineage potentially elevated to a distinct genus.

Geography of diversification within Geomyidae. No subgenera have been recognized in *Geomys*, but the analyses in the present study reveal a large p -distance between members of this genus from different sides of the Mississippi

Table 4. Average and range of genetic differences based on Cytb and COI within each of the taxa examined in the family Geomyidae. *Only one species has been sequenced. ** Only two species have been sequenced.

Taxa	Cytb	COI
	Average (Min – Max)	Average (Min – Max)
<i>Cratogeomys</i> (genus)	11.81% (4.64 - 15.08)	9.45% (2.59 - 11.96)
<i>Pappogeomys</i> (genus)	*	*
<i>Zygogeomys</i> (genus)	*	*
<i>Orthogeomys</i> (genus)	*	*
<i>Heterogeomys</i> (genus)	10.62% (3.91 – 17.67)	8.62% (6.84 - 10.96)
<i>Heterogeomys</i> (subgenus)	7.01%**	1.09%**
<i>Macrogeomys</i> (subgenus)	7.92% (3.91 - 11.31)	7.50% (6.77 - 8.69)
<i>Geomys</i> (genus)	13.58% (3.24 – 19.03)	11.76% (6.93 - 15.93)
<i>Geomys</i> (W Mississippi)	12.40% (4.90 – 19.03)	10.05% (6.93 – 13.34)
<i>Geomys</i> (E Mississippi)	*	*
<i>Thomomys</i> (genus)	16.09% (4.21 – 21.22)	14.40% (6.28 - 19.49)
<i>Megascapheus</i> (subgenus)	14.01% (4.21 - 18.21)	12.69% (6.29 - 15.61)
<i>Thomomys</i> (subgenus)	17.71% (7.01 – 20.08)	14.46% (12.74 – 16.12)

River. Animals from west of the river include the *bursarius* and *breviceps* species groups, while animals from east of the river include species in the *pinetis* group (Davis 1940; Hall 1981; Sudman et al. 2006). More broadly, patterns of evolutionary diversification differ markedly between the two recognized tribes of geomyids. While the Thomomyini contains two genera, the Geomyini consists of at least seven genera. The Geomyidae are typically considered to be a fast-evolving group, with much of their diversity emerging during the Late Miocene. This coincides with the expansion of open grass-dominated habitats during the Cenozoic (Strömberg 2011; Anderman et al. 2022), which may have facilitated diversification of these herbivorous rodents. Divergence within the Geomyidae is thought to have been driven by multiple factors, including fluctuations in climatic conditions and their impacts on vegetation, notably the relative expansions and contractions of forests versus grasslands (Castañeda-Rico et al. 2024). At the same time, geographic barriers have no doubt played a role in this dynamic, as has been suggested for the role of the Trans-Mexican Volcanic Belt (TMVB) in determining the distributional limits of multiple genera of geomyids and generating a unique habitat for species in the genera *Pappogeomys* and *Zygogeomys*. It seems likely that the Mississippi River has also functioned as an important geographic barrier, particularly within *Geomys*, which is the only currently recognized genus of pocket gophers to cross this river. Accordingly, it is not surprising that there are marked genetic and morphological differences between members of this genus located on the western versus eastern sides of this major riverine barrier.

Concluding thoughts. Based on our findings that members of the genus *Geomys* form two genetically distinct lineages that are separated by the Mississippi River, we suggest that formal revision of the genus is warranted, with attention to whether differences between these lineages are sufficient to justify recognition of each as a distinct genus. Our analyses are based on sequence data from two mitochondrial locus indicate that levels of genetic differentiation (p-distances) are greater than those for other pairs of genera within the Geomyidae. These differences are also supported by previous studies describing morphological differences between these lineages. We assert that, given these differences, the two lineages should be formally distinguished using taxonomic categories recognized by the ICZN (1999). We believe that elevation of the western lineage to genus status is more appropriate than description of the two lineages as species groups or complexes as the latter designations lack ICZN (1999) oversight and often add unnecessary complexity to efforts to resolve mammalian taxonomy (Tate 1933; Voss et al. 2014). At the same time, we recognize that an integrated approach—one that makes use of multiple data sets—is critical when diagnosing new taxonomic units. A formal revision of genera within the Geomyidae, in particular evaluation of our proposal that *Geomys* be divided into two genera, will benefit from examination of nuclear sequence data as well as empirical evaluation of apparent

morphological differences between lineages. More generally, significant revision is needed for other portions of the Geomyidae. Although our analyses have focused on generic level differences within this family, revision at other levels is also needed, such as a revision of species-level differentiation with *Thomomys*. We hope the analyses included here will provide the foundation for a more extensive and comprehensive revision of the taxonomy of the family Geomyidae. Given the ecological and evolutionary importance of these animals, a thorough understanding of their taxonomic diversity should generate critical insights into numerous aspects of mammalian biology.

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Appendix 1

SYSTEMATICS

We propose that pocket gophers in the family Geomyidae be classified into nine genera, as defined, diagnosed, and discussed in the following generic accounts. For the sake of reference completeness, the literature cited provides the full citations for each of the generic-level names ([Merriam 1895](#); [Elliot 1903](#)).

Tribe Thomomyini (Clade A)

Genus *Megascapheus* Elliot 1903

1903. *Megascapheus* Elliot, Field Columb. Mus., Publ. 76, Zool. Ser., 3(11):190. Type species. *Diplostoma bulbivorum* (Richardson, 1829).

Content. Thirteen allopatric species of *Megascapheus* are recognized: *Megascapheus atrovarius* (Allen, 1898), *Megascapheus baileyi* (Merriam, 1901), *Megascapheus bottae* (Eydoux and Gervais, 1836), *Megascapheus bulbivorus* (Richardson, 1829), *Megascapheus connectens* (Hall, 1936), *Megascapheus fulvus* (Woodhouse, 1852), *Megascapheus laticeps* (Baird, 1855), *Megascapheus nayarensis* (Mathis *et al.*, 2013), *Megascapheus nigricans* (Rhoads, 1895), *Megascapheus ruidosae* (Hall, 1932), *Megascapheus sheldoni* (Bailey, 1915), *Megascapheus townsendii* (Bachman, 1839), and *Megascapheus umbrinus* (Richardson, 1829).

Etymology. The name *Megascapheus* is derived from the Greek *Mega*, meaning “great” and *skapherus*, “a digger”: the great digger ([Jaeger 1955](#)).

Diagnosis. The species in the genus *Megascapheus* can be distinguished from those in the genus *Thomomys* by having the upper incisors procumbent and their root between the fourth upper premolars and the first upper molars; sphenoidal fissure open; angular process continuous, with a well-developed flange along the ventral ramus side; rostrum heavy; base of the first lower premolars inclined anteriorly; infraorbital canal openings anterior to the incisive foramina; anterior enamel plate of the first lower premolars not recurved; anterior enamel plate of the first lower premolars narrow and broadly separated from the lateral enamel plate on the lingual side; chromosome number of living forms from 74 to 82 ([Nelson and Goldman 1934](#); [Russell 1968a](#); [Álvarez-Castañeda 2024](#)).

Distribution. *Megascapheus* ranges from southern Oregon, Idaho, and Colorado southward through Michoacán, State of Mexico, Mexico City, Puebla, and Veracruz and eastward through New Mexico, Texas, Coahuila, Nuevo Leon, San Luis Potosí, and Veracruz.

Comments. *Megascapheus* and *Thomomys* were considered two subgenera of *Thomomys*, with clear morphological differences. Morphological and genetic data support considering these differences sufficient at the genus level. The subspecies of *M. fulvus* should be reviewed, increasing the number of sequences of the recognized subspecies to carry out a detailed analysis. The nomenclature used in the genus is supported in the studies of [Hall and Kelson \(1959\)](#), [Anderson \(1966, 1972\)](#), [Patton and Dingmen \(1968\)](#), [Thealer \(1968a, b, 1972, 1977, 1980\)](#), [Hoffmeister \(1969, 1986\)](#), [Patton \(1973, 1993, 2005\)](#), [Thaeler and Hinesley \(1979\)](#), [Patton and Smith \(1981, 1990\)](#), [Patton *et al.* \(1984\)](#), [Álvarez-Castañeda \(2010\)](#), [Hafner *et al.* \(2011\)](#), [Trujano-Álvarez and Álvarez-Castañeda \(2013\)](#), [Mathis *et al.* \(2013a, 2013b, 2014\)](#), [Álvarez-Castañeda *et al.* \(2017\)](#), and [Bradley *et al.* \(2023\)](#).

Morphological difference between *Megascapheus* in relation to *Thomomys* are: the upper incisors procumbent and their root between the fourth upper premolars and the first upper molars vs upper incisors not procumbent and their root above the fourth upper premolars; sphenoidal fissure open vs closed (except for some specimens of *T. clusius*); angular process continuous, with a well-developed flange along the ventral ramus side vs not continuous, with a weakly developed flange along the ventral ramus side; rostrum heavy vs rostrum slender; base of the first lower premolars inclined anteriorly vs nearly perpendicular to the occlusal surface of the toothrow; infraorbital canal openings anterior to the incisive foramina vs directly above or slightly posterior to the incisive foramina; anterior enamel plate of the first lower premolars not recurved vs recurved, frequently forming a shallow re-entrant angle; anterior enamel plate of the first lower premolars narrow and broadly separated from the lateral enamel plate on the lingual side, vs only slightly separated from the posterior enamel plate (rarely continuous), with the lateral enamel plate on the lingual side; chromosome number of living forms from 74 to 82 vs from 40 to 60 ([Nelson and Goldman 1934](#); [Russell 1968a](#); [Álvarez-Castañeda 2024](#)).

Megascapheus atrovarius (Allen, 1898)

(Southern pocket gopher, tuza de Sinaloa)

1898. *Thomomys atrovarius* (J. A. Allen), Bull. Amer. Mus. Nat. Hist., 10:148. Type locality “Tatemales (near Rosario), Sinaloa”.

2024. *Megascapheus atrovarius*: (this study).

1. *M. a. atrovarius* (Allen, 1898). For type locality see above. Range from the central Sinaloa coast south through northwestern Jalisco.

2. *M. a. parviceps* (Nelson and Goldman, 1934). Type locality "Chacala, 3000 ft., Durango". Known only from central and northeastern Sinaloa and western Durango.
3. *M. a. simulus* (Nelson and Goldman, 1934). Type locality "Alamos, 1200 ft., Sonora". Known only from southeastern Sonora and northeastern Sinaloa.
4. *M. a. sinaloae* (Merriam, 1901). Type locality "Altata, Sinaloa". Range in coastal central and northern Sinaloa.

Megascapheus baileyi (Merriam, 1901)

Southwestern Texas pocket gopher, tuza del suroeste de Texas

1901. *Thomomys baileyi* Merriam, Proc. Biol. Soc. Washington, 14:109. Type locality "Sierra Blanca, Hudspeth Co., Texas".

2024. *Megascapheus baileyi*: (this study).

