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SYSTEMATIC REVISION OF POCKET GOPHERS OF THE *CRATOGEOMYS GYMNURUS* SPECIES GROUP

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The genus *Cratogeomys*, particularly members of the *Cratogeomys gymnurus* species group, account for much of the high species diversity of pocket gophers in the Trans-Mexican Volcanic Belt. Recent molecular studies of this species group have shown strong discordance between genetically defined clades and current species taxonomy. Accordingly, we investigated relationships among the 5 species in the *C. gymnurus* species group using mitochondrial and nuclear DNA, chromosomes, and morphological characters. Although quantitative morphometrics provided little discrimination among species or clades within this group, the molecular data sets were consistent in identifying 5 allopatric clades, none of which corresponded to any of the 5 currently recognized species. Four of these 5 genetically defined clades lack clear diagnosability, and so are grouped into the single polytypic species, *C. fumosus*. The fifth clade is diagnosable based on multiple characters, including nuclear genotype, chromosomal diploid number, parasite fauna, and qualitative morphological characters. Accordingly, we resurrect Merriam's (1895) species *planiceps* to represent members of this clade, which occurs in the Volcán de Toluca and Valle de Bravo regions of central Mexico. Based on the observation that differences in diploid number usually signal reproductive isolation between populations of pocket gophers, we hypothesize that *C. fumosus* and *C. planiceps* are reproductively incompatible. We provide synonymies and descriptions for these 2 species, along with a key to this species group, which is now called the *C. fumosus* species group.

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

Rodents of the New World family Geomyidae (pocket gophers) range from southern Canada into northwestern Colombia and reach their highest diversity in the Trans-Mexican Volcanic Belt (TMVB) between latitudes 18° and 22°N (Alberico 1990; Hall 1981; Fig. 1). This tectonically and volcanically active region (Johnson and Harrison 1990) contains some of the highest peaks in North America, and the geologic and physiographic complexity of the TMVB doubtlessly has contributed to the high diversity of pocket gophers in this region. The TMVB supports species belonging to 5 of the 6 extant genera of geomyids; only *Geomys* does not occur in the TMVB, whereas the genera *Pappogeomys* and *Zygogeomys* are restricted to the TMVB.

High taxonomic diversity of pocket gophers can result from an increase in number of genera or species (or both), but it also can be a taxonomic artifact caused by oversplitting of taxa. The high species diversity of pocket gophers in southern Central America (between latitudes 6° and 10°N; Fig. 1) involves only a single genus (*Orthogeomys*) with 6 species. With the exception of *O. thaeleri* (Alberico 1990; Sudman and Hafner 1992), the taxonomic validity of these species has been upheld in recent studies (Demastes et al. 1996; Hafner 1991; Sudman and Hafner 1992). High gopher diversity in the mountains, deserts, and gulf-coast regions of northern Mexico and southern United States (30°–34°N; Fig. 1) involves 3 genera (*Cratogeomys*, *Geomys*, and *Thomomys*), each of which has been the subject of recent taxonomic investigations (e.g., Demastes et al. 2002; Jolley et al. 2000; Patton and Smith 1990). High gopher diversity observed in the TMVB (18°–22°N) results mainly from an increase in number of genera (5 in total), but also from an increase in number of species in the genus *Cratogeomys*. The taxonomic status of the 5 genera of the TMVB has been validated repeatedly (e.g., Hafner 1982; Hafner et al. 1994; Honeycutt and Williams 1982), and this high genus-level diversity suggests that the TMVB might have been the center of origin of the Geomyidae from ancestral rodent stock.

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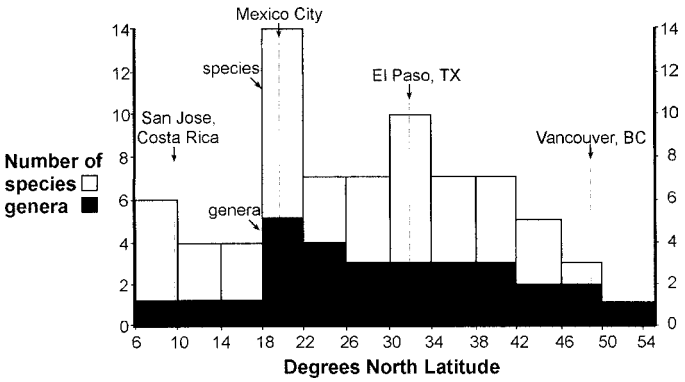

FIG. 1.—Number of pocket gopher species (open bars) and genera (solid bars) represented in 4° latitudinal increments from northwestern Colombia (left) to southern Canada (right). The 3 peaks in species diversity coincide with major physiographic and bioclimatic features. The southernmost diversity peak (near the latitude of San José, Costa Rica) coincides with the extreme topographic diversity (central highlands and coastal lowlands) at these latitudes. The peak in diversity near the latitude of Mexico City coincides with the Trans-Mexican Volcanic Belt and the interdigitation of temperate and tropical habitats at these latitudes. The northernmost peak in diversity (near the latitude of El Paso, Texas) coincides with the presence of 3 disparate habitats (mountain, desert, and gulf coast habitats) at these latitudes. Taxonomic conclusions of this study and those of Demastes et al. (2003) together reduce the number of geomyid species in the 18°–22°N latitudinal increment from 14 to 10 species.

