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EVOLUTIONARY RELATIONSHIPS OF POCKET GOPHERS OF THE GENUS *PAPPOGEOMYS* (RODENTIA: GEOMYIDAE)

MARK S. HAFNER,* DAVID J. HAFNER, JAMES W. DEMASTES, GERALD L. HASTY, JESSICA E. LIGHT, AND THERESA A. SPRADLING

Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, LA 70803, USA (MSH, GLH, JEL)
New Mexico Museum of Natural History, Albuquerque, NM 87104, USA (DJH)
Department of Biology, University of Northern Iowa, Cedar Falls, IA 50614, USA (JWD, TAS)
Present address of GLH: P.O. Box 1088, Lihue, HI 96766, USA
Present address of JEL: Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843, USA

Once encompassing as many as 9 species of pocket gophers spread across most of the Mexican Altiplano, the genus *Pappogeomys* is now restricted to a single species, *P. bulleri*, occupying the mountains, tablelands, and coastal plains near the western end of the Trans-Mexican Volcanic Belt in west-central Mexico. Herein, we review the taxonomic history of *Pappogeomys* and examine relationships among populations of *P. bulleri* from throughout the geographic range of the species based on analyses of nonpreferentially stained karyotypes and mitochondrial and nuclear sequence data. Results of these analyses are concordant and reveal 3 major clades of *P. bulleri* that are separated by major physiographic features of the region, including the Sierra Madre del Sur and drainages of the Río Grande de Santiago, Río Ameca, Río Ayuquila, and Río Armería. We reduce the number of subspecies of *P. bulleri* from 9 to 5 valid forms and provide a revised synonymy of the species.

Key words: chromosomes, mitochondrial DNA, nuclear DNA, *Pappogeomys*, pocket gophers, systematics

Pappogeomys Merriam, 1895, is a monotypic genus of pocket gophers endemic to the states of Colima, Jalisco, and Nayarit in west-central Mexico. *Pappogeomys* is sister to *Cratogeomys* within the Geomyidae (Merriam 1895), and the phylogenetic position of these taxa relative to other geomyids was investigated 1st by Russell (1968a) based on morphological characters, then by Honeycutt and Williams (1982), DeWalt et al. (1993), and Demastes et al. (2002) based on molecular characters. Russell's (1968a) examination of both fossil and extant geomyids led him to place *Cratogeomys* as a subgenus of *Pappogeomys*, and this taxonomy was followed by most authorities (e.g., Hall 1981; Patton 1993) until recently (Patton 2005). Because studies of molecular characters (e.g., Demastes et al. 2002; DeWalt et al. 1993; Honeycutt and Williams 1982) have documented considerable genetic divergence between *Cratogeomys* and *Pappogeomys*, most modern authorities have returned to the original taxonomy of Merriam (1895) in which *Cratogeomys* and *Pappogeomys* are recognized as valid genera (Hafner et al. 2008; Patton 2005).

* *Correspondent: namark@lsu.edu*

The single species of *Pappogeomys*, *P. bulleri*, is a small geomyid, with total length rarely >270 mm and body mass usually <250 g. The species occupies a wide variety of habitats, including forested highlands, mountain meadows, sparsely vegetated plains, and coastal lowlands from near sea level to >3,000 m at the western end of the Trans-Mexican Volcanic Belt (Fig. 1). In sharp contrast with virtually all other geomyids, *P. bulleri* appears to avoid cultivated fields in valley bottoms. Specimens of *P. bulleri* show the suite of adaptations characteristic of fossorial mammals, including a stocky build, fusiform shape, powerful jaws and incisors, large and powerful forelimbs, and reduced hind limbs and hips. Since its original description in 1892, *P. bulleri* has been the subject of several taxonomic revisions in which authors have recognized 1 species with 2 subspecies (Merriam 1895), 1 species with 8 subspecies (Goldman 1939), 2 species with 8 subspecies (Russell 1968b), or 1 species with 5 subspecies (this study).

Taxonomic history of P. bulleri.—In August of 1892, Oldfield Thomas described *Geomys bulleri* from a single fluid-preserved specimen collected by Dr. A. C. Buller near the town of Talpa in Jalisco, Mexico (Thomas 1892). One month later, Merriam (1892), who was apparently unaware of Thomas' new species, described *Geomys nelsoni* from a series of 6 specimens collected by E. W. Goldman from the north slope of the Sierra Nevada de Colima, also in Jalisco, Mexico.