1. *M. b. actuosus* (Kelson, 1951). Type locality " Corona, Lincoln Co., New Mexico". Known only from central New Mexico.
2. *M. b. analogus* (Goldman, 1938a). Type locality " Sierra Guadalupe, about 12 mi. S General Cepeda, Coahuila". Range in southeastern Coahuila, southwestern Coahuila, and Nuevo León.
3. *M. b. baileyi* (Merriam, 1901). For type locality see above. Known only from type locality.
4. *M. b. confinalis* (Goldman, 1936). Type locality " 35 mi. E Rock Springs, 2450 ft., Texas". Known only from Sutton County, southwestern Texas.
5. *M. b. cultellus* (Kelson, 1951). Type locality " Halls Peak, Mora Co., New Mexico". Known only from Mora County, northeastern New Mexico.
6. *M. b. guadalupensis* (Goldman, 1936). Type from McKittrick Canyon, 7800 ft., Guadalupe Mts., Texas." Known only from Guadalupe Mountains New Mexico and Texas.
7. *M. b. humilis* (Baker, 1953). Type locality " 3 mi. W Hda. San Miguel, 2200 ft., Coahuila". Known only from northern Coahuila.
8. *M. b. lachuguilla* (Bailey, 1902). Type locality " arid foothills near El Paso, El Paso Co., Texas". Range in southern New Mexico and western Texas.
9. *M. b. limitaris* (Goldman, 1936). Type locality "4 mi. W Boquillas, Brewster Co., Texas". Known only from southwestern Texas.
10. *M. b. limpiae* (Blair, 1939). Type locality " Limpia Canyon, 1 mi. N Fort Davis, 4700 ft., Jeff Davis Co., Texas". Known only from Jeff Davis County, western Texas.
11. *M. b. opulentus* (Goldman, 1935). Type locality " Las Palomas, on the Rio Grande, Sierra Co., New Mexico". Known only from Sierra County, central New Mexico.
12. *M. b. pectoralis* (Goldman, 1936). Type locality "Vicinity of Carlsbad Cave, Carlsbad Cave National Monument, Eddy Co., New Mexico". Known only from Carlsbad Cave National Monument.
13. *M. b. pervagus* (Merriam, 1901). Type locality "Española, Rio Arriba Co., New Mexico". Known from northern New Mexico.
14. *M. b. retractus* (Baker, 1953). Type locality "Fortin, 3300 ft., 20 mi. N, 2 mi. E San GerOnimo, Coahuila". Known only from northern Coahuila.
15. *M. b. robertbakeri* (Beauchamp-Martin *et al.* 2019). Type locality "2.5 mi. E McCamey, Upton County, Texas". Known only from southern-central Texas.
16. *M. b. scotophilus* (Davis, 1940). Type locality "1 1/2 W Bat Cave, Sierra Diablo, Hudspeth Co., Texas. Known only from Sierra Diablo Texas.
17. *M. b. spatiosus* (Goldman, 1938). Type locality "Alpine, 4500 ft., Brewster Co., Texas". Known only from Brewster County, western Texas.
18. *M. b. sturgisi* (Goldman, 1938a). Type locality "Sierra del Carmen, 6000 ft., Coahuila". Range from central Coahuila to northwestern Coahuila.
19. *M. b. texensis* (Bailey, 1902). Type locality "head of Limpia Creek, 5500 ft., Davis Mts., Jeff Davis Co., Texas". Known only from southwestern Texas.
20. *M. b. tularosae* (Hall, 1932). Type locality "Cook Ranch, 1/2 mi. W Tularosa, Otero Co., New Mexico". Known only from Tularosa are in New Mexico.
21. *M. b. villai* (Baker, 1953). Type locality "7 mi. S, 2 mi. E Boquillas, 1800 ft., Coahuila". Known only from type locality.

Megascapheus bottae (Eydoux and Gervais, 1836)

Botta's pocket gopher, tuza del norte

1836. *Oryctomys (Saccophorus) bottae* Eydoux and Gervais, Mag. de Zool., Paris, 6:23. Type locality "Coast of California"; name applied by Baird (Proc. Acad. Nat. Sci. Philadelphia, 7:335) to the gopher occurring in vie. Monterey.

1966. *Thomomys bottae*: Anderson, Syst. Zool., 15:192.

2024. *Megascapheus bottae*: (this study).

1. *M. b. bottae* (Eydoux and Gervais, 1836). For type locality see above. Range in western coast of California from San Francisco Bay south through Ventura County.
2. *M. b. mewa* (Merriam, 1908). Type locality "Raymond, Madera Co., California". Known only from Maderas County, central California.
3. *M. b. navus* (Merriam, 1901). Type locality "Red Bluff, Tehama Co., California". Known only from Tehama County, northern California.
4. *M. b. pascalis* (Merriam, 1901). Type locality "Fresno, San Joaquin Valley, Fresno Co., California". Known only from Fresno County, central California.

Megascapheus bulbivorus (Richardson, 1829)

Camas pocket gopher, tuza del Valle de Camas

1829. *Diplostoma bulbivorum* Richardson, Fauna Boreali Americana, 1:206. Type locality "Banks of the Columbia River, Oregon," probably Portland, the only place near the Columbia River where it has been taken since. The type was reported as in the Hudson Bay Museum but has not been found (*vide* V. Bailey, N. Amer. Fauna, 39:40, November 15, 1915).

1855. *Thomomys bulbivorus*: Beiträge zur nähern Kenntniss der Säugethiere Russland's. St. Pétersburg Acad. Sci. Mem., 9:188.

2024. *Megascapheus bulbivorus*: (this study).

Megascapheus connectens (Hall, 1936)

(New Mexico pocket gopher, tuza de Nuevo Mexico)

1936. *Thomomys umbrinus connectens* Hall, Jour. Washington Acad. Sci., 26:296. Type locality "Clawson Dairy, 5 mi. N Albuquerque, 4943 ft., Bernalillo Co., New Mexico". Known only from Bernalillo County, New Mexico.

2024. *Megascapheus connectens*: (this study).

Megascapheus fulvus (Woodhouse, 1852)

Fulvus pocket gopher, tuza del suroeste

1852. *Geomys fulvus* Woodhouse, Proc. Acad. Nat. Sci. Philadelphia, 6:201. Type locality "San Francisco Mtn., Coconino Co., Arizona".

2010. *Thomomys fulvus*: Álvarez-Castañeda, Mol. Phylog. Evol., 54:679.

2024. *Megascapheus fulvus*: (this study).

1. *M. f. abstrusus* (Hall and Davis, 1935). Type locality "Fish Spring Valley, 2 mi. SE Tulle Peak, 7000 ft., Nye Co., Nevada". Known only from Nye County, southern Nevada.
2. *M. f. albicaudatus* (Hall, 1930). Type locality "Provo, 4510 ft., Utah Co., Utah". Known only from Utah County, central Utah.
3. *M. f. alexandrae* (Goldman, 1933b). Type locality "plain 5 mi. SW Rainbow Lodge, near Navajo Mtn., 6200 ft., Coconino Co., Arizona". Known only from Coconino County, northern Arizona.
4. *M. f. alpinus* (Merriam, 1897). Type locality "Big Cottonwood Meadows, 10,000 ft., 8 mi. SE Mt. Whitney peak, High Sierra, Inyo Co., California". Known only from Mount Whitney, Inyo County, western California.
5. *M. f. angustidens* (Baker, 1953). Type locality "Sierra del Pino, 5250 ft., 6 mi. N, 6 mi. W Acebuches, Coahuila". Known only from Sierra del Pino, Coahuila.
6. *M. f. apache* (Bailey, 1910). Type locality "Lake La Jara, 7500 ft., Jicarilla Apache Indian Reservation, New Mexico". Known only from Sandoval County, northern New Mexico.
7. *M. f. aureiventris* (Hall, 1930). Type locality "Fehlman Ranch, 3 mi. N Kelton, 4225 ft., Boxelder Co., Utah". Known only from Box Elder County, northern Utah.

8. *M. f. aureus* (Allen, 1893). Type locality " Bluff City, San Juan Co., Utah". Known only from San Juan County, southwestern Utah.
9. *M. f. basilicae* (Benson and Tillotson, 1940). Type locality " La Misión, 2 mi. W Magdalena, Sonora". Known only from central Sonora.
10. *M. f. birdseyei* (Goldman, 1937a). Type locality " Pine Valley Mts., 5 mi. E Pine Valley, 8300 ft, Washington Co., Utah". Restricted to Washington County, southwestern Utah.
11. *M. f. bonnevilliei* (Durrant, 1946). Type locality " Fish Springs, 4400 ft., Juab Co., Utah". Known only from Juab County, western Utah.
12. *M. f. brevidens* (Hall, 1932a). Type locality " Breen Creek, 7000 ft., Kawich Range, Nye Co., Nevada". Known only from Nye County, southern Nevada.
13. *M. f. camoae* (Burt, 1937). Type locality " Camoa, Rio Mayo, Sonora". Known only from central-southern coast Sonora.
14. *M. f. canus* (Bailey, 1910). Type locality " Deep Hole, N end Smoke Creek Desert, Washoe Co., Nevada". Known only from Smoke Creek Desert, Washoe County, northwestern Nevada.
15. *M. f. catalinae* (Goldman, 1931). Type locality " Swnmerhaven, Santa Catalina Mts., 7500 ft., Pima Co., Arizona". Known only from Pima County, southern Arizona.
16. *M. f. cervinus* (Allen, 1895). Type locality " Phoenix, Maricopa Co., Arizona". Known only from Maricopa County, southwestern Arizona.
17. *M. f. cinereus* (Hall, 1932a). Type locality " West Walker River, Smiths Valley, 4700 ft., Lyon Co., Nevada". Known only from Lyon County, Nevada.
18. *M. f. collis* (Hooper, 1940). Type locality " Shuman's Ranch, 30 mi. S Grants, sec. 30, T. 6 N, R. 10 W, Valencia Co., New Mexico". Known only from Valencia County, western New Mexico.
19. *M. f. concisor* (Hall and Davis, 1935). Type locality " Pott's Ranch, 6900 ft., Monitor Valley, Nye Co., Nevada". Known only from Nye County, southern Nevada.
20. *M. f. contractus* (Durrant, 1946). Type locality " Scipio, 5315 ft., Millard Co., Utah". Known only from Millard County, western Utah.
21. *M. f. convergens* (Nelson and Goldman, 1934)". Type locality " Costa Rica Ranch, delta Sonora River, SW of Hermosillo, Sonora". Known only from the Sonora River delta, Sonora.
22. *M. f. convexus* (Durrant, 1939). Type locality " E side Clear Lake, 4600 ft., Millard Co., Utah". Known only from Millard County, western Utah.
23. *M. f. cultellus* (Kelson, 1951). Type locality " Halls Peak, Mora Co., New Mexico". Known only from Mora County, northeastern New Mexico.
24. *M. f. curtatus* (Hall, 1932a). Type locality " San Antonio, 5400 ft., Nye Co., Nevada". Known only from Nye County, southern Nevada.
25. *M. f. depressus* (Hall, 1932a). Type locality " Dixie Meadows (at S end Humboldt Salt Marsh), 3500 ft., Churchill Co., Nevada". Known only from Churchill County, western Nevada.
26. *M. f. desertorum* (Merriam, 1901). Type locality " Mud Spring, Detrital Valley, Mohave Co., Arizona". Known only from Detrital Valley, Mohave Country, southeastern Arizona.
27. *M. f. dissimilis* (Goldman, 1931). Type locality " E slope Mt. Ellen, 8000 ft., Henry Mts., Garfield Co., Utah". Known only from Garfield County, southern Utah.
28. *M. f. divergens* (Nelson and Goldman, 1934). Type locality " 4 mi. W Huachinera, 4000 ft., Rio Bavispe, Sonora". Known only from Huachinera, eastern Sonora.
29. *M. f. estanciae* (Benson and Tillotson, 1939). Type locality " La Estancia, 6 mi. N Nacori, Sonora". Known only from Nacori, eastern Sonora.
30. *M. f. fulvus* (Woodhouse, 1852). For type locality see above. Range from central Arizona to western New Mexico.
31. *M. f. fumosus* (Hall, 1932a). Type locality " Milman Ranch, Moores Creek, 19 mi. SE Millett P.O., Nye Co., Nevada". Known only from Nye County, southern Nevada.
32. *M. f. howelli* (Goldman, 1936). Type locality " Grand Junction, 4600 ft., Mesa Co., Colorado". Known only from Mesa County, western Colorado.
33. *M. f. internatus* (Goldman, 1936). Type locality " Salida, 7000 ft., Chaffee Co., Colorado". Known only from Chaffee County, southern Colorado.