Half of the geomyid species of the TMVB (7 of 14 species) belong to the genus *Cratogeomys*, which has not been formally revised since Russell's (1968) morphological study. A recent molecular investigation of *Cratogeomys* by Demastes et al. (2002) called into question the taxonomic validity of several species in the *C. gymnurus* species group, which raises the possibility that the high species diversity of geomyids in the TMVB (Fig. 1) might result, in part, from oversplitting of taxa. In this study, we investigate the taxonomic status of the *C. gymnurus* species group.

TAXONOMIC HISTORY OF THE *Cratogeomys GYMNURUS* SPECIES GROUP

Merriam (1895) recognized 3 genera of large-bodied, highland pocket gophers in Mexico: *Zygogeomys*, *Cratogeomys*, and *Platygeomys*. The taxonomy of *Zygogeomys* has been studied by Hafner (1982), Hafner and Barkley (1984), Honeycutt and Williams (1982), and Russell (1968), and this genus is not considered further in this study. Merriam's (1895) concept of *Cratogeomys* included the species *castanops*, *merriami*, *fulvescens*, *perotensis*, *estor*, *oreocetes*, and *peregrinus*, and his genus *Platygeomys* included the species *fumosus*, *gymnurus*, *tylorhinus*, and *planiceps*. In 1946, Hooper synonymized *Platygeomys* under *Cratogeomys*, arguing that the morphological distinction between Merriam's *Cratogeomys* and *Platygeomys* did not warrant generic status (Hooper 1946). Two decades later, Russell (1968) recognized *Cratogeomys* as a subgenus of *Pappogeomys* (Merriam 1895), which prior to 1968 included only 2 small-bodied species of pocket gopher (*bulleri* and *alcorni*) from western Mexico. Honeycutt and Williams (1982) returned the subgenus *Cratogeomys* to generic level, and most geomyid specialists today recognize both genera (*Pappogeomys* and *Cratogeomys*). According to most authorities (including the upcoming 3rd edition of *Mammal Species of the World* by Wilson and Reeder, in press), the genus *Pappogeomys* contains the species *bulleri* and *alcorni* (although *alcorni* has been synonymized under *bulleri* recently by Demastes et al. 2003), and the genus *Cratogeomys* contains all large-bodied, highland gophers of Mexico, except *Zygogeomys trichopus*.

Russell (1968) divided *Cratogeomys* into 2 morphological groups: the *castanops* group, including the species *castanops* and *merriami*; and the *gymnurus* group, including *gymnurus*, *fumosus*, *tylorhinus*, *neglectus*, and *zinseri*. Lee and Baker (1987:13) reported two karyotypes within *C. castanops* (2n = 46 and 42) and concluded that, "At this time, it probably is best to recognize two species. . .[*castanops* and *goldmani*, respectively]." They did not offer a formal taxonomic revision because of discontinuities between morphologically (Russell 1968) and karyotypically defined groups within *castanops* and uncertainty as to the oldest available name (*goldmani* or *subnubilus*). Reciprocal monophyly of the *castanops* and *gymnurus* species groups is supported by morphological (Russell 1968), chromosomal (Berry and Baker 1972), and molecular (Demastes et al. 2002; DeWalt et al. 1993; Honeycutt and Williams 1982) evidence.

Berry and Baker (1972) reported indistinguishable karyotypes for 4 species of the *gymnurus* group (*fumosus*, *tylorhinus*, *zinseri*, and *gymnurus*; diploid chromosomal number [2n] = 40, fundamental number [FN] = 76), and León et al. (2001) reported the same karyotype for the 5th member of this group, *C. neglectus*. Lee and Baker (1987) used the karyotype of *gymnurus* for outgroup comparison to study chromosomal evolution within the *castanops* group of *Cratogeomys*. Although they affirmed that members of the *gymnurus* group "have indistinguishable nondifferentially stained karyotypes" (Lee and Baker 1987:3), they figured and described a 2n = 38 karyotype for a specimen of *C. gymnurus* without comment. Thus, Lee and Baker's (1987) statement and figured karyotype are at odds. With the exception of this single conflicting report by Lee and Baker (1987), all previously reported karyotypes for the *gymnurus* group have 2n = 40 and FN = 76.