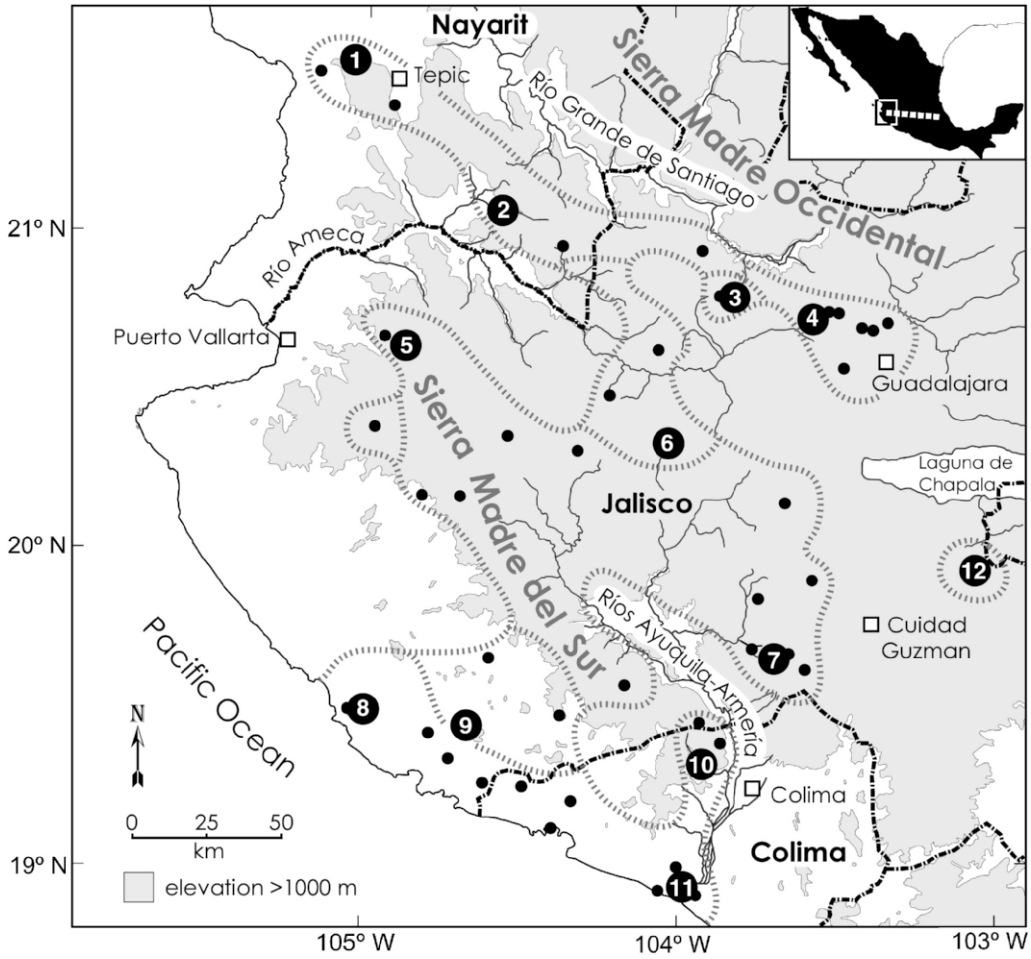

Fig. 1.—Collecting localities of pocket gophers (*Pappogeomys bulleri*) sampled for this analysis (numbered circles). Complete locality information is listed in Appendix I. Smaller (filled) circles show all other localities from which *P. bulleri* is known to date. Shaded area indicates elevations above 1,000 m. Dashed lines show approximate distributions of the 9 currently recognized subspecies of *P. bulleri*. Dashed line in inset shows approximate east–west extent of the Trans-Mexican Volcanic Belt.

Realizing that Thomas' name, *bulleri*, had priority over his name, *nelsoni*, Merriam synonymized *nelsoni* under *bulleri* and recognized *G. bulleri* as the type species of a new genus, *Pappogeomys*, in his 1895 monographic revision of the Geomyidae (exclusive of *Thomomys*). In that same publication, Merriam (1895) also described a new species, *P. albinasus*, on the basis of a single specimen collected near Guadalajara, Mexico. In the spring of 1897, E. W. Nelson and E. A. Goldman collected 25 additional specimens of *Pappogeomys* from Jalisco and Nayarit, and 42 years later Goldman (1939) published a revision of the genus based largely on those specimens. In his revision, Goldman (1939) synonymized Merriam's *P. albinasus* with *P. bulleri* and recognized 8 subspecies of *P. bulleri*: *albinasus* (Merriam 1895), *amecensis* (new), *bulleri* (Thomas 1892), *burti* (new), *flammeus* (new), *lagunensis* (new), *nayaritensis* (new), and *nelsoni* (Merriam 1892).

In 1957, Russell recognized an isolated population of *Pappogeomys* from the mountains south of Lake Chapala as a new species, *P. alcorni* (Russell 1957). In his subsequent revision of the genus, Russell (1968b) recognized 2 species (*P. alcorni* and *P. bulleri*) and 7 subspecies within *P. bulleri*, including 5 of Goldman's (1939) 8 subspecies (*albinasus*, *amecensis*, *bulleri*, *burti*, and *nayaritensis*) and 2 new subspecies (*infuscus* and *lutulentus*). One year later, Genoways and Jones (1969) described an 8th subspecies of *Pappogeomys*, *P. b. melanurus*, from the mountains of southwestern Jalisco near the town of Tecomate.

Demastes et al. (2003) used mitochondrial DNA (mtDNA) and morphometric data to examine the species status of *P. alcorni* and concluded that Russell's (1957) *P. alcorni* warrants recognition only as a subspecies of *P. bulleri* (*P. b. alcorni*). Thus, the genus *Pappogeomys* currently comprises a single species, *P. bulleri*, and 9 subspecies: *albinasus*, *alcorni*, *amecensis*, *bulleri*, *burti*, *infuscus*, *lutulentus*, *melanurus*, and *nayaritensis*. Herein, we reexamine relationships among populations of *P. bulleri* based on nonpreferentially stained karyotypes and mtDNA and nuclear DNA (nuDNA) sequences.

Materials and Methods

Specimens examined.—We examined 23 specimens of *P. bulleri* from 11 localities (Fig. 1; Appendix I) for 2 mitochondrial genes (cytochrome *b* [*Cytb*] and cytochrome *c* oxidase subunit I [*CoI*]) and 1 nuclear gene (β-fibrinogen [β-*fib*]). One

additional specimen (Fig. 1, locality 12) was sampled for *Cytb* only. *Cytb* sequence data for 4 specimens of *P. bulleri* were taken from Demastes et al. (2002—GenBank accession numbers AF302168 and AF302177), Demastes et al. (2003—AF454094–AF454096 [3 fragments from a single specimen]), and DeWalt et al. (1993—L11900). One β-*fib* sequence was taken from Spradling et al. (2004—AY331249). Outgroup taxa consisted of specimens of *Cratogeomys castanops*, *C. goldmani*, *C. fumosus*, and *C. merriami*. Sequence data for these species were obtained from Demastes et al. (2002—AF302161, AF302171, AF302176, and AF302179) and Hafner et al. (2004—AY545538) for *Cytb*, Spradling et al. (2004—AY331076, AY331077, and AY331243) for *CoI*, and Hafner et al. (2005—AY880903) for β-*fib*. The remaining specimens are new to this study and were collected using standard trapping methods approved by the American Society of Mammalogists (Gannon et al. 2007). Species designations follow the taxonomy of Hafner et al. (2004, 2005).

Chromosomal analysis.—Nonpreferentially stained chromosome preparations were made from 14 individuals from 9 localities (Appendix I) following the postmortem field protocol described by Hafner and Sandquist (1989). Diploid number (2n) and fundamental number (FN) were determined for each individual based on counts of at least 10 cells and inspection of several digital images from each individual.