34. *M. f. lacrymalis* (Hall, 1932a). Type locality " Arlemont [Chiatovich Ranch, Fish Lake Valley], 4900 ft., Esmeralda Co., Nevada". Known only from Esmeralda County, western Nevada.
35. *M. f. latus* (Hall and Davis, 1935). Type locality " Cherry Creek, 6500 ft., White Pine Co., Nevada". Known only from White Pine County, eastern Nevada.
36. *M. f. lenis* (Goldman, 1942). Type locality " Richfield, 5308 ft., Sevier Co., Utah". Known only from Sevier County, central Utah.
37. *M. f. levidensis* (Goldman, 1942). Type locality " Manti, about 5500 ft., Sanpete Co., Utah". Known only from Sanpete County, central Utah.
38. *M. f. lucrificus* (Hall and Durham, 1938)". Type locality " Eastgate, Churchill Co., Nevada". Known only from Churchill County, western Nevada.
39. *M. f. mearnsi* (Bailey, 1914). Type locality " Grays Ranch, 5000 ft., Animas Valley, Grant Co., New Mexico". Known only from the southwest corner of New Mexico.
40. *M. f. minimus* (Durrant, 1939). Type locality " Stansbury Island, Great Salt Lake, Tooele Co., Utah". Known only from Tooele County, northwestern Utah.
41. *M. f. modicus* (Goldman, 1931). Type locality " La Osa (near Mexican boundary), southern end of Altar Valley, Pima Co, Arizona". Known only from northern Sonora.
42. *M. f. morulus* (Hooper, 1940). Type locality " Bill Porter's Ranch, 8 mi. SE Paxton, Valencia Co., New Mexico". Only known of Cibola County, western New Mexico.
43. *M. f. nanus* (Hall, 1932a). Type locality " S end Belted Range, 5½ mi. NW White Rock Spring, 7200 ft, Nye Co., Nevada". Known only from Nye County, southern Nevada.
44. *M. f. nesophilus* (Durrant, 1936). Type locality " Antelope Island, Great Salt Lake, Davis Co., Utah". Known only from Antelope Island, Davis County, northern Utah.
45. *M. f. operarius* (Merriam, 1897). Type locality " Keeler, E side Owens Lake, Inyo Co., California". Only known from Inyo County, eastern California.
46. *M. f. operosus* (Hatfield, 1942). Type locality " Peoples Valley, 4400 ft., 6 mi. N Yarnell, Yavapai Co., Arizona". Known only from Yavapai County, central Arizona.
47. *M. f. optabilis* (Goldman, 1936). Type locality " Coventry, 6500 ft., Montrose Co., Colorado". Known only from Montrose County, western Colorado.
48. *M. f. osgoodi* (Goldman, 1931). Type locality " Hanksville, Wayne Co., Utah". Known only from Wayne County, central Utah.
49. *M. f. paguatae* (Hooper, 1940). Type locality " ½ mi. N Cebolleta (Seboyeta P.O.), Valencia Co., New Mexico". Known only from Valencia County, western central New Mexico.
50. *M. f. perampus* (Goldman, 1931). Type locality "Wheatfields Creek, 7000 ft. [about 27 mi. E Chin Lee], W slope Tunitcha Mts., Apache Co., Arizona". Known only from Apache County, northwestern Arizona.
51. *M. f. perditus* (Merriam, 1901). Type locality "Lampazos, Nuevo León". Range from eastern Coahuila and western Nuevo León.
52. *M. f. perpallidus* (Merriam, 1886). Type locality "Palm Springs, Riverside Co., California". Known only from Riverside County, southern California.
53. *M. f. pervagus* (Merriam, 1901). Type locality "Española, Rio Arriba Co., New Mexico". Known only from Rio Arriba and Santa Fe counties, northern New Mexico.
54. *M. f. phelleoecus* (Burt, 1933). Type locality "Hidden Forest, 8500 ft., Sheep Mts., Clark Co., Nevada". Known only from Clark County, southern Nevada.
55. *M. f. pinalensis* (Goldman, 1938b). Type locality "Oak Flat, 5 mi. E Superior, Pinal Mts., Pinal Co., Arizona". Known only from Gila County, central Arizona.
56. *M. f. planirostris* (Burt, 1931). Type locality "Zion National Park, Washington Co., Utah". Known only from Washington County, southwestern Utah.
57. *M. f. planorum* (Hooper, 1940). Type locality "1 ½ mi. SW San Mateo, Valencia Co., New Mexico". Known only from Valencia County, western-central New Mexico.
58. *M. f. powelli* (Durrant, 1955). Type locality "Hall Ranch, Salt Gulch, 8 mi. W Boulder, 6000 ft., Garfield Co., Utah". Known only from Garfield County, southern Utah.
59. *M. f. pusillus* (Goldman, 1931). Type locality "Coyote Mis., 3000 ft., Pima Co., Arizona". Known only from Pima County, southern Arizona.

60. *M. b. riparius* (Grinnell and Hill, 1936a). Type locality "Blythe, Riverside Co., California". Known only from Riverside County, southern California.
61. *M. f. robustus* (Durrant, 1946). Type locality "Orr's Ranch, 4300 ft., Skull Valley, Tooele Co., Utah". Known only from Tooele County, northwestern Utah.
62. *M. f. sevieri* (Durrant, 1946). Type locality "Swasey Spring, 6500 fl., House Mtn., Millard Co., Utah". Known only from Millard County, western Utah.
63. *M. f. solitarius* (Grinnell, 1926). Type locality "Fingerrock Wash, 5400 ft., Stewart Valley, Mineral Co., Nevada". Known only from Mineral County, western Nevada.
64. *M. f. stansburyi* (Durrant, 1946). Type locality "South Willow Creek, Stansbury Mts., 7500 ft., Tooele Co., Utah". Known only from Tooele County, northwestern Utah.
65. *M. f. subsimilis* (Goldman, 1933). Type locality "Harquahala Mt., 3000 ft., Yuma Co., Arizona". Known only from Yuma County, southwestern Arizona.
66. *M. f. tivius* (Durrant, 1937). Type locality "Oak Creek Canyon, 6 mi. E Oak City, 6000 ft., Millard Co., Utah". Known only from Millard County, western Utah.
67. *M. f. toltecus* (Allen, 1893). Type locality "Colonia Juarez, 4500 ft., Casas Grandes River, Chihuahua". Range from southern New Mexico and northern Chihuahua.

Megascapheus laticeps (Baird, 1855)

Northern California pocket gopher, tuza del norte de California

1855. *Thomomys laticeps* Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:335. Type locality. Humboldt Bay, Humboldt Co., California.

2024. *Megascapheus laticeps*: (this study).

1. *M. l. agriculturalis* (Grinnell, 1935). Type locality "Stralock Farm, 3 mi. W Davis, Yolo Co., California". Known only from Yolo County, California.
2. *M. l. awahnee* (Merriam, 1908). Type locality "Yosemite Valley, 4000 ft., near old Sentinel Hotel, Mariposa Co., California". Range in southern Sierra Nevada, California.
3. *M. l. detumidus* (Grinnell, 1935). Type locality "1 1/2 mi. S (town of) Pistol River, 250 ft., Curry Co., Oregon". Known only from Curry County, Oregon.
4. *M. l. laticeps* (Baird, 1855). For type locality see above. Range from Humboldt County, California north through southern Oregon.
5. *M. l. leucodon* (Merriam, 1897). Type locality "Grant Pass, Rogue River Valley, Oregon". Range in highlands around the northern Central Valley, California, and southwestern Oregon.
6. *M. l. saxatilis* (Grinnell, 1934). Type locality "1 mi. N Susan-ville, 4400 ft., Lassen Co., California". Known only from Lassen County, California.

Megascapheus nayarensis (Mathis *et al.*, 2013)

Nayarit pocket gopher, tuza del Nayar

2013. *Thomomys nayarensis* Mathis, Hafner, Hafner, and Demastes; Jour. Mamm 94:989. Type locality. 8.5 km N, 7 km W Mesa del Nayar (formerly listed by Hafner *et al.* [2011] as "22 km S, 3 km E Santa Teresa), 2,200 m (22.290, _104.721), Nayarit, México".

2024. *Megascapheus nayarensis*: (this study).

Megascapheus nigricans (Rhoads, 1895)

California pocket gopher, tuza de Baja California

1895. *Thomomys fulvus nigricans* Rhoads; Proc. Acad. Nat. Sci. Philadelphia, 47:36. Type locality. Witch Creek, 2753 ft., 7 mi. W Julian, San Diego Co., California.

2013. *Thomomys nigricans*: Trujano-Álvarez and Álvarez-Castañeda, Zool. Jour. Linn. Soc. 168:886.

2024. *Megascapheus nigricans*: (this study).

1. *M. n. anitae* (Allen, 1898). Type locality "Santa Anita, Baja California [Sur]". Range from southern Vizcaino Desert south to the southern tip of Baja California Peninsula.

2. *M. n. martirensis* (Allen, 1898). Type locality "La Grulla Meadow, Sierra San Pedro Mártir, 7400 ft., Baja California". Range from Sierra Juárez south through the Central Desert, Baja California.
3. *M. n. nigricans* (Rhoads, 1895). For type locality see above. Known only from southern California and northwestern Baja California.
4. *M. n. russeolus* (Nelson and Goldman, 1909). Type locality "San Angel, WSW San Ignacio, Baja California". Known only from the Vizcaíno Desert, northern Baja California Sur, and southern Baja California.

Megascapheus ruidosae (Hall, 1932)

Ruidoso pocket gopher, tuza de Ruidoso

1932. *Thomomys umbrinus ruidosae* Hall, Proc. Biol. Soc. Washington, 45:96. Type locality "Ruidoso, 6700 ft., Lincoln Co., New Mexico.
2024. *Megascapheus ruidosae*: (this study).

Megascapheus sheldoni (Bailey, 1915)

Sheldon's pocket gopher, tuza de la Sierra Madre

1915. *Thomomys sheldoni* V. Bailey, N. Amer. Fauna, 39:93, November 15. Type locality "Santa Teresa, 6800 ft., Sierra del Nayarit, Nayarit".

2024. *Megascapheus sheldoni*: (this study).

1. *M. s. chihuahuae* (Nelson and Goldman, 1934). Type locality "Sierra Madre, 7000 ft., about 65 mi. E Batopilas, Chihuahua". Known only from the Sierra Madre Occidental highlands, Chihuahua.
2. *M. s. sheldoni* (Bailey, 1915). For type locality see above. Known only from the Sierra Madre Occidental highlands, western Durango, northeastern Nayarit, and western Zacatecas.

Megascapheus townsendii (Bachman, 1839)

Townsend's pocket gopher, tuza de las montañas del oeste

1839. *Geomys townsendii* Bachman, Jour. Acad. Nat. Sci. Philadelphia, 8:105. Type locality. Erroneously given as "Columbia River," but probably near Nampa, Canyon Co., Idaho, where Townsend's party camped to trade with Indians, August 22, 1834 (V. Bailey, N. Amer. Fauna, 39:42, November 15, 1915).

1968. *Thomomys townsendii*: Thaler, Univ. California Pub. Zool. 86.

2024. *Megascapheus townsendii*: (this study).

1. *M. t. nevadensis* (Merriam, 1897). Type locality "Reese River Valley, 5 mi. W Austin, Lander Co., Nevada". Central-northern Nevada, southeastern Oregon, and California.
2. *M. t. townsendii* (Bachman, 1839). For type locality see above. Known only from Snake River, western Idaho, and eastern Oregon.

Megascapheus umbrinus (Richardson, 1829)

Southern pocket gopher, tuza mexicana

1829. *Geomys umbrinus* Richardson, Fauna Boreali-Americana, 1:202. Type locality "southern México; probably vic. Boca del Monte, Veracruz"; type said to have come from "Cadadaguois, a town in southwestern Louisiana"; see V. Bailey, Proc. Biol. Soc. Washington, 19:3-6, January 29, 1906.

1855. *Thomomys umbrinus*: Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:332.

2024. *Megascapheus umbrinus*: (this study).

1. *M. u. durangi* (Nelson and Goldman, 1934). Type locality "Durango, Durango". Range from southwestern Durango to extreme northwestern Zacatecas.
2. *M. u. goldmani* (Merriam, 1901). Type locality "Mapimi, 3800 ft., Durango". Range in central Chihuahua south through central-eastern Durango and southwestern Coahuila.
3. *M. u. intermedius* (Mearns, 1897). Type locality "summit Huachuca Mts., 9000 ft., Arizona". Range from southeastern Arizona south through Sonora and northwestern Chihuahua.
4. *M. u. umbrinus* (Richardson, 1829). For type locality see above. Range from eastern-central Zacatecas south through the Eje Neovolcánico in Veracruz.

Thomomys Wied-Neuwied, 1839

1839. *Thomomys* Wied-Neuwied, Nova Acta Phys.-Med. Acad. Caesar. Leop.-Carol., 19(pt. 1):377. Type species. *Thomomys rufescens* Wied-Neuwied, 1839.

Content. Five allopatric species of *Thomomys* are recognized: *Thomomys clusius* Coues, 1875, *Thomomys idahoensis* Merriam, 1901, *Thomomys mazama* Merriam, 1897, *Thomomys monticola* J. A. Allen, 1893, and *Thomomys talpoides* (Richardson, 1828).

Etymology. The name *Thomomys* is derived from the Greek *thomos*, meaning “pile”, and *mys*, “mouse”: related to the pile of earth accumulated at the entrance of its burrows.