Demastes et al. (2002) used mitochondrial DNA (mtDNA) sequence data to investigate relationships within the genera *Cratogeomys* and *Pappogeomys*, including the 5 species in Russell's (1968) *gymnurus* group of *Cratogeomys*. Although 5 mtDNA clades were identified within the *C. gymnurus* species group (clades A–E in figure 2 of Demastes et al. 2002), these clades did not correspond to the 5 recognized species within the group. Demastes et al. (2002) concluded that Russell's (1968) morphology-based study, in which species descriptions were based largely on body size and fur coloration, was most likely confounded by convergent evolution of morphological characters that now are known to be highly plastic in geomyids (Patton and Brylski 1987; Smith and Patton 1988; Wilkins and Swearingen 1990). The present research expands upon the

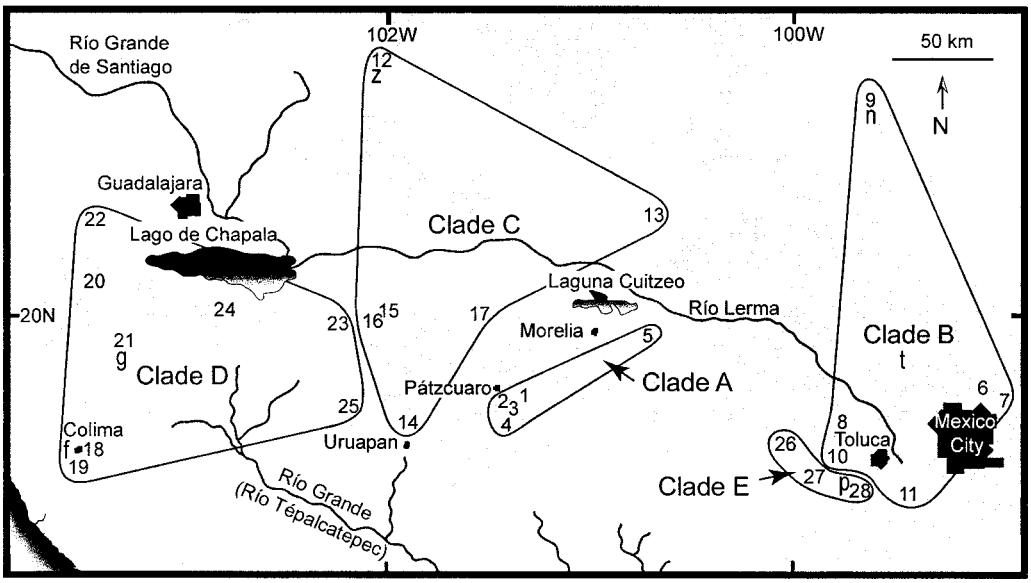

FIG. 2.—Geographic distribution of *Cratogeomys* clades A–E in central Mexico. Shading depicts areas above 2,000 m elevation, and numbers refer to collecting localities listed in Appendix I. Lowercase letters indicate type localities, as follows: f = *Cratogeomys fumosus*; g = *C. gymnurus*; n = *C. neglectus*; p = *C. planiceps*; t = *C. tylorhinus*; z = *C. zinseri*.

Demastes et al. (2002) study of the *C. gymnurus* species group by adding new collection localities and new data sets, including chromosomes, morphometrics, and nuclear DNA sequence data.

MATERIALS AND METHODS

Specimens examined.—A combined total of 35 specimens representing the 5 species in the *C. gymnurus* species group were used in the mtDNA, nuclear DNA, and chromosomal analyses (Appendix I). Samples included at least 1 specimen from the type locality (or as near as possible to the type locality) for each species, except *C. tylorhinus* (Fig. 2). Cytochrome-*b* (*Cytb*) sequence data for 22 of these specimens were taken from DeWalt et al. (1993—GenBank accession nos. L11903, L11905, L11909) and Demastes et al. (2002—GenBank accession nos. AF 302155, 302156, 302162–302167, 302169, 302170, 302173–302175, 302178–302183). The remaining 13 specimens are new to this study and were captured in the wild using standard trapping methods approved by the American Society of Mammalogists (Animal Care and Use Committee 1998). Outgroup taxa consisted of 3 *Cratogeomys* species in the *castanops* species group (Appendix I). Sequence data for these species were obtained from the literature (DeWalt et al. 1993—GenBank accession nos. L11904, L11906, L11908). The morphometric analysis involved a total of 293 specimens (Appendix II).