Mitochondrial DNA analysis.—Whole DNA was extracted (DNeasy Tissue Kit; QIAGEN, Inc., Valencia, California) from 20–25 mg of tissue. Extractions followed the manufacturer's protocol, with the 2 final elutions of 100 μl combined for each sample. Extractions were amplified by polymerase chain reaction for the mitochondrial loci *CoI* (1,551 base pairs [bp]) and *Cytb* (1,140 bp). Polymerase chain reaction and sequencing protocols were performed as described in Hafner et al. (2008). All sequenced regions received at least 2 times coverage, by sequencing in both strand directions or by repeated coverage using different sequencing primers and reactions. Sequences were submitted to GenBank (GenBank accession numbers EU880351–EU880373 for *CoI* and EU880374–EU880394 for *Cytb*).

Phylogenetic analyses were conducted using PAUP* version 4.0b10 (Swofford 2002) for maximum-likelihood analyses and MrBayes version 3.1.1 (Ronquist and Huelsenbeck 2003) for Bayesian analyses. Phylogenetic congruence of the locus-specific data was tested by the incongruence length difference test (''homogeneity partition test'' of PAUP*) as a prelude to combining the separate locus-specific data into a single data set. MODELTEST version 3.7 (Posada and Crandall 1998) was used as an aid in selecting nucleotide substitution models used in phylogenetic analyses.

For maximum-likelihood analyses, branch support was estimated as nonparametric bootstrap support from 1,000 replicates of random taxon addition in a heuristic search using tree-bisection-reconnection branch swapping. All Bayesian analyses consisted of paired runs of 4 Markov chain Monte Carlo analyses each, using default settings and iterated for 10^7 generations sampled every 100 generations, and discarding the initial 500 trees sampled. In the default settings, elements of substitution rate matrices are assigned equal priors, equilibrium nucleotide frequencies have equal priors, branch lengths have an exponential prior distribution, and alternative topologies have equal prior support.

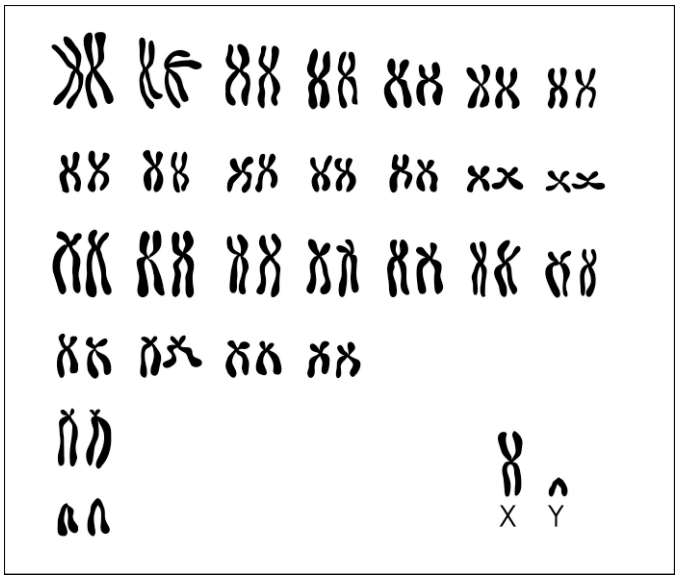

FIG. 2.—Nonpreferentially stained karyotype of *Pappogeomys bulleri*, 2n = 56, FN = 106 (LSUMZ 36568) from 8 km west of Ahuacatlán, Nayarit, México.

Nuclear DNA sequence analysis.—Sequence data were obtained for 23 specimens of *P. bulleri* from 11 collecting localities. Amplification of the 7th intron of β-*fib* and a small portion (11 bp) of exon-8 was accomplished using the FIB-B17U and FIB-B17L primers of Prychitko and Moore (1997) as outlined by Spradling et al. (2004). β-*fib* polymerase chain reaction products were prepared for sequencing using the QIAquick PCR Purification Kit (QIAGEN, Inc.). Sequencing reactions were performed at Iowa State University's DNA Facility using their ABI 3730 DNA Analyzer (Applied Biosystems, Inc., Foster City, California). Sequences were aligned and heterozygosity was evaluated by eye using Sequencher 4.1.2 software (Gene Codes Corporation, Ann Arbor, Michigan). Sequences were submitted to GenBank (GenBank accession numbers EU880395–EU880416). Sequences were analyzed using parsimony (PAUP* version 4.0b10—Swofford, 2002).

RESULTS

Chromosomal variation.—Each of 8 individuals from 5 populations (populations 2, 4, 7, 9, and 10 in Fig. 1) for which 2n and FN could confidently be determined possessed identical nonpreferentially stained karyotypes with 2n = 56 and FN = 106 (Fig. 2). These karyotypes had approximately equal numbers of metacentric–submetacentric and subtelocentric chromosomes, a single pair of small-to-medium acrocentric chromosomes, and a unique pair of large subtelocentric (nearly acrocentric) chromosomes (Fig. 2). The Y-chromosome is a small acrocentric and the X-chromosome is a large metacentric chromosome. Although poor-quality preparations precluded