Diagnosis. The species of the genus *Thomomys* can be distinguished from those of *Megascapheus* by having the upper incisors no procumbent and their root above the fourth upper premolars; sphenoidal fissure close (except for some specimens of *T. clusius*); angular process not continuous, with a weakly-developed flange along the ventral ramus side; rostrum slender; base of the first lower premolars nearly perpendicular to the occlusal surface of the toothrow; infraorbital canals opening directly above or slightly posterior to the incisive foramina; anterior enamel plate of the first lower premolars recurved, frequently forming a shallow re-entrant angle; anterior enamel plate of the first lower premolars broad and only slightly separated from the posterior enamel plate (rarely continuous), with the lateral enamel plate on the lingual side; diploid chromosome numbers from 40 to 60 (Nelson and Goldman 1934; Russell 1968a; Álvarez-Castañeda 2024).

Distribution. *Thomomys* ranges from southern British Columbia, Alberta, Saskatchewan, and Manitoba southward through California, Nevada, Arizona, and New Mexico; eastward through North Dakota, South Dakota, Nebraska, and Colorado; and from Washington, Oregon, and California east through Manitoba, eastern North Dakota, and South Dakota, southwestern Nebraska, eastern Colorado, and central New Mexico.

Comments. Thaeler (1980) suggests that the current *T. talpoides* could be split into 10–12 separate species. The genetic data show that *T. talpoides* is a species complex and should be reviewed in detail.

Thomomys clusius Coues, 1875

Wyoming pocket gopher, tuza de Wyoming

1875. *Thomomys clusius* Coues, Proc. Acad. Nat. Sci. Philadelphia 27:138. Type locality “Bridger Pass, 18 mi. SW Rawlins, Carbon Co., Wyoming”.

Thomomys idahoensis Merriam, 1901

Idaho pocket gopher, tuza de Idaho

1901. *Thomomys idahoensis* Merriam, Proc. Biol. Soc. Washington, 14:114. Type locality “Brich Creek, Clark Co., Idaho”.

1. *T. i. confinis* Davis, 1937. Type locality “Gird Creek, near Hamilton, Ravalli Co., Montana”. Known only from Ravalli County, Montana.
2. *T. i. idahoensis* Merriam, 1901. For type locality see above. Range in southeastern Idaho and southwestern Montana.
3. *T. i. pygmaeus* Merriam, 1901. Type locality “Montpelier Creek, 6700 ft., about 10 mi. NE Montpelier, Bear Lake Co., Idaho”. Range in southwestern Wyoming and southeastern Idaho.

Thomomys mazama Merriam, 1897

Western pocket gopher, tuza del oeste

1897. *Thomomys mazama* Merriam, Proc. Biol. Soc. Washington, 11:214. Type locality “Anna Creek, 6000 ft., near Crater Lake, Mt. Mazama, Klamath Co., Oregon”.

1. *T. m. couchi* Goldman, 1939. Type locality “4 mi. N Shelton, Mason Co., Washington”. Known only from Mason County, Washington.
2. *T. m. glacialis* Dalquest and Scheffer, 1942. Type locality “prairie 2 mi. S Roy, Pierce Co., Washington”. Known only from Pierce County, Washington.
3. *T. m. helleri* Elliot, 1903. Type locality “Goldbeach, mouth of Rogue River, Curry Co., Oregon”. Known only from Curry County, Oregon.
4. *T. m. hesperus* Merriam, 1901. Type locality “Tillamook, Tillamook Co., Oregon”. Range in coastal area of northwestern Oregon.
5. *T. m. louiei* Gardner, 1950. Type locality “12 mi, NNE Cathlamet (Crown-Zellerbach's Cathlamet Tree Farm), 2500 ft., Wahkiakum Co., Washington”. Known only from Wahkiakum County, Washington.

6. *T. m. mazama* Merriam, 1897. For type locality see above. Range in central-western Oregon and northern California.
7. *T. m. melanops* Merriam, 1899. Type locality "timberline at head Soledue River, Olympic Mts., Clallam Co., Washington". Range in northern Olympia peninsula, Washington.
8. *T. m. nasicus* Merriam, 1897. Type locality "Farewell Bend, Deschutes River, Deschutes Co., Oregon". Known only from central-western Oregon.
9. *T. m. niger* Merriam, 1901. Type locality "Seaton (= Mapleton), near mouth Umpqua River (= head tidewater, Siuslaw River), Lane Co., Oregon". Known only from Benton and Lane Counties, Oregon.
10. *T. m. oregonus* Merriam, 1901. Type locality "Ely, near Oregon City, Willamette Valley, Clackamas Co., Oregon". Known only from northwestern Oregon.
11. *T. m. premaxillaris* Grinnell, 1914. Type locality "2 mi. S South Yolla Bolly Mtn., 7500 ft., Tehama Co., California". Known only from Tehama County, California.
12. *T. m. pugetensis* Dalquest and Scheffer, 1942. Type locality "3 mi. S Olympia, Thurston Co., Washington". Known only from Thurston County, Washington.
13. *T. m. tacomensis* Taylor, 1919. Type locality "6 mi. S Tacoma, Pierce Co., Washington". Known only from Tacoma County, Washington.
14. *T. m. tumuli* Dalquest and Scheffer, 1942. Type locality "7 mi. N Tenino, Thurston Co., Washington". Known only from Thurston County, Washington.
15. *T. m. yelmensis* Merriam, 1899. Type locality "Tenino, Yelm Prairie, Thurston Co., Washington". Known only from Thurston County, Washington.

Thomomys monticola J. A. Allen, 1893

Mountain pocket gopher, tuza de las montañas

1893. *Thomomys monticola* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 5:48. Type locality "Mt. Tallac, 7500 ft., El Dorado Co., California".

Thomomys talpoides (Richardson, 1828)

Northern pocket gopher, tuza del norte

1828. *Cricetus talpoides* Richardson, Zool. Jour., 3:518. Type locality "Fixed at near Fort Carlton (Carlton House), Saskatchewan River, Saskatchewan, Canada".

1858. *Thomomys talpoides*: Baird, Mammals, in Repts. Expl. Surv., 8(1):403.

1. *T. t. aequalidens* Dalquest, 1942. Type locality "Abel Place, 2200 ft., 6 mi. SSE Dayton, Columbia Co., Washington". Known only from southeastern Oregon.
2. *T. t. agrestis* Merriam, 1908. Type locality "Medano Ranch, San Luis Valley, Colorado". Known only from southern-central Colorado.
3. *T. t. andersoni* Goldman, 1939. Type locality "Medicine Hat, South Saskatchewan River, Alberta". Known only from southwestern Alberta.
4. *T. t. attenuatus* Hall and Montague, 1951. Type locality "3½ mi. W Horse Creek P.O., 7000 ft., Laramie Co., Wyoming". Range in southeastern Wyoming and northeastern Colorado.
5. *T. t. bridgeri* Merriam, 1901. Type locality "Harvey's Ranch, Smith Fork, 6 mi. SW Old Fort Bridger, Uinta Co., Wyoming". Range in southeastern Idaho, western and southwestern California.
6. *T. t. bullatus* Bailey, 1914. Type locality "Powderville, Custer Co., Montana". Range in southern Saskatchewan, eastern Montana, and northeastern Wyoming.
7. *T. t. caryi* Bailey, 1914. Type locality "head Trapper Creek, 9500 ft., Bighorn Mts., Bighorn Co., Wyoming". Range in central-northern Wyoming and southern-central Montana.
8. *T. t. cheyennensis* Swenk, 1941. Type locality "2 mi. S Dalton, Cheyenne Co., Nebraska". Known only from western Nebraska.
9. *T. t. cognatus* Johnstone, 1955. Type locality "Crowsnest Pass, British Columbia". Known only from southeastern British Columbia.
10. *T. t. columbianus* Bailey, 1914. Type locality "Touchet, Walla Walla Co., Washington". Known only from northern-central Oregon.

11. *T. t. devexus* Hall and Dalquest, 1939. Type locality "1 mi. WSW Neppel, Grant Co., Washington". Known only from central-southeastern Washington.
12. *T. t. douglasii* (Richardson, 1829). Type locality "near mouth Columbia River, probably near Vancouver, Washington". Known only from southwestern Washington.
13. *T. t. durranti* Kelson, 1949. Type locality "Johnson Creek, 14 mi. N Blanding, 7500 ft., San Juan Co., Utah". Range in eastern Idaho and western-central Colorado.
14. *T. t. falcifer* Grinnell, 1926. Type locality "Bells Ranch, 6890 ft., Reese River Valley, Nye Co., Nevada". Known only from central Nevada.
15. *T. t. fisheri* Merriam, 1901. Type locality "Beckwith, Sierra Valley, Plumas Co., California". Range in western California and eastern Nevada.
16. *T. t. fossor* Allen, 1893. Type locality "Florida, 7200 ft., La Plata Co., Colorado". Range in northeastern Arizona, southwestern Colorado, and northern New Mexico.
17. *T. t. fuscus* Merriam, 1891. Type locality "Summit Creek in mountains, head Big Lost River, Custer Co., Idaho". Known only from central Idaho.
18. *T. t. gracilis* Durrant, 1939. Type locality "Pine Canyon, 6600 ft., 17 mi. NW Kelton, Boxelder Co., Utah". Range in northwestern Idaho, northern, central, and northeastern Nevada.
19. *T. t. immunis* Hall and Dalquest, 1939. Type locality "5 mi. S Trout Lake, Klickitat Co., Washington". Known only from central-southern Washington.
20. *T. t. incensus* Goldman, 1939. Type locality "Shuswap, Yale District, British Columbia". Known only from southern British Columbia.
21. *T. t. kaibabensis* Goldman, 1938. Type locality "De Motte Park, 9000 ft., Kaibab Plateau, Coconino Co., Arizona". Known only from northern-central Arizona.
22. *T. t. kelloggi* Goldman, 1939. Type locality "West Boulder Creek, Absaroka Mts., 18 mi. SE Livingston, Park Co., Montana". Known only from Park County, Montana.
23. *T. t. levis* Goldman, 1938. Type locality "Seven Mile. Flat, 10,000 ft., 5 mi. N Fish Lake, Fish Lake Plateau, Sevier Co., Utah". Known only from central Idaho.
24. *T. t. limosus* Merriam, 1901. Type locality "White Salmon, Gorge of the Columbia, Klickitat Co., Washington". Known only from southern Washington.
25. *T. t. loringi* Bailey, 1914. Type locality "South Edmonton, Alberta". Known only from central-western Alberta.
26. *T. t. macrotis* Miller, 1930. Type locality "D' Arey Ranch, 2 mi. N Parker, Douglas Co., Colorado". Known only from Douglas County, Colorado.
27. *T. t. medius* Goldman, 1939. Type locality "Silver King Mine, summit Toad Mtn., 6 mi. S Nelson, West Kootenay District, British Columbia". Known only from southeastern British Columbia.
28. *T. t. meritus* Hall, 1951. Type locality "8 mi. N, 19½ mi. E Savery, 8800 ft., Carbon Co., Wyoming". Known only from central-northern Colorado.
29. *T. t. monoensis* Huey, 1934. Type locality "Dexter Creek Meadow, 6800 ft., at confluence Dexter and Wet creeks, Mono Co., California". Range in eastern California and western Nevada.
30. *T. t. moorei* Goldman, 1938. Type locality "1 mi. S Fairview, 6000 ft., Sanpete Co., Utah". Known only from central Utah.
31. *T. t. nebulosus* Bailey, 1914. Type locality "Jack Boyden's Ranch, 3750 ft., Sand Creek Canyon, 15 mi. NE Sundance, Crook Co., Wyoming". Range in western South Dakota and eastern Wyoming.
32. *T. t. ocius* Merriam, 1901. Type locality "Mountainview, Smiths Fork, 4 mi. (by airline) SE Fort Bridger, Uinta Co., Wyoming". Range in southwestern Wyoming, northwestern Colorado, and northeastern Utah.
33. *T. t. oquirrhensis* Durrant, 1939. Type locality "Settlement Creek, 6500 ft., Oquirrh Mts., Tooele Co., Utah". Known only from central-northern Utah.
34. *T. t. parowanensis* Goldman, 1938. Type locality "Brian Head, 11,000 ft., Parowan Mts., Iron Co., Utah". Known only from southern Utah.
35. *T. t. pierreicolus* Swenk, 1941. Type locality "Wayside, Dawes Co., Nebraska". Known only from western Nebraska.
36. *T. t. pryori* Bailey, 1914. Type locality "head Sage Creek, 6000 ft., Pryor Mts., Carbon Co., Montana". Known only from southern Montana.