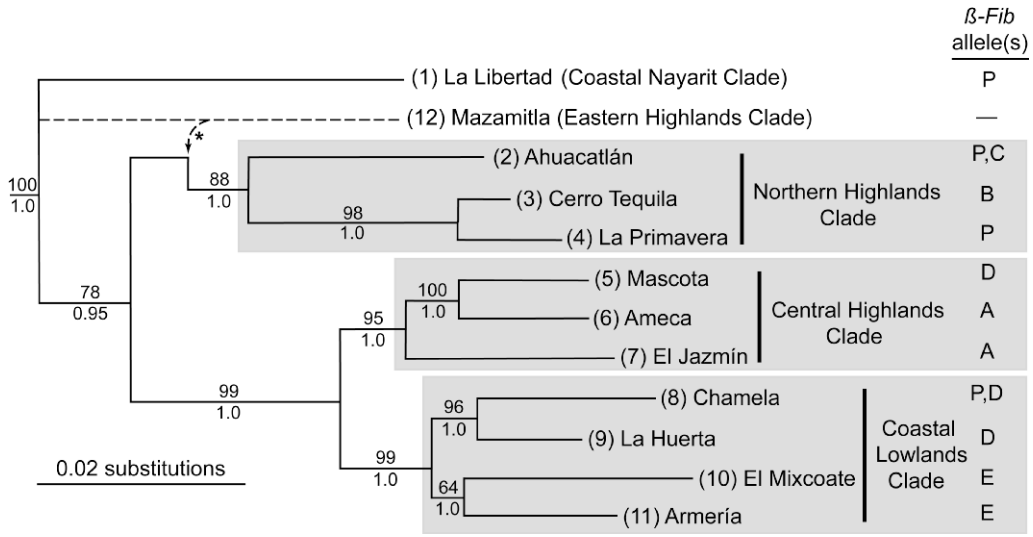

Fig. 3.—Maximum-likelihood phylogram for 12 populations of pocket gophers (*Pappogeomys bulleri*) collected in western Mexico (Fig. 1). The phylogram is based on combined sequences obtained from the mitochondrial *Cytb* and *CoI* genes. Numbers above the branches show maximum-likelihood bootstrap support and numbers below are Bayesian posterior probability values. Locality numbers refer to the map (Fig. 1), and full localities are listed in Appendix I. Nuclear β-fibrinogen alleles present at each locality are listed on the right, and presumed relationships among these alleles are shown in Fig. 4. Mitochondrial DNA sequences for the specimen from locality 12 (Mazamitla, Jalisco) were obtained from a 48-year-old study skin (Demastes et al. 2003). This specimen formed an unresolved polytomy at the base of the tree (this analysis) or grouped with pocket gophers from the Northern Highlands clade (indicated by an asterisk [Demastes et al. 2003]).

confident determination of 2n and FN in 6 additional individuals, specimens from localities 1, 5, and 6 possessed the 2 characteristic pairs of acrocentric and subtelocentric chromosomes.

Mitochondrial DNA analysis.—The amount of locus-specific sequence obtained varied across samples. As a result, all 1,551 bp of *CoI* data and 1,011 bp (positions 130–1,140) of *Cytb* were retained for analysis (total of 2,562 bp). Alignments resulted in nucleotide variability across samples and loci consisting entirely of substitutions (no indels). Two nucleotide substitution models were chosen for use in the maximum-likelihood and partitioned Bayesian analyses. In MODELTEST terminology, the models (with number of free parameters) were GTR+I (9) for *Cytb* and TVM+I+G (9) for *CoI*. These were drawn from the 95% Akaike's information criterion (95% AIC) credibility set constructed by MODELTEST and included the best-supported models as indicated by MODELTEST AIC. One maximum-likelihood tree was recovered for each analysis, and all Bayesian analyses converged on stationarity of tree log-likelihood values within 1,000 generations.

Independent phylogenetic analyses of the *CoI* and *Cytb* data returned very similar topological results (data available on request). The only difference (discussed below) involved placement of the sample from locality 1 (Fig. 1). The incongruence length difference test found no significant incongruence between the 2 data sets ($P = 0.532$), so the *CoI* and *Cytb* data sets were combined in subsequent maximum-likelihood analyses, which used the GTR+I+G model.

In both the maximum-likelihood and Bayesian analyses, *P. bulleri* was monophyletic relative to the outgroups, and outgroup selection did not affect topology within *P. bulleri*. In all analyses of both genes, ingroup specimens from 10 of the 12 localities were consistently separated into 3 major clades: 1 from the highlands of southern Nayarit and central Jalisco (''Northern Highlands clade''), another from the highlands of western Jalisco (''Central Highlands clade''), and the 3rd from the lowlands of coastal Jalisco and Colima (''Coastal Lowlands clade'' [Fig. 3]). The latter 2 grouped together in all analyses with ≥99% bootstrap support in the maximum-likelihood analysis and 1.0 posterior probability in Bayesian analyses of both genes.

The sample of *P. bulleri* from coastal Nayarit (''Coastal Nayarit clade'' [Fig. 3]) was consistently placed as the outgroup to all other samples of *P. bulleri*, except in the maximum-likelihood analysis of the *Cytb* sequences, in which the coastal Nayarit sample was grouped with the Northern Highlands clade with weak (61%) bootstrap support. DNA extracted from a study skin of the presumed extinct subspecies, *P. b. alcorni* (Fig. 1, locality 12) by Demastes et al. (2003) yielded only 427 bp of *Cytb*. Phylogenetic analyses in which *Cytb* samples from all specimens were trimmed to 427 bp consistently placed *P. b. alcorni* (''Eastern Highlands clade'') near the base of the tree, creating a polytomy (Fig. 3). Thus, in total, 5 phylogenetic lineages were identified: 3 major clades, each represented by specimens from several localities within distinct physiographic regions (i.e., Northern Highlands, Central Highlands, and Coastal Lowlands), plus the Coastal Nayarit and Eastern Highlands clades, both detected at single localities.

Substructure within the 3 major clades of *P. bulleri* also was consistent across analyses of mtDNA. Within each clade, samples clustered in accordance with an isolation-by-distance model, with geographically close samples grouping together to the exclusion of more distant samples. The only exception was 1 of 3 individuals from El Jazmín, Jalisco (CNMA 43265 from locality 7; see Appendix I for museum acronyms) that grouped

consistently with a specimen collected >150 km away near Mascota, Jalisco (LSUMZ 36580; locality 5) rather than with the other 2 specimens collected at the El Jazmín locality. CNMA 43265 from El Jazmín and the Mascota specimen were identical at the *Cytb* locus and showed only 2 differences (1 transition [TS] and 1 transversion [TV]) at the *CoI* locus. In contrast, CNMA 43265 from El Jazmín showed 3.8% (uncorrected *p*-distance) and 4.0% (Kimura 2-parameter [K2P] distance) *Cytb* divergence (35 TS, 4 TV) and 2.9% (*p*-distance) and 3.0% (K2P distance) *CoI* divergence (38 TS, 7 TV) from the 2 other specimens of *P. bulleri* collected on the same day at the same locality (the other 2 individuals were identical at both loci). DNA contamination or accidental switching of tissues can be ruled out because laboratory errors of that sort would have caused CNMA 43265 from El Jazmín to be identical to the Mascota specimen at both, rather than just 1, of the 2 mitochondrial loci. It appears that the pocket gopher population at El Jazmín contains 2 divergent *Cytb* haplotypes, 1 of which is very similar to that at Mascota. This conclusion is supported by nuDNA evidence, in that all 3 individuals collected at El Jazmín, including the individual with the divergent mtDNA haplotype, share the same β-*fib* allele.