37. *T. t. quadratus* Merriam, 1897. Type locality "The Dalles, Wasco Co., Oregon". Known only from southeastern Oregon.
38. *T. t. ravus* Durrant, 1946. Type locality "19 mi. N Vernal, 8000 ft., Uintah Co., Utah". Known only from northeastern Utah.
39. *T. t. relicinus* Goldman, 1939. Type locality "Twin Springs, 20 mi. N Minidoka, Snake River Desert, Minidoka Co., Idaho". Known only from central-southern Idaho.
40. *T. t. retrorsus* Hall, 1951. Type locality "Flagler, Kit Carson Co., Colorado". Known only from eastern Colorado.
41. *T. t. rostralis* Hall and Montague, 1951. Type locality "1 mi. E Laramie, 7164 ft., Albany Co., Wyoming". Range in southern-central Wyoming and central Colorado.
42. *T. t. rufescens* Wied-Neuwied, 1839. Type locality "Minnetaree Village, now Old Fort Clark, about 6 mi. S Stanton, Mercer Co., North Dakota". Range in southwestern Saskatchewan and Manitoba south through South Dakota.
43. *T. t. saturatus* Bailey, 1914. Type locality "Silver, near Saltese, Coeur d'Alene Mts., Missoula Co., Montana". Range in northern Idaho, northwestern Montana, and southeastern British Columbia.
44. *T. t. segregatus* Johnstone, 1955. Type locality "Goat Mtn., E side Kootenay River, near Wynndel, British Columbia". Known only from near Wynndel, southeastern British Columbia.
45. *T. t. shawi* Taylor, 1921. Type locality "Owyhigh Lake, 5100 ft., Mt. Rainier, Pierce Co., Washington". Range in central-southern Washington.
46. *T. t. talpoides* (Richardson, 1828). For type locality see above. Range in western Alberta, central Saskatchewan, central-western Manitoba, and northern-central Montana.
47. *T. t. taylori* Hooper, 1940. Type locality "6 mi. NE summit Mt Taylor, about 8900 ft., near Fernandez summer camp, Valencia Co., New Mexico". Known only from Valencia County, central New Mexico.
48. *T. t. tenellus* Goldman, 1939. Type locality "Whirlwind Peak, 10,500 ft., Absaroka Range, Park Co., Wyoming". Range in northwestern Wyoming and southern Montana.
49. *T. t. trivialis* Goldman, 1939. Type locality "near head Big Timber Creek, 5200 ft., about 15 mi. NW Big Timber, Crazy Mts., Sweetgrass Co., Montana". Known only from central Montana.
50. *T. t. uinta* Merriam, 1901. Type locality "Blacks Fork, 10,000 ft., N base Gilbert Peak, Uinta Mts., Summit Co., Utah". Known only from central-northern Utah.
51. *T. t. wallowa* Hall and Orr, 1933. Type locality "Catherine Creek, 3500 ft., 7 mi. E Telocaset, Union Co., Oregon". Known only from northeastern Oregon.
52. *T. t. wasatchensis* Durrant, 1946. Type locality "Midway, 5500 ft., Wasatch Co., Utah". Known only from northern Utah.
53. *T. t. whitmani* Drake and Booth, 1952. Type locality "Whitman National Monument, 750 ft., 6 mi. W Walla Walla, Walla Walla Co., Washington". Known only from Walla Walla County, eastern Washington.
54. *T. t. yakimensis* Hall and Dalquest, 1939. Type locality "Selah, Yakima Co., Washington". Range in central-southern Washington.

Tribe Geomyini (Clade B)

Sub-clade B1

Genus *Cratogeomys* Merriam, 1895

1895. *Cratogeomys* Merriam, N. Amer. Fauna, 8:150. Type species. *Geomys merriami* (Thomas, 1893).

Content. Seven allopatric species are recognized species of *Cratogeomys* are recognized: *Cratogeomys castanops* (Baird, 1852), *Cratogeomys fulvescens* Merriam, 1895, *Cratogeomys fumosus* (Merriam, 1892), *Cratogeomys goldmani* Merriam, 1895, *Cratogeomys merriami* (Thomas, 1893), *Cratogeomys perotensis* Merriam, 1895, and *Cratogeomys planiceps* (Merriam, 1895).

Etymology. The name *Cratogeomys* is derived from the Greek *krataios*, meaning "strong"; *geo*, "earth"; and *mys*, "mouse": strong earth mouse, referring to strong and large specimens within the gophers ([Jaeger 1955](#)).

Diagnosis. Dorsal pelage in different colors, mainly shades of brown; fur of underparts paler than in the dorsum; tail short and slightly darker dorsally; body compact and cylindrical; hair silky and long, approximately 8.0 mm; skull large and massive; no ridge on the squamosal but a sagittal crest mainly in adult and old males; interorbital region narrower than the rostrum; zygomatic lateral angle with a plate-shaped expansion. The genus *Cratogeomys* can be differentiated from other species of the family Geomyidae by the following characteristics: rostrum wider than the interorbital region, zygomatic without an anterior angle plate-shaped expansion, and third upper molars not clearly showing two lobes ([Merriam 1895](#); [Nelson and Goldman 1934](#); [Russell 1968a](#); [Álvarez-Castañeda 2024](#)).

Distribution. The species of *Cratogeomys* range from Colorado, Kansas, Oklahoma, New Mexico, and Texas southward throughout the Altiplano Mexicana to the Eje Volcánico Transversal the Oriental Basin, eastern Puebla, western Veracruz, and western Tlaxcala throughout Jalisco, Colima, and Nayarit (Russell 1968a, Hall 1981; Hafner et al. (2004, 2005, 2008)). All species of *Cratogeomys* have allopatric distribution.

Comments. Revisions of the species in the genus *Cratogeomys* have been performed by Russell (1968b) and Hafner et al. (2004, 2005, 2008). The genus *Cratogeomys* comprises two species groups: *castanops* (*C. castanops*, *C. fulvescens*, *C. goldmani*, *C. merriami*, and *C. perotensis*) and *fumosus* (*C. fumosus* and *C. planiceps*; Hafner et al. 2004). The revision of *C. castanops* by Hafner et al. (2008) considered that it should be split into two different species, with the boundary between the species located at the Nazas River and Sierra de Parras. *C. castanops* is distributed north of this boundary and *C. goldmani* ranges to the south; all other subspecies should be considered junior synonyms. *C. castanops castanops* includes *C. c. angusticeps*, *C. c. bullatus*, *C. c. convexus*, *C. c. dalquesti*, *C. c. hirtus*, *C. c. parviceps*, *C. c. perplanus*, *C. c. pratensis*, *C. c. simulans*, *C. c. tamaulipensis*, *C. c. torridus*, and *C. c. ustulatus* as junior synonyms. The subspecies *C. c. consitus* includes the subspecies *C. c. excelsus*, *C. c. goldmani* (part of the distribution), *C. c. jucundus*, *C. c. perexiguus*, *C. c. sordidulus*, *C. c. subsimus*, and *C. c. surculus* (part of the distribution). *C. goldmani* is distributed south of the Nazas River and Sierra de Parras, and comprises two subspecies: *C. g. goldmani*, which includes the subspecies of *C. castanops*: *C. c. goldmani* as a junior synonym (part of the distribution), *C. c. rubellus*, and *C. c. surculus* (part of the distribution). The subspecies *C. g. subnubilus* includes the subspecies *C. c. subnubilus*, *C. c. elibatus*, *C. c. maculatus*, *C. c. peridoneus*, and *C. c. planifrons*. The populations previously considered subspecies of *C. merriami* (Russell 1968b), namely *C. m. perotensis* and *C. m. fulvescens*, were elevated to full species (Hafner et al. 2005). On the other hand, *C. merriami estor*, *C. m. peraltus*, *C. m. irolonis*, and *C. m. saccharalis* are not considered valid subspecies, the first are junior synonyms of *C. perotensis* and the later of *C. merriami* (Hafner et al. 2005). *Cratogeomys fumosus angustirostris*, *C. f. imparilis* and *C. f. tylorhinus* were considered subspecies of *C. fumosus*. *C. f. angustirostris* comprises *Pappogeomys zinseri* and *P. tylorhinus brevisrostris* as junior synonyms. *C. f. fumosus* includes *P. gymnurus gymnurus*, *P. g. inclarus*, *P. g. tellus*, *P. tylorhinus atratus*, *P. t. zodiacus*, and *C. zinseri morulus*; *C. f. tylorhinus* includes *P. neglectus* and *C. t. arvalis* (Hafner et al. 2004).

The morphological differences that differentiate *Pappogeomys* from *Cratogeomys* include the tail usually naked and less than one-half of the head-and-body length vs tail short and slightly darker dorsally; claws on the forefeet larger vs smaller; interorbital region wider vs narrower than the rostrum; sagittal crest absent vs present; zygomatic without an anterior angle and plate-shaped expansion vs lateral angles with a plate-shaped expansion (Merriam 1895; Nelson and Goldman 1934; Russell 1968a; Álvarez-Castañeda 2024). The characteristics that differentiate *Pappogeomys* from *Orthogeomys* include size less than 350 mm vs size greater than 350.0 mm; body mass less than 600 g vs greater than 800 g; third upper molars clearly with two lobes, outer lingual angle well developed vs third upper molars not clearly with two lobes, outer lingual angle not well developed; upper premolars usually with an enamel plate on the back restricted to the lingual region vs upper premolars never with an enamel plate in the lingual region (Russell 1968a; Hall 1981; Álvarez-Castañeda 2024). The characteristics listed above are easily observed and useful for separating *Pappogeomys* from *Cratogeomys* and *Orthogeomys*, as many of the authors cited previously have demonstrated.

Cratogeomys castanops (Baird, 1852)

Yellow-faced pocket gopher, tuza de cara amarilla

1852. *Pseudostoma castanops* Baird, in Rept. Stan bury' s Expl. Surv. ... Great Salt Lake of Utah... , App. C, p. 313. Type locality "prairie road to Bent's Fort, near present town of Las Animas, Bent Co., Colorado".

1985. *Cratogeomys castanops*: Merriam, N. Amer. Fauna, 8:159.

1. *C. c. castanops* (Baird, 1852). For type locality see above. Range from northern Tamaulipas, Coahuila, and Chihuahua north through Colorado, Kansas, Oklahoma, New Mexico, and Texas.

2. *C. c. consitus* Nelson and Goldman, 1934. Type locality "Gallego, 5500 ft., Chihuahua". Range from northern Tamaulipas, Coahuila, Chihuahua, and Sonora south through the Nazas River and Sierra de Parras, Coahuila, and Durango".

Cratogeomys fulvescens Merriam, 1895

Oriental Basin pocket gopher, tuza de la Cuenca Oriental

1895. *Cratogeomys fulvescens* Merriam, N. Amer. Fauna, 8:161. Type locality "Chalchicomula [= Ciudad Serdán], 8200 ft., Puebla".

Cratogeomys fumosus (Merriam, 1892)

Smoky pocket gopher, tuza del centro de México

1892. *Geomys fumosus* Merriam, Proc. Biol. Soc. Washington, 7:165. Type locality "3 mi. W Colima, 1700 ft., Colima".

1948. *Cratogeomys fumosus*: Hooper, Jour. Mamm., 29:302.

1. *C. f. angustirostris* (Merriam, 1903). Type locality "Cerro Patambán, 10,000 ft., Michoacán". Known only from the southwestern central Mexican Plateau.
2. *C. f. fumosus* (Merriam, 1892). For type locality see above. Patchily distributed on western Michoacán, eastern slopes of the Sierra Madre del Sur in Jalisco and Colima.
3. *C. f. imparilis* (Goldman, 1939). Type locality "Pátzcuaro, Michoacán". Patchily distributed in central Michoacán.
4. *C. f. tylorhinus* (Merriam, 1895). Type locality "Tula, 6800 ft., Hidalgo". Patchily distributed across the southeastern central Mexican Plateau.

Cratogeomys goldmani Merriam, 1895

Goldman's pocket gopher, tuza del Altiplano

1895. *Cratogeomys castanops goldmani* Merriam, N. Amer. Fauna, 8:160. Type locality "Cañitas, Zacatecas".

1987. *Cratogeomys goldmani*: Lee and Baker, Occ. Pap., Mus. Texas Tech Univ. 114:13.