Nuclear DNA sequence analysis.—Of the 434 bp of the β-*fib* intron-7 examined, there were 9 nucleotide positions that varied in the 23 specimens of *P. bulleri* sampled. All variable nucleotide sites were in the intron. There were 6 unique β-*fib* alleles (Figs. 3 and 4), and 1 individual (TTU 45109 from Chamela) showed a pattern of nucleotide heterozygosity consistent with it being the result of the combination of the D and P alleles. One allele (P) matched the outgroup (*C. merriami*, GenBank AY331243) at all sites that were variable within the ingroup, thus parsimony analysis using outgroup rooting placed this allele as the most likely ancestral sequence to all other alleles (Fig. 4). This presumed primitive allele (P) was found in 4 populations of *P. bulleri* (localities 1, 2, 4, and 8) that span the range of the species, and this allele likely represents a retained ancestral allele in each of these populations. Parsimony analysis of β-*fib* allele sequences yielded a tree with no apparent homoplasy; alleles A–E each appear to be independently derived from the P allele sequence (Fig. 4). Patterns of β-*fib* allele sharing generally were consistent with results from the mtDNA sequence analysis (Fig. 3); allele A was found only in the Central Highlands clade, allele E was found only in the El Mixcoate–Armería subclade of the Coastal Lowlands clade, and alleles B and C are unique to individual clades. The single disagreement between the mtDNA and β-*fib* results involves allele D, which appears to unite the Mascota individual (locality 5) from the Central Highlands clade with the Chamela (locality 8) and La Huerta (locality 9) individuals from the Coastal Lowlands clade.

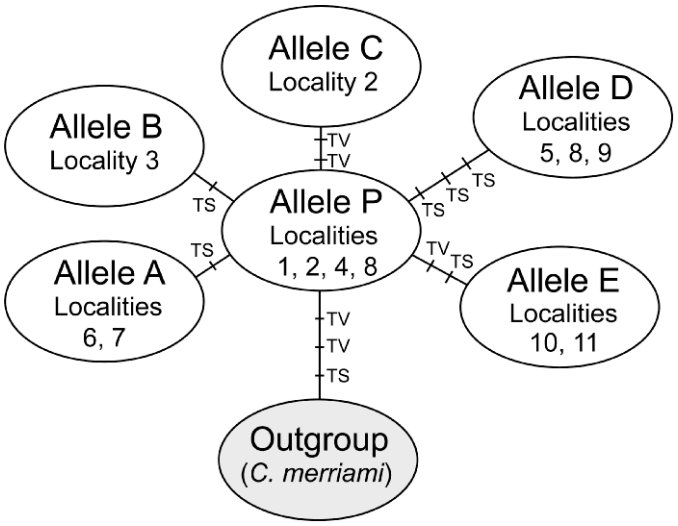

FIG. 4.—Network of 6 β-fibrinogen alleles found in *Pappogeomys bulleri* (locality numbers from Fig. 1 and Appendix I). Base substitutions are indicated as either transitions (TS) or transversions (TV).

DISCUSSION

Our karyotype of *P. bulleri* (2n = 56) disagrees with the 2n = 58 karyotype reported for the genus by Honeycutt and Williams (1982:214). The report of Honeycutt and Williams (1982) was based on a personal communication from R. J. Baker, and the 2n = 58 karyotype was not figured and locality information and museum specimen number for the karyotyped individual were not provided. Although the report of Honeycutt and Williams (1982) suggests presence of 2n variation within *P. bulleri*, our finding of identical karyotypes (2n and FN) in specimens representing 4 of the 5 genetically defined lineages within *P. bulleri* suggests absence of chromosomal variation.

The combined mtDNA and nuDNA data sets support a well-resolved tree with 3 major clades and 5 lineages within *P. bulleri* (Fig. 3). The Central Highlands clade occupies the mountains and plateaus above 1,000 m elevation east of the main arc of the Sierra Madre del Sur (Fig. 5). This clade is approximately 4.5% (*Cytb* uncorrected *p*-distance; 4.6% K2P distance) genetically divergent from the Coastal Lowlands clade and is separated from that clade by the intervening Sierra Madre del Sur and the common drainage of the Río Ayuquila and Río Armería. All specimens of the Coastal Lowlands clade collected to date have occurred below approximately 500 m elevation. To the north, the Central Highlands clade is separated from the Northern Highlands clade by the Río Ameca drainage (Fig. 5). The Central Highlands clade is approximately 7% (*Cytb* uncorrected *p*-distance; 7.2% K2P distance) genetically divergent from the Northern Highlands clade, which extends from the vicinity of Guadalajara, Jalisco, west into southern Nayarit at elevations between 1,000 and 3,000 m. The combined Central Highlands and Coastal Lowlands clades show approximately 7.5% (*Cytb* uncorrected *p*-distance; 7.4% K2P distance) genetic divergence from the Northern Highlands clade. Finally, specimens from the Coastal Nayarit clade (locality 1) and the Eastern Highlands clade (locality 12) show an average of almost 8% (*Cytb* uncorrected *p*-distance; 8.3% K2P distance) genetic divergence from all other clades of *P. bulleri* (Fig. 5). These rather high levels of genetic divergence between clades of *P. bulleri*, plus the fact that multiple individuals from certain localities and clades (e.g.,