1. *C. g. goldmani* Merriam, 1895. For type locality see above. Ranges from Nazas River and Sierra de Parras, Coahuila, and Durango south through San Luis Potosí and Zacatecas.
2. *C. g. subnubilus* Nelson and Goldman, 1934. Type locality "Cameros, Coahuila". Range from Monterrey, Nuevo León, along western Tamaulipas, and San Luis Potosí.

Cratogeomys merriami (Thomas, 1893)

Merriam's pocket gopher, tuza del Valle de México

1893. *Geomys merriami* Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:271. Type locality "southern Mexico (Probably the Valley of Mexico according to Merriam, N. Amer. Fauna, 8:152, 1895.)"

1982. *Cratogeomys merriami*: Honeycutt and Williams, Jour. Mamm. 63:212.

Cratogeomys perotensis Merriam, 1895

Perote pocket gopher, tuza de Perote

1895. *Cratogeomys perotensis* Merriam, N. Amer. Fauna, 8:154. Type locality "Cofre de Perote, 9500 ft., Veracruz".

Cratogeomys planiceps (Merriam, 1895)

Toluca Volcano pocket gopher, tuza del Nevado de Toluca

1895. *Platygeomys planiceps* Merriam, N. Amer. Fauna, 8:168. Type locality "N slope Volcán de Toluca, 9000 ft., México".

2004. *Cratogeomys planiceps*: Hafner, Spradling, Light, Hafner, and Demboski. Jour. Mamm 85:1178.

Orthogeomys Merriam, 1895

1895. *Orthogeomys* Merriam, N. Arner. Fauna, 8:172. Type species. *Geomys scalops* (Thomas, 1894).

Content. Only one species of *Orthogeomys* is recognized: *O. grandis* (Thomas, 1893).

Etymology. The name *Orthogeomys* is derived from the Greek *orthos*, meaning "straight"; *geo*, "earth"; and *mys*, "mouse". The name refers to the unusual shape of the skull ([Merriam 1895](#)).

Diagnosis.— *Orthogeomys* has the largest members of the family Geomyidae; dorsal pelage reddish cinnamon to brownish; fur of underparts paler; body compact and cylindrical; hair sparse and bristly; skull large and massive; ridge on the squamosal joining the temporal in adult and old males; rostrum narrower than the interorbital region, no interorbital constriction; frontal bone wide and inflated; anterior surface of the upper incisors with one deep groove; last upper molars semi-lobular, only one labial groove; an enamel plate covering the front and re-entrant angle edge of the first upper and lower molariforms; first lower molariforms with an enamel plate and first upper molariforms without a small plate on the lingual side; fourth upper premolars without an enamel plate, although a small plate restricted to the lingual end of the wall rarely present ([Russell 1968a](#); [Hall 1981](#); [Álvarez-Castañeda 2024](#)).

Distribution. Patchily distributed along the Pacific coast Colima and Jalisco southward to southwestern Honduras, including Guatemala and El Salvador; altitudinal range from near sea level to at least 2,700 m ([Hall 1981](#); [Spradling et al. 2016](#)).

Comments. *Orthogeomys ciniculus* was considered as a valid species, but the genetic analyses with nDNA and mtDNA show the absence of reciprocal monophyly. Given this finding, it is considered a junior synonym of *O. grandis*.

Orthogeomys grandis (Thomas, 1893)

Giant pocket gopher, tuza gigante del Pacífico

1893. *Geomys grandis* Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:270. Type locality "Dueñas, Guatemala".1895. *Orthogeomys grandis*, Merriam, N. Amer. Fauna, 8:175.

1. *O. g. alleni* Nelson and Goldman, 1930. Type locality "near Acapulco, Guerrero, Mexico (altitude 2,000 feet)". Range in southeastern Jalisco coastal plains through central Oaxaca.
2. *O. g. alvarezi* Schaldach, 1966. Type locality "ridge above Lachao (pass above Kilometer 183), on road from Oaxaca City to Puerto Escondido, approximately 40 kms. N. San Gabriel Mixtepec, Municipio de Juquila, Oaxaca, Mexico, altitude approximately 1700 m". Known only from San Gabriel Mixtepec, Oaxaca.
3. *O. g. annexus* Nelson and Goldman, 1933. Type locality "Tuxtla Gutierrez, 2600 ft., Chiapas". Known only from Tuxtla Gutiérrez.
4. *O. g. carbo* Goodwin, 1956. Type locality "Ecurano, 2500 ft., Cerro de San Pedro, 20 km W Mixtequilla, Oaxaca [Mexico]". Known only from the central coast of Oaxaca.
5. *O. g. cuniculus* Elliot, 1905. Type locality "Zanatepec, Oaxaca". Known only from type locality.
6. *O. g. engelhardi* Felten, 1957. Type locality "Finca El Carmen (1,319 m), Volcán de San Vicente, [San Vicente Department] El Salvador". Known only from type locality.
7. *O. g. felipensis* Nelson and Goldman, 1930. Type locality "Cerro San Felipe, 10 miles north of Oaxaca, Oaxaca, Mexico (altitude 10,000 feet)". Known only from the Central Valleys of Oaxaca.
8. *O. g. grandis* (Thomas, 1893). Type see above. Known only from the volcano arch of Guatemala.
9. *O. g. guerrerensis* Nelson and Goldman, 1930. Type locality "El Limon, in the valley of the Rio de las Balsas about 20 miles northwest of La Union, Guerrero [Mexico]". Known only from the central lowlands of Guerrero.
10. *O. g. huixtlae* Villa R., 1944. Type locality "Finca Lubeca, 12 km NE Huixtla, 850 m, Chiapas [Mexico]". Known only from southeastern Chiapas.
11. *O. g. latifrons* Merriam, 1895. Type locality "Guatemala (exact locality unknown, but probably lowlands of southern Guatemala)". Known only from Guatemala.
12. *O. g. nelsoni* Merriam, 1895. Type locality "Mt. Zempoaltepec, 8000 ft., Oaxaca". Known only from Sierra Norte of Oaxaca.
13. *O. g. pluto* Lawrence, 1933. Type locality "Cerro Cantoral, north of Tegucigalpa, Honduras". Known only from type locality.
14. *O. g. pygacanthus* Dickey, 1928. Type locality "Cacaguatique, 3500 ft. Department of San Miguel, El Salvador". Known only from western and central El Salvador.
15. *O. g. scalops* (Thomas, 1894). Type locality "Tehuantepec, Oaxaca". Known only from the Isthmus of Tehuantepec, Oaxaca.
16. *O. g. soconuscensis* Villa R., 1949. Type locality "Finca Esperanza, 710 m, 45 km (by road) NW Huixtla, Chiapas [Mexico]". Known only from the coast of Chiapas.
17. *O. g. vulcani* Nelson and Goldman, 1931. Type locality "Volcan Santa Maria, Quezaltenango, Guatemala (altitude 9,000 feet)".

Genus *Pappogeomys* Merriam, 18951895. *Pappogeomys* Merriam, N. Amer. Fauna, 8:145. Type species. *Geomys bulleri* (Thomas, 1892).Content. One species of *Pappogeomys* is recognized: *Pappogeomys bulleri* (Thomas, 1892).Etymology. The name *Pappogeomys* is derived from the Greek *pappos*, meaning "grandfather"; *geo*, "earth", and *mys*, "mouse": the grandfather of the earth mouse ([Jaeger 1955](#)).Diagnosis. Buller's pocket gopher is medium-sized; total length 200.0 mm to 249.0 mm, skull length 39.2 mm to 42.9 mm. Pelage medium in length and soft, except in coastal populations which have short and sparse pelage; color light brown to dark gray; fur of underparts paler than in the dorsum; most specimens with a small nasal patch consisting of white or pale buffy hairs; body compact and cylindrical; tail usually naked and less than one-half of the head-and-body length; claws on forefeet larger than in *Cratogeomys*; skull large and massive; rostrum wider than the interorbital region; incisors without grooves in the frontal phase; without a zygomatic anterior angle with a plate-shaped expansion ([Merriam 1895](#); [Nelson and Goldman 1934](#); [Russell 1968a](#); [Hafner et al. 2009](#); [Álvarez-Castañeda 2024](#)).

Distribution. *Pappogeomys bulleri* is known from the mountains, tablelands, and coastal plains near the western end of the Trans-Mexican Volcanic Belt in west-central México, including the states of Nayarit, Jalisco, and Colima (Hafner *et al.* 2009).

Comments. *Cratogeomys* was first considered a subgenus of *Pappogeomys* (Nelson and Goldman 1934; Russell 1968a); it is currently a full genus (Honeycutt and Williams 1982; Demastes *et al.* 2002). Hafner *et al.* (2009) reviewed the *Pappogeomys bulleri* complex (considering that the previous subspecies of *P. bulleri* are junior synonyms of the following subspecies: *P. b. albinasus* includes *P. b. infuscus* and *P. b. nayaritensis* (part of the species); *P. b. bulleri* includes *P. b. amecensis*, *P. b. flammeus*, *P. b. lagunensis*, and *P. b. lutulentus*; and *P. b. burti* includes *P. b. melanurus*. *Cratogeomys* differs from all the other species of the family Geomyidae in the following characteristics: rostrum wider than the interorbital region; without a zygomatic anterior angle with a plate-shaped expansion, and third upper molars not clearly showing two lobes.

Pappogeomys bulleri (Thomas, 1892)

Buller's pocket gopher, tuza de Jalisco

1892. *Geomys bulleri* Thomas, Ann. Mag. Nat. Hist., ser. 6, 10:196. Type locality "near Talpa, W slope Sierra de Mascola, 8500 (probably about 5000) ft., Jalisco".

1895. *Pappogeomys bulleri*, Merriam, N. Amer. Fauna, 8:159.

1. *P. b. albinasus* Merriam, 1895. Type locality "Atemajac, a suburb of Guadalajara, Jalisco". Known only from central Jalisco and southeastern Nayarit.
2. *P. b. alcorni* Russell, 1957. Type locality "4 mi. W Mazamitla, 6600 ft., Jalisco". Range in eastern and central Jalisco.
3. *P. b. bulleri* (Thomas, 1892). For type locality see above. Known only from the Sierra Madre del Sur highlands, Jalisco.
4. *P. b. burti* Goldman, 1939. Type locality "Tenacatita Bay, southwestern coast of Jalisco". Known only from coastal areas and lowlands of Colima and Jalisco.
5. *P. b. nayaritensis* Goldman, 1939. Type locality "about 10 mi, S Tepic, 5000 ft., Nayarit". Known only from lowlands of Nayarit.

Zygozemys Merriam, 1895

1895. *Zygozemys* Merriam, N. Amer. Fauna, 8:195. Type species *Zygozemys trichopus* Merriam, 1895.

Content. One species of *Zygozemys* is recognized: *Zygozemys trichopus* Merriam, 1895.

Etymology. The name *Zygozemys* is derived from the Greek *zygos*, meaning "zygomatic"; *geo*, "earth"; and *mys*, "mouse": related to the shape of the zygomatic arch, which is characteristic of the genus (Merriam 1895).

Diagnosis. Body compact and cylindrical; eyes, ears, and limbs small; fore- and hindfoot claws well-developed; tail short and slightly darker dorsally; upper incisors bisulcate, a major sulcus on the inner side of the median line and a minor sulcus on the inner convexity; third upper molars conspicuously bicolumnar, longer than wide owing to the elongation of the posterior loph; rostrum narrow relative to its length; maxillary and squamosal roots of the zygomatic arches in contact above the jugal, and antero-external angles rounded rather than expanded; zygomata not widely spreading and slender; sagittal crest short but well-developed (Merriam 1895, Russell 1968a, Álvarez-Castañeda 2024).

Distribution. *Zygozemys* is known only from Nahuatzen, Pátzcuaro, Cerros Tancítaro, and Patambán, all in the state of Michoacán, Mexico (Merriam 1895, Russell 1968a; Hall 1981).

Comments. *Zygozemys trichopus* can be found in sympatry with *Cratogeomys fumosus*, which is normally more common and abundant. *Zygozemys trichopus* can be distinguished from *Cratogeomys* by having two grooves in the anterior surface of the upper incisors (the internal grooves are very notorious, can be detected by passing a pencil tip or a thumb nail).

Zygozemys can be differentiated from all other genera mainly by having the upper incisors bisulcate, a major sulcus on the inner side of the median line and a minor sulcus on the inner convexity; third upper molars conspicuously bicolumnar, longer than wide owing to the elongation of the posterior loph and maxillary and squamosal roots of the zygomatic arches in contact above the jugal clearly morphologically distinct from other members of the sub-clade (Merriam 1895, Russell 1968a, Álvarez-Castañeda 2024).

Zygozemys trichopus Merriam, 1895

Michoacán pocket gopher, tuza de Michoacán

1895. *Zygozemys trichopus* Merriam, N. Amer. Fauna, 8:196. Type locality "Nahuatzen, Michoacán".

1. *Z. t. tarascensis* Goldman, 1938. Type locality "6 mi. SE Patzcuaro, 8000 ft., Michoacán". Known only from Pátzcuaro area, Michoacán.

2. *Z. t. trichopus* Merriam, 1895. For type locality see above. Known only from Nahuatzen, Cerros Tancítaro, and Patambán, Michoacán.

Sub-clade B2

Genus *Heterogeomys* Merriam, 1895

1895. *Heterogeomys* Merriam, N. Amer. Fauna, 8:179. Type species. *Geomys hispidus* Le Conte, 1852.

Content. Two species of the subgenus *Heterogeomys* are recognized: *Heterogeomys (Heterogeomys) hispidus* (Le Conte, 1852) and *Heterogeomys (Heterogeomys) lanius* Elliot, 1905, and five of the subgenus *Macrogeomys* are recognized: *Heterogeomys (Macrogeomys) cavator* (Bangs, 1902), *Heterogeomys (Macrogeomys) cherriei* (J. A. Allen, 1893), *Heterogeomys (Macrogeomys) dariensis* (Goldman, 1912), *Heterogeomys (Macrogeomys) heterodus* (Peters, 1865), and *Heterogeomys (Macrogeomys) underwoodi* (Osgood, 1931).

Etymology. The name *Heterogeomys* is derived from the Greek *Hetero*, meaning "other, different"; *geo*, "earth"; and *mys*, "mouse": the other earth mouse or the different earth mouse ([Jaeger 1955](#)).

Diagnosis. The genus *Heterogeomys* comprises large specimens; coloration dark brown; pelage harsh and stiff; frontal bone narrow and not markedly inflated; interorbital region decidedly constricted; zygomata more widely spreading; post-orbital bar (process) weakly developed; anterior margin of the mesoptergoid fossa even with the plane of the posterior wall of third upper molars; first upper incisors unisulcate; surface of incisors flat on both sides of the sulcus; sulcus wholly on the inner side of the median line and deep and abrupt on the inner third in some specimens; anteroposterior occlusal length of the third upper molars equal to or shorter than the combined lengths of the first and second upper molars; fourth upper premolars with a short enamel plate and restricted to the lingual end of the wall ([Russell 1968a](#); [Hall 1981](#)).

Comments. *Heterogeomys* was first described as a full genus ([Merriam 1895](#)) and was later considered a subgenus of *Orthogeomys* ([Russell 1968a](#)). Molecular data supports its reassignment at the genus level, including *Macrogeomys* as a subgenus ([Spradling et al. 2016](#)).

Subgenus *Heterogeomys* Merriam, 1895

Heterogeomys (Heterogeomys) hispidus (Le Conte, 1852)

Hispid pocket gopher, tuza gigante tropical

1852. *G[geomys]. hispidus* Le Conte, Proc. Acad. Nat. Sci. Philadelphia, 6:158. Type locality "near Jalapa, Veracruz".

2016. *Heterogeomys hispidus* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:415

1. *H. h. cayoensis* Burt, 1937. Type locality "Mountain Pine Ridge, 12 mi. S El Cayo, British Honduras [Belize]."
2. *H. h. chiapensis* Nelson and Goldman, 1929. Type locality "Tenejapa, 16 mi. NE San Cristobal, Chiapas". Range in all Chiapas, except northwestern.
3. *H. h. concavus* Nelson and Goldman, 1929. Type locality "Pinal de Amoles, Queretaro". Range in San Luis Potosí, Querétaro, and northwestern Veracruz.
4. *H. h. hispidus* (Le Conte, 1852). For type locality see above. Range in western Veracruz and eastern Puebla.
5. *H. h. hondurensis* Davis 1966. Type locality "8 mi. W Tela, Honduras". Known only from type locality.
6. *H. h. isthmicus* Nelson and Goldman, 1929. Type locality "Jaltipan, Veracruz". Known only from southeastern Veracruz.
7. *H. h. latirostris* Hall and Álvarez, 1961. Type locality "Hda. Tamiahua, Cobo Rojo, Veracruz". Known only from north-eastern Veracruz.
8. *H. h. negatus* Goodwin, 1953. Type locality "Gómez Feras [= Farías], 1300 ft., about 45 mi. S Ciudad Victoria, 10 mi. W Pan American Highway, Tamaulipas". Known only from southern Tamaulipas.
9. *H. h. teapensis* Goldman, 1939. Type locality "Teapa, Tabasco. Known only from type locality". Known only from southern Tabasco and northwestern Chiapas.
10. *H. h. tehuantepecus* Goldman, 1939. Type locality "mountains 12 mi. NW Santo Domingo and about 60 mi. N Tehuantepec, 1600 ft., Oaxaca". Known only from northern Oaxaca.
11. *H. h. torridus* Merriam, 1895. Type locality "Chichicaxtle, Veracruz". Known only from central Veracruz.
12. *H. h. yucatanensis* Nelson and Goldman, 1929. Type locality "Campeche, Campeche". Range in Yucatán peninsula, Belize, and Guatemala.

Heterogeomys (Heterogeomys) lanius Elliot, 1905

Big pocket gopher, tuza gigante de Veracruz

1905. *Heterogeomys lanius* Elliot, Proc. Biol. Soc. Washington, 18:235. Type locality "Xuchil, Veracruz". Known only from type locality.

Subgenus *Macrogeomys* (Peters, 1895)*Heterogeomys (Macrogeomys) cavator* (Bangs, 1902)

Chiriquí Pocket Gopher

1902. *Macrogeomys cavator* Bangs, Bull. Mus. Comp. Zool., 39:42. Type locality "Boquete [Chiriqui Province, Panama] 4,000 to 7,000 feet".

2016. *Heterogeomys cavator* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:416.

1. *H. c. cavator* (Bangs, 1902). For type locality see above. Known only from Chiriqui Province, Panama.
2. *H. c. nigrescens* (Goodwin, 1934). Type locality "El Muñeco (Rio Navarro), 10 miles south of Cartago, Province Cartago, Costa Rica, altitude 4,000 feet". Known only from type locality.
3. *H. c. pansa* (Bangs, 1902). Type locality "Bogaba [Bugaba], Chiriqui Province, Panama". Known only from type locality.

Heterogeomys (Macrogeomys) cherriei (J. A. Allen, 1893)

Cherrie's Pocket Gopher

1893. *Geomys cherriei* J. A. Allen, Bull. Amer. Mus. Nat. Hist., 5:337. Type locality "Santa Clara, Costa Rica.

2016. *Heterogeomys cherriei* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:416.

1. *H. c. carlosensis* (Goodwin, 1934). Type locality "Cataratos, San Carlos, Province Alajuela, Costa Rica, about 400 feet elevation". Known only from Province Alajuela, Costa Rica.
2. *H. c. cherriei* (J. A. Allen, 1893). For type locality see above. Known only from Santa Clara area, Costa Rica.
3. *H. c. costaricensis* (Merriam, 1895). Type locality "Pacuare, Costa Rica". Known only from Pacuare Basin, Costa Rica.
4. *H. c. matagalpae* (J. A. Allen, 1910). Type locality "Pena [Peña] Blanca, Matagalpa, Nicaragua". Range in central area of Nicaragua.

Heterogeomys (Macrogeomys) dariensis (Goldman, 1912)

Darién Pocket Gopher

1912. *Macrogeomys dariensis* Goldman, Smiths. Misc. Coll., 60(2):8. Type locality "Cana (altitude 2,000 feet) in the mountains of eastern Panama".

2016. *Heterogeomys dariensis* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:416.

1. *H. d. dariensis* (Goldman, 1912). For type locality see above. Known only from The Darien, southern Panama.
2. *H. d. thaeleri* (Alberico, 1990). Type locality "ca. 7 km S Bahía Solano, Municipio Bahía Solano, Departamento del Chocó, Colombia, ca. 100 m". Known only from Municipio Bahía Solano northwestern Colombia.

Heterogeomys (Macrogeomys) heterodus (Peters, 1865)

Variable Pocket Gopher

1865. *Geomys heterodus* Peters, Monatsb. preuss. Akad. Wiss., Berlin, p. 177). Type locality "Costa Rica".

2016. *Heterogeomys heterodus* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:417.

1. *H. h. cartagoensis* (Goodwin, 1934). Type locality "Paso Ancho, Province Cartago, Costa Rica". Central area of Costa Rica.
2. *H. h. dolichocephalus* (Merriam, 1895). Type locality "San Jose, Costa Rica". Known only from the area of San José, Costa Rica.
3. *H. h. heterodus* (Peters, 1865). For type locality see above. Known only from the area of Escazú, Costa Rica.

Heterogeomys (Macrogeomys) underwoodi (Osgood, 1931)

Underwood's Pocket Gopher

1931. *Macrogeomys underwoodi* Osgood, Field Mus. Nat. Hist., Publ. 295, Zool. Ser., 18(5):143. Type locality "Alto de Jabillo Pirris, between San Geronimo and Pozo Azul, western Costa Rica".

2016. *Heterogeomys underwoodi* Spradling, Demastes, Hafner, Milbach, Cervantes, and Hafner, Jour. Mamm. 97:417.

Sub-clade B3

Genus *Geomys* Rafinesque, 1817

1817. *Geomys* Rafinesque, Amer. Month. Mag., 2:45. Type *Geomys pinetis* Rafinesque, 1817.

Content. Thirteen allopatric species are recognized species of *Geomys* are recognized: *Geomys arenarius* Merriam, 1895, *Geomys attwateri* Merriam, 1895, *Geomys breviceps* Baird, 1855, *Geomys bursarius* (Shaw, 1800), *Geomys jugossicularis* Hooper, 1940, *Geomys knoxjonesi* Baker and Genoways, 1975, *Geomys lutescens* Merriam, 1890, *Geomys mobilensis* (Merriam, 1895), *Geomys personatus* True, 1889, *Geomys pinetis* Rafinesque, 1817, *Geomys streckeri* Davis, 1943, *Geomys texensis* Merriam, 1895, *Geomys tropicalis* Goldman, 1915.

Etymology. The name *Geomys* is derived from the Greek *geo*, "earth", and *mys*, "mouse": earth mouse ([Álvarez-Castañeda and Álvarez 1996](#)).

Diagnosis. Dorsal pelage reddish to grayish brown; fur of underparts paler than in the dorsum; back of the rostrum and head darker, contrasting with the nape and back; rump generally paler; whitish gray coloration from chin to neck; body compact and cylindrical; eyes, ears, and limbs small; claws of limbs well-developed; skull large and massive; ridge on the squamosal joining the temporal in adult and old males; interorbital region narrower than the rostrum; middle part of anterior surface of upper incisors with two grooves: one large, deep, and medial; the other small and flanked on the inner side; first upper molars without an enamel plate and larger than the first lower molars; upper molariforms not prominently bicolumnar and almost as long as wide; all molariforms elliptical with a small anterior-posterior axis; anterior and posterior margins of molariforms with enamel, other margins with dentin; sagittal crest poorly developed ([Russell 1968a](#); [Baker and Williams 1974](#); [Sudman et al. 2006](#); [Álvarez-Castañeda 2024](#)).

Distribution. *Geomys* ranges east of the Mississippi River in Alabama, Georgia, and Florida, associated with deep sandy soils and open areas in long-leaf pinewood forests, and west of the Mississippi River from southern Manitoba, Canada, southward throughout northeastern Tamaulipas, Mexico, and westward throughout eastern Wyoming, Colorado, central New Mexico, western Texas, and northern Chihuahua.