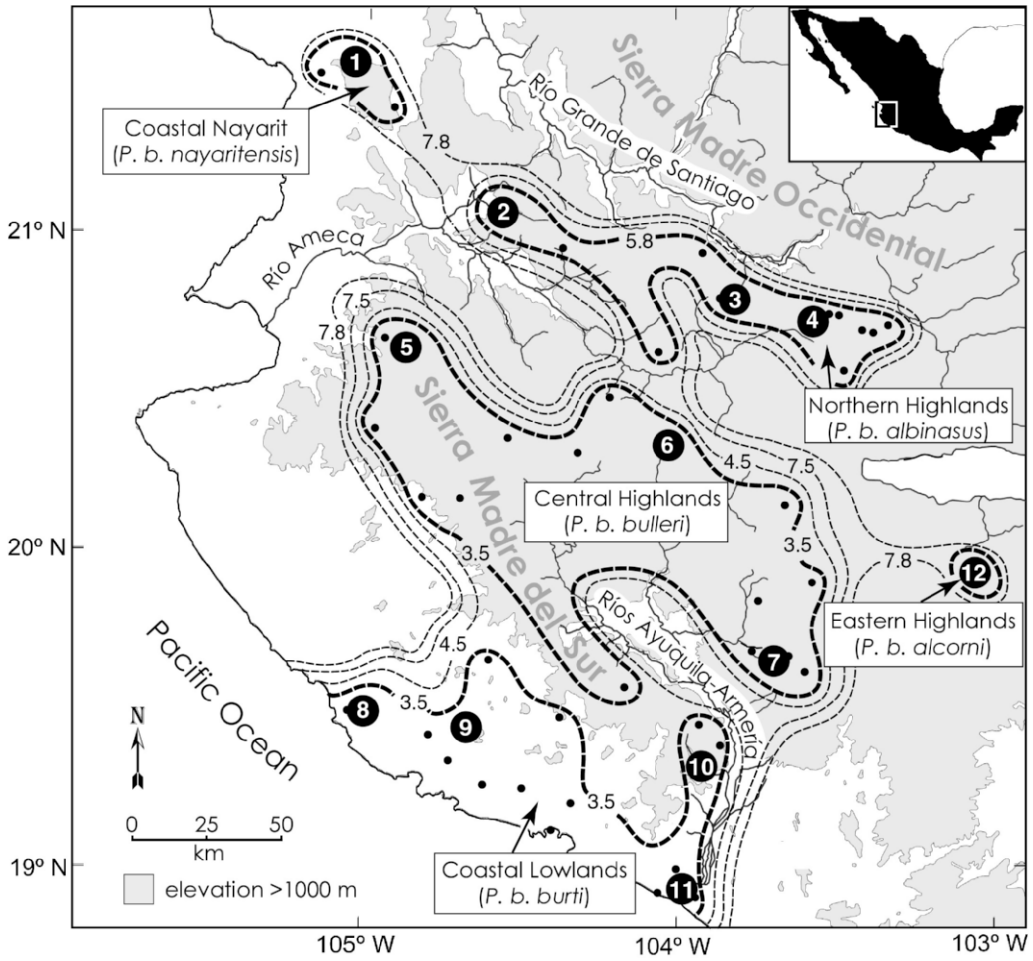

FIG. 5.—Map of the study area showing the approximate geographic distribution of the 5 subspecies of *Pappogeomys bulleri* recognized in this study (Fig. 3). Average percent *Cytb* sequence divergences (uncorrected *p*-distances) are indicated on the dashed lines linking the clades. Major river drainages and elevational shifts separate the subspecies of *P. bulleri*.

7 of 8 individuals from the Ahuacatlán locality, and 5 of 6 individuals from the Central Highland clade) are fixed for unique β-*fib* alleles suggests that the clades of *P. bulleri* have been separated genetically for a long period of time. However, observed levels of *Cytb* divergence within *P. bulleri* are consistent with those measured between 4 conspecific clades of *C. fumosus* (average uncorrected *p*-distance = 7.4%, range 4.0–8.8% [Hafner et al. 2004]) and 26 conspecific populations of *Thomomys bottae* (average *p*-distance = 11.8%, range 0.8–15.8% [Smith 1998]).

The single disagreement between the mtDNA and β-*fib* results—presence of the β-*fib* D allele in populations that belong to different mtDNA clades (Fig. 3)—could result from retention of a primitive allele in the Central Highlands and Coastal Lowlands clades (which are sister clades), allelic convergence, or from secondary contact between these clades. The possibility that the D allele signals a special phylogenetic relationship between specimens from localities 5, 8, and 9 is contradicted by morphological evidence. All specimens of the Coastal Lowlands clade (*P. bulleri burti*; see ''Taxonomic Conclusions'') are exomorphologically distinguishable from all other specimens of *P. bulleri* by presence of short, sparse pelage that is dark gray in color. The specimens from localities 8 and 9 share this feature with all other members of the Coastal Lowlands clade (Fig. 3), whereas the specimen from locality 5 has the longer, browner pelage characteristic of animals of the Central Highlands clade (*P. b. bulleri*).

Relationships among chewing lice hosted by Pappogeomys.—In their morphological investigation of chewing lice (*Geomydoecus*) hosted by *P. bulleri*, Price and Hellenthal (1989) recognized 2 species and 5 subspecies of lice whose distributions showed little correspondence with the distributions of the 9 currently recognized subspecies of *P. bulleri* (Fig. 1). However, louse distributions match very closely the distributions of the genetically defined clades of their hosts identified in this study (Fig. 5). For example, the louse subspecies *Geomydoecus b. bulleri* is restricted to populations of pocket gophers belonging to the Central Highlands clade (localities 5–7 in Figs. 1 and 5). Three taxa of lice (*G. b. melanuri*, *G. b. intermedius*, and *G. burti*) are restricted to hosts of the Coastal Lowlands clade (localities 8–11), and the louse *Geomydoecus nadleri* is restricted to populations of *P. bulleri* from coastal Nayarit (locality 1) plus populations of hosts belonging to the Northern Highlands clade (localities 2–4).

Although gophers from coastal Nayarit (locality 1) are not closely related to gophers of the Northern Highlands clade (localities 2–4), these clades probably come into contact in southeastern Nayarit, which may explain presence of the same louse species (*G. nadleri*) in both clades.

Taxonomic Conclusions

The 9 currently recognized subspecies of *P. bulleri* were described almost entirely on the basis of differences in body size and pelage coloration (e.g., Genoways and Jones 1969; Goldman 1939; Russell 1968b), characteristics that are now known to be highly labile in pocket gophers. The ecophenotypic plasticity of body size in pocket gophers has been amply demonstrated (Hafner et al. 2008; Patton and Brylski 1987; Smith and Patton 1988; Wilkins and Swearingen 1990), and it is widely known that pelage color can vary dramatically in pocket gophers, even among closely related and geographically proximate populations (e.g., Krupa and Geluso 2000).

The limited taxonomic value of the characters used to define the current subspecies of *P. bulleri* (body size and pelage coloration) may explain why the genetically defined clades identified in this analysis (Figs. 3 and 5) show little correspondence to traditional subspecies boundaries (Soler-Frost et al. 2003; Patton 2005; Fig. 1). Instead, the boundaries of the genetically defined clades show close correspondence to key physiographic features in this region of Mexico, including major river drainages and mountain chains (Fig. 5).

We have chosen to recognize subspecies within *P. bulleri* based primarily on genetic groups rather than retain subspecific determinations based on morphological characters that we know to be of limited taxonomic value in pocket gophers. Our recognition of subspecies is in agreement with genetic definitions outlined by Lidicker (1960, 1962) and expanded by Endler (1977). Patton and Smith (1990) and Hafner et al. (2008) used similar logic to reduce the number of subspecies in the pocket gophers they studied by 67% and 85%, respectively. Analyses of mtDNA and nuDNA were generally concordant in defining 3 major clades and a total of 5 lineages within *P. bulleri*, which we herein recognize as subspecies.

Pappogeomys Merriam, 1895

Geomys Thomas, 1892:196. Type species *Geomys bulleri* Thomas.

Pappogeomys Merriam, 1895:145. Redesignation of *Geomys bulleri* Thomas. The genus *Pappogeomys* is monotypic.

Pappogeomys bulleri (Thomas, 1892)

Buller's Pocket Gopher

(Synonymy under subspecies.)

Geographic range.—Endemic to west-central Mexico, including portions of southern Nayarit, central and southern Jalisco, and Colima. Patchily distributed in a wide variety of habitats, including forested highlands, mountain meadows, sparsely vegetated plains, and coastal lowlands. Elevational range sea level to approximately 3,000 m.

Description.—Body size small for family. Total length rarely exceeds 270 mm, and most individuals are much smaller (approximately 200–230 mm). Pelage medium in length and covering most of body, except in coastal form (*P. b. burti*), which has short, sparse pelage. Color varies geographically from light brown to dark gray. Most specimens have a small nasal patch consisting of white or pale buffy hairs. Tail is usually naked, white, and less than one-half the combined length of the head and body.

Pappogeomys bulleri albinasus Merriam, 1895

P. albinasus Merriam, 1895:149. Type locality "Atemajac, a suburb of Guadalajara, Jalisco, Mexico." Type specimen adult female, skin and skull, United States National Museum number 34138/46215, collected 21 May 1892 by E. W. Nelson, original number 2654.

P. b. albinasus Goldman, 1939. First use of current name combination.

P. b. infuscus Russell, 1968b:610. Type locality "Cerro Tequila, 10,000 feet, 7 mi. S and 2 mi. W Tequila, Jalisco, Mexico."

P. b. nayaritensis Goldman, 1939:94. Type locality "Jalisco [Xalisco], about 10 miles south of Tepic, Nayarit, Mexico (altitude 5,000 feet)." Part, only specimens east of approximately −104.7° longitude are referable to *P. b. albinasus* as it is currently understood.

Geographic range.—Known from sparsely vegetated plains and forested slopes of central Jalisco and southeastern Nayarit between the drainages of the Río Grande de Santiago and the Río Ameca. Longitudinal range from approximately −103° (vicinity of Guadalajara, Jalisco) to approximately −104.8° (east of Tepic, Nayarit). Elevational range approximately 1,000–3,000 m.

Comments.—*Pappogeomys b. albinasus* is equivalent to the "Northern Highlands clade" as defined genetically in this report (Fig. 3).

Pappogeomys bulleri alcorni Russell, 1957

P. alcorni Russell, 1957:359. Type locality "4 mi. W Mazamitla, 6600 ft., Jalisco, Mexico." Type specimen adult female, skin and skull, University of Kansas Museum of Natural History number KU 39806, collected by J. R. Alcorn on 18 October 1950, original number 12835.

P. b. alcorni Demastes et al., 2003. First use of current name combination.

Geographic range.—Known only from vicinity of type locality in the forested mountains south of Laguna de Chapala. Elevation approximately 2,000 m.

Comments.—*Pappogeomys b. alcorni* is equivalent to the "Eastern Highlands clade" as defined genetically in this report (Fig. 3). This subspecies is known from only 4 museum specimens, all collected between the years 1950 and 1966, and

recent attempts have failed to locate individuals in the wild (Demastes et al. 2003). In April 1993, the authors (MSH, DJH, JWD, and TAS) set traps for pocket gophers on a steep, densely forested hillside about 8 km (by road) west of Mazamitla. The leaf litter was thick, making it extremely difficult to locate active burrows. The narrow diameter of the burrows suggested that their occupants were *P. b. alcorni* (and not individuals of the much larger species *C. fumosus*, which was abundant in the nearby agricultural fields), but we were unable to capture a specimen. We returned to this locality in March of 1997 and found no active burrows in the forested areas, but again noted high levels of activity of *C. fumosus* in the surrounding meadows and agricultural fields.

Pappogeomys bulleri bulleri (Thomas, 1892)

Geomys bulleri Thomas, 1892:196. Type locality ''Talpa, Mascota, Jalisco, Mexico, 8500 feet.'' Type specimen adult female preserved in alcohol with skull extracted, British Museum of Natural History number 1892.10.7.16, collected by A. C. Buller (date of collection and original number unknown).

G. nelsoni Merriam, 1892:164. Type locality ''north slope of the Sierra Nevada de Colima, Jalisco, Mexico (altitude 1,980 meters or 6,500 feet).''