Comments. *G. p. colonus*, *G. p. cumberlandius*, and *G. p. floridanus* were recognized as distinct species ([Hall 1981](#); [Laerm 1981](#)), but not by [Patton \(1993, 2005\)](#) and [Baker et al. \(2003\)](#). The subspecies *G. p. austrinus*, *G. p. colonus*, *G. p. cumberlandius*, *G. p. floridanus*, *G. p. goffi*, *G. p. mobiliensis* are considered junior synonyms of *G. p. pinetis* ([Williams and Genoway 1980](#)). [Sudman et al. \(2006\)](#) considered that *G. p. mobilensis* may represent a species different from *G. pinetis*. No other species of the genus *Geomys* occurs anywhere near its range. *G. pinetis* cannot be differentiated morphologically from any other species west to the Mississippi River. The chromosome number is $2n = 42$, $FN = 80$.

Geomys shows a high genetic difference (17.6 % [16.1 %–19.0 %]) relative to all other species east of the Mississippi River, higher than the difference within species within any genus of the family Geomyidae and the species east of the Mississippi River 12.4 % (2.8 %–15.3 %). Additionally, *Geomys* compared to all other species of eastern of the Mississippi River have presence-absence of lice species ([Hafner et al. 1994](#)), protein ([Kennedy 1988](#)), mtDNA restriction patterns, and allozyme loci ([Avise et al. 1979](#)), with the Mississippi River acting as an impassable barrier that isolated *Geomys* from all other species of eastern of the Mississippi River.

Geomys shows a high inner variation, so its analysis considered two geographical groups in relation to the Mississippi River determined based on the following conditions: 1) presence of different species complexes determined by several authors ([Russell 1968a](#); [Williams and Genoway 1980](#); [Hall 1981](#); [Sudman et al. 2006](#)); 2) the marked difference in the nasal shape, being straight in western specimens vs nasals with a strong constriction near the middle in eastern specimens (hourglass-shaped); interorbital area narrow (western) vs a notorious narrow interorbital area (eastern); the east-of-Mississippi population is a different clade from the population thriving in the west side, and is considered basal ([Russell 1968a](#); [Penney and Zimmerman 1976](#); [Sudman et al. 2006](#)). The Mississippi River is a mayor barrier for the gopher dispersion, flows from northern Minnesota to the Gulf of Mexico, dividing inland plains by a large stream that is virtually impossible to cross by gophers. We consider the crossing of the river as a hypothesis, which a population was located near the boundary of a meander belt and dispersed into the neck of one lobe of the river that later was cut-off from the mainstream, the population could have crossed the river and diversified. The Mississippi River was established as a geographic barrier that prevented subsequent dispersion events.

Geomys arenarius Merriam, 1895

Desert pocket gopher, tuza del desierto

1895. *Geomys arenarius* Merriam, N. Amer. Fauna, 8:139. Type locality "El Paso Co., Texas".

1. *G. a. arenarius* Merriam, 1895. For type locality see above. Range in southern New Mexico, northern Chihuahua, and southwestern Texas.
2. *G. a. brevisrostris* Hall, 1932. Type locality "E edge [white] sand [9 mi. W Tularosa], Tularosa-Hot Springs Road, Otero Co., New Mexico". Known only from central-southern New Mexico.

Geomys attwateri Merriam, 1895

Attwater's pocket gopher, tuza de Corpus Christi

1895. *Geomys breviceps attwateri* Merriam, N. Amer. Fauna, 8:135. Type locality "Rockport, Texas".

1. *G. a. ammophilus* Davis, 1940. Type locality "Cuero, De Witt Co., Texas". Known only from the Brazos River Basin near the coast, central-southeastern Texas.
2. *G. a. attwateri* Merriam, 1895. For type locality see above". Known only from the Colorado and Guadalupe River basins near the coast of southeastern Texas.

Geomys breviceps Baird, 1855

Baird's pocket gopher, tuza texana del este

1855. *Geomys breviceps* Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:335. Type locality "Prairie Mer Rouge, Louisiana. Known only from Morehouse Parish".

1. *G. b. breviceps* Baird, 1855. For type locality see above. Range from southeastern Oklahoma and southwestern Arkansas south through eastern Texas and western Louisiana.
2. *G. b. ozarkensis* Elrod, Zimmerman, Sudman, and Heidt, 2000. Type locality "from 3 mi S Melbourne, IZard County, Arkansas". Range in northern-central Arkansas.
3. *G. b. sagittalis* Merriam, 1895. Type locality "Clear Creek, Galveston Bay, Galveston Co., Texas". Known only from Galveston Bay, Texas.

Geomys bursarius (Shaw, 1800)

Plains pocket gopher, tuza de las planicies

1800. *Mus bursarius* Shaw, Trans. Linnean Soc. London, 5:227. Type locality "somewhere in upper Mississippi Valley (Restricted to Elk River, Sherburne Co., Minnesota, by Swenk, Missouri Valley Fauna, 1:6.)".

1829. *Geomys bursarius*, Richardson, Fauna BorealiAmericana 1:203.

1. *G. b. bursarius* (Shaw, 1800). For type locality see above. Range from southern Manitoba south through eastern Dakotas, Minnesota, and northwestern Wisconsin.
2. *G. b. illinoensis* Komarek and Spencer, 1931. Type locality "1 mi, S Momence, Kankakee Co., Illinois". Range in central Illinois and central-western Indiana.
3. *G. b. majusculus* Swenk, 1939. Type locality "Lincoln, Nebraska". Range from Iowa and northern-central Missouri west through southeastern Nebraska and eastern Kansas.
4. *G. b. missouriensis* McLaughlin, 1958. Type locality "2 mi. N Manchester, St. Louis Co., Missouri". Range in eastern Missouri.
5. *G. b. wisconsinensis* Jackson, 1957. Type locality "Lone Rock, Richland Co., Wisconsin". Range in western Wisconsin.

Geomys jugossicularis Hooper, 1940

Hall's pocket gopher, tuza de las planicies centrales

1940. *Geomys lutescens jugossicularis* Hooper, Occas. Pap. Mus. Zool., Univ. Michigan, 420:1. Type locality "Lamar, Prowers Co., Colorado".

1. *G. j. halli* Sudman, Choates and Zimmerman, 1987. 1 3/4 mi. E Ellis (T13S, R20W, NE 1/4 Sec. 10), Ellis Co., Kansas. Range from eastern Colorado east through southwestern Kansas, Oklahoma, and northeastern New Mexico.
2. *G. j. jugossicularis* Hooper, 1940. For type locality see above. Oklahoma and southwestern Kansas.

Geomys knoxjonesi Baker and Genoways, 1975

Jones's pocket gopher, tuza texana del oeste

1975. *Geomys bursarius knoxjonesi* Baker and Genoways, Occas. Pap. Mus. Texas Tech Univ., 29:1. Type locality "4.1 mi. N, 5.1 mi. E Kermit, Winkler Co., Texas".

Geomys lutescens Merriam, 1890

Sandy hill pocket gopher, tuza arenera

1890. *Geomys bursarius lutescens* Merriam, N. Amer. Fauna, 4:51. Type locality "sandhills on Birdwood Creek, Lincoln Co., Nebraska".

1. *G. l. industrius* Villa and Hall, 1947. Type locality "1 1/2 mi. N Fowler, Meade Co., Kansas". Known only from southwestern Kansas.
2. *G. l. lutescens* Merriam, 1890. For type locality see above. Range from South Dakota south through central-eastern Colorado and central Kansas.
3. *G. l. major* Davis, 1940. Type locality "8 mi. W Clarendon, Donley Co., Texas". Range from southern Kansas south through.

Geomys personatus True, 1889

Texas pocket gopher, tuza texana del sur

1889. *Geomys personatus* True, Proc. U.S. Nat. Mus., 11:159 for 1888. Type locality "Padre Island, Cameron Co., Texas".

1. *G. p. davisii* Williams and Genoways, 1981. Type locality "3 mi N, 2.8 mi W Zapata, Zapata Co., Texas". Known only from southern Texas.
2. *G. p. fallax* Merriam, 1895. Type locality "S side Nueces Bay, Nueces Co. Texas". Known only from southeastern Texas.
3. *G. p. fuscus* Davis, 1940. Type locality "Fort Clark [Bracketville], Kinney Co., Texas". Known only from Kinney and Valverde counties, southern Texas.
4. *G. p. maritimus* Davis, 1940. Type locality "Flour Bluff, 11 mi. SE Corpus Christi, Nueces Co., Texas". Known only from Baffin Bay and Flour Bluff, southern Texas.
5. *G. p. megapotamus* Davis, 1940. Type locality "4 mi. SE Oilton, Webb Co., Texas". Range in southern Texas and north-eastern Tamaulipas.
6. *G. p. personatus* True, 1889. For type locality see above. Known only from the Mustang and Padre islands, southern Texas.

Geomys pinetis Rafinesque, 1817

Southeastern pocket gopher, tuza del sureste

1806. *Mus tuza* Barton, Mag. fur den neusten Zustand der Naturkunde (ed. J. H. Voight), 12(6):488 (Type locality restricted to pine barrens near Augusta, Georgia, by Bangs, Proc. Boston Soc. Nat. Hist., 28:175. According to Harper, Proc. Biol. Soc. Washington, 65:36, 952, *tuza* of Barton is of uncertain application and is regarded as not available.)

1817. *Geomys pinetis* Rafinesque, Amer. Month. Mag., 2(1):45. Type locality "Georgia in the region of the pines (More restrict-edly, Screven County according to Harper, Proc. Biol. Soc. Washington, 65:36, 1952.)" Regarded as identical with *tuza* by Merriam, N. Amer. Fauna, 8:113, January 31, 1895.

1. *G. p. fontanelus* (Sherman, 1940). Type locality "7 mi. NW Savannah, Chatham Co., Georgia". Known only from Chatham County, eastern Georgia.
2. *G. p. pinetis* (Rafinesque, 1817). For type locality see above. Range in Georgia and Florida.

Geomys mobilensis Merriam, 1895

Southeastern Pocket Gopher of Mobile Bay, tuza del sureste de la bahía de Mobile

1895. *Geomys tuza mobilensis* Merriam, N. Amer. Fauna, 8:119. Type locality "Point Clear, Mobile Bay, Baldwin Co., Alabama".

2006. *Geomys mobilensis*: Sudman, Wickliffe, Horner, Smolen, Bickham, and Bradley, J. Mamm. 87:674.

Geomys streckeri Davis, 1943

Strecker's pocket gopher, tuza texana del Carrizo

1940. *Geomys personatus minor* Davis, Texas Agric. Exp. Station Bull., 590:29. Type locality "Carrizo Springs, Dimmit Co., Texas". Not *Geomys minor* Gidley, 1922, a fossil. Known only from type locality.

Geomys texensis Merriam, 1895

Llano pocket gopher, tuza del centro de Texas

1895. *Geomys texensis* Merriam, N. Amer. Fauna, 8:137. Type locality "Mason, Mason Co., Texas.

1. *G. t. bakeri* Smolen, Pitts and Bickham, 1993. Type locality "1 mile E D'Hanis, Medina Co., Texas". Known only from Medina, Uvalde, and Zavala counties, central-south Texas.
2. *G. t. llanensis* Bailey, 1905. Type locality "Llano, Texas". Known only from Gillespie, Kimble, and Zavala counties, central-southern Texas.
3. *G. t. texensis* Merriam, 1895. For type locality see above. Known only from Mason, McCulloch, and San Saba counties, central Texas.

Geomys tropicalis Goldman, 1915

Tropical pocket gopher, tuza tropical

1915. *Geomys personatus tropicalis* Goldman, Proc. Biol. Soc. Washington, 28:134. Type locality "Altamira, Tamaulipas".

Supplementary material

Supplementary material 1. GenBank accession numbers for the cytochrome b and cytochrome oxidase subunit 1 sequences and the authors who recorded the sequences in GenBank used in the present study.

<https://mastozoologiamexicana.com/therya/index.php/THERYA/article/view/6153/1468>

Supplementary material 2. Phylogenetic inference using neighbor-joining for the cytochrome b sequences using the large set of data.

<https://mastozoologiamexicana.com/therya/index.php/THERYA/article/view/6153/1469>

Supplementary material 3. Phylogenetic inference using neighbor-joining, unweighted pair group method with arithmetic mean (UPGMA), maximum-parsimony, maximum-likelihood, and Bayesian inference for the cytochrome b and cytochrome oxidase subunit 1 sequences.

<https://mastozoologiamexicana.com/therya/index.php/THERYA/article/view/6153/1470>

Supplementary material 4. Percentage of genetic differences of Cytb between the species examined in the family Geomyidae.

<https://mastozoologiamexicana.com/therya/index.php/THERYA/article/view/6153/1471>