P. bulleri Merriam, 1895. Redesignation of *Geomys bulleri*.

P. b. bulleri Goldman, 1939. First use of current name combination.

P. b. amecensis Goldman, 1939:97. Type locality ''mountains near Ameca, Jalisco, Mexico (altitude 6,500 feet).''

P. b. flammeus Goldman, 1939:95. Type locality ''Milpillas, 5 miles southwest of San Sebastian, northwestern Jalisco, Mexico (altitude 3,800 feet).''

P. b. lagunensis Goldman, 1939:96. Type locality ''La Leguna, Sierra de Juanacatlan, northwestern Jalisco, Mexico (altitude 6,500 feet).''

P. b. lutulentus Russell, 1968b:612. Type locality ''Sierra de Cuale, 7,300 feet, 9 km N El Teosinte (= Desmoronado), Jalisco, Mexico.''

Geographic range.—Patchily distributed in the Sierra Madre del Sur and tablelands of west-central Jalisco south of the Río Ameca drainage and east of the Río Ayuquila and Río Armería drainages. Known elevational range approximately 1,000–3,000 m.

Comments.—*Pappogeomys b. bulleri* is equivalent to the ''Central Highlands clade'' as defined genetically in this report (Fig. 3).

Pappogeomys bulleri burti Goldman, 1939

P. b. burti Goldman, 1939:97. Type locality ''Tenacatita Bay, southwest coast of Jalisco, Mexico.'' Type specimen adult female, skin and skull, Museum of Zoology, University of Michigan number UMMZ 81017, collected by W. H. Burt on 19 February 1938, original number unknown.

P. b. melanurus Genoways and Jones, 1969:748. Type locality ''7.5 mi. SE Tecomate, 1500 ft, Jalisco, Mexico.''

Geographic range.—Coastal plain and foothills of Colima and Jalisco west of the Sierra Madre del Sur. Elevational range from near sea level to approximately 500 m.

Comments.—*Pappogeomys b. burti* is equivalent to the ''Coastal Lowlands clade'' as defined genetically in this report (Fig. 3).

Pappogeomy bulleri nayaritensis Goldman, 1939

P. b. nayaritensis Goldman, 1939:94. Type locality ''Jalisco [Xalisco], about 10 miles south of Tepic, Nayarit, Mexico (altitude 5,000 feet).'' Type specimen adult male, skin and skull, United States National Museum number USNM 88124, collected by E. W. Nelson and E. A. Goldman on 10 April 1897, original number 10886. Goldman (1951:201) lists the town of Jalisco as ''... about 5 miles south of Tepic,'' and the present-day town of Xalisco is located approximately 4 miles (6.4 km) south of Tepic, Nayarit. Part, specimens east of approximately −104.7° longitude probably are referable to *P. b. albinasus*.

Geographic range.—Known only from the forested mountains west and south of Tepic, Nayarit. Elevational range 1,000–1,500 m.

Comments.—*Pappogeomys b. nayaritensis* is equivalent to the ''Coastal Nayarit clade'' as defined genetically in this report (Fig. 3).

Resumen

Alguna vez incluyó hasta 9 especies de tuzas distribuidas a través de la mayor parte del Altiplano Mexicano, el género *Pappogeomys* se encuentra ahora restringido a una sola especie, *P. bulleri*, ocupando montañas, mesetas, y las planicies costeras cerca del límite occidental de la Faja Volcánica Transmexicana en el occidente-centro de México. Aquí, nosotros revisamos la historia taxonómica de *Pappogeomys* y examinamos las relaciones entre las poblaciones de *P. bulleri* a través del rango geográfico de la especie basados en análisis de cariotipos teñidos no preferenciales y de datos de secuencias de ADN mitocondrial y nuclear. Los resultados de estos análisis concuerdan y revelan 3 clados principales y 2 clados marginales de *P. bulleri* que se encuentran separados por las principales características fisiográficas de la región, incluyendo la Sierra Madre del Sur y las cuencas del Río Grande de Santiago, Río Ameca, Río Ayuquila, y Río Armería. Reducimos el número de subespecies de *P. bulleri* de 9 a 5 formas válidas y proveemos una sinonimia revisada de las especies.

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APPENDIX I

Specimens examined.—Specimens of *Pappogeomys bulleri* new to this study are housed in the Mammal Collection of Louisiana State University Museum of Natural Science (LSUMZ) or in the Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA). Specimens also used in previous studies of *P. bulleri* (Demastes et al. 2002, 2003; DeWalt et al. 1993) are housed in the Museum, Texas Tech University (TTU) or the Museum of Natural History, University of Kansas (KU). All specimens were collected in Mexico, and all were used in the molecular analyses. Specimens designated by "[k]" also were used in the chromosomal analysis. Locality numbers (in parentheses) are indicated in Figs. 1, 3, and 5. COLIMA: (10) 1 km SE El Mixcoate, 530 m (CNMA 43269 [k]); (11) 4 km S Armería, 10 m (LSUMZ 36563 [k], CNMA 41925 [k]); JALISCO: (3) Cerro Tequila, 7 miles S, 2 miles W Tequila, 2,900 m (LSUMZ 36082); (4) 1 km SW La Primavera, 1,585 m (LSUMZ 36565 [k]); (5) 9 miles NW Mascota, 1,300 m (LSUMZ 36580 [k]); (6) 20 km S Ameca, 2,223 m (LSUMZ 36581 [k]); (7) El Jazmín, 1,763 m (LSUMZ 36578, CNMA 43265 [k], 43266, 43267); (8) 5 km S Chamela, adjacent to N side of Chamela Station (TTU 45109); (9) 8.6 km (by road) SW La Huerta, 374 m (LSUMZ 36562 [k]); (12) 3 miles (5 km) WSW Mazamitla, Sierra del Tigre (KU 61328); NAYARIT: (1) La Libertad, 10 km NE Jalcocotán, 1,034 m (LSUMZ 36574 [k], CNMA 43263 [k]); (2) 8.4 km W Ahuacatlán, 1,100 m (LSUMZ 34338) and 8 km W Ahuacatlán, 1,000 m (LSUMZ 36567 [k], 36568 [k], CNMA 41927 [k], 41930–41933).