Mitochondrial DNA analysis.—Genomic DNA was isolated from liver or kidney tissue using the DNeasy Tissue Kit (QIAGEN Inc., Valencia, California). Amplification by polymerase chain reaction (PCR) and sequencing of the mitochondrial gene cytochrome-*b* (1140 base pairs [bp]) were performed using combinations of the following primers: L14724, L15513 (Irwin et al. 1991), L15049, H15579, H15906 (Spradling et al. 2001), and H15154 (''MVZ04'' in Smith and Patton 1993). PCR amplifications were performed in 50 μl reaction volumes usually using primers L14724 with H15906. If this primer pair failed to yield acceptable internal sequences, PCR amplifications were performed in 50 μl reaction volumes using primers L14724 with H15154, L15049 with H15579, and L15513 with H15906. Each PCR amplification included 2.5 μl of each primer (10 μM), 4 μl of $MgCl_2$ (10 mM), 2 μl of deoxynucleotide-triphosphate mixture (10 mM solution; dATP, dGTP, dCTP, and dTTP, each 100 mM), 5 μl of 10× *Taq* buffer, and 0.2 μl of *Taq* DNA polymerase. The amplification protocol required an initial denaturation stage of 94°C for 2 min, followed by 38 PCR cycles of 94°C (1 min), 47°C (1 min; 4 cycles), then 56°C (1 min; 34 cycles), and 72°C (1 min), and a final extension of 72°C for 10 min.

Prior to sequencing, amplified products were purified using the QIAquick PCR Purification Kit protocol (QIAGEN, Inc., Valencia, California). Amplified products were sequenced in both directions at the Museum of Natural Science, Louisiana State University. Each 10 μl reaction included 2 μl of BigDye™ (Applied Biosystems, Perkin-Elmer Corporation, Boston, Massachusetts), 3.2 μl of 0.5 μM primer, 1.8 μl of double-distilled H_2O, and 3 μl of amplification product. Samples were sequenced for 30 cycles at 96°C (10 s), 50°C (5 s), and 60°C (4 min). Sequences were purified with Centri-Sep spin columns (Princeton Separations, Adelphia, New Jersey) and were electrophoresed using an ABI Prism 377 Genetic Analyzer (Perkin Elmer, Foster City, California). Sequences were edited using Sequencher Version 4.1 software (Gene Codes Corporation, Ann Arbor, Michigan) and then aligned using Se-Al v2.0a11 (http://evolve.zps.ox.ac.uk/Se-Al/Se-Al.html) and submitted to GenBank (GenBank accession nos. AY545529–AY545541).

To generate the best maximum-likelihood tree for these data, Modeltest (Version 3.06; Posada and Crandall 1998) was used to examine the fit of 56 models of nucleotide substitution to the sequence data. Of the models tested, the general time-reversible model including invariant sites and among-site rate variation (GTR+I+Γ—Gu et al. 1995; Yang 1994) was chosen for subsequent analyses because it provided the best approximation of the *C. gymnurus Cytb* data using the fewest parameters, as assessed by likelihood-ratio tests (Huelsenbeck and Rannala 1997). A full heuristic maximum likelihood search was conducted using the successive-approximations approach with the GTR+I+G model in PAUP* 4.0b10 (Swofford 2002). A full heuristic bootstrap (200 pseudoreplicates) also was performed using the GTR+I+Γ model on a Beowolf cluster (8 alpha-processor nodes).

For comparative purposes, maximum parsimony and Bayesian analyses also were performed on the mtDNA data. Equally weighted maximum parsimony searches were performed with 100 random taxon addition replicates and tree-bisection-reconnection branch swapping (PAUP*4.0b10, Swofford 2002). A full heuristic bootstrap (1,000 replicates) was performed using parsimony criteria. Bayesian phylogenetic analyses were performed using MrBayes 2.01 (Huelsenbeck and Ronquist 2001). The GTR+I+Γ model was used in all analyses and model parameters were treated as unknown variables with uniform priors and were estimated as part of the analysis. Bayesian analyses were initiated with random starting trees, run for 2×10^6 generations with 4 incrementally heated chains (Metropolis-coupled Markov chain Monte Carlo—Huelsenbeck and Ronquist 2001), and sampled at intervals of 100 generations. Two independent Bayesian analyses were run to avoid entrapment on local optima, and log-likelihood scores were compared for convergence (Huelsenbeck and Bollback 2001; Leaché and Reeder 2002). Stationarity was assessed by plotting the log likelihood scores of sample points against generation time. All burn-in points (the first 2,500 trees) were discarded. The retained equilibrium samples were used to generate a 50% majority rule consensus tree with the percentage of samples recovering any particular clade representing that clade's posterior probability (Huelsenbeck and Ronquist 2001).

In an effort to adjust for potential biases between purines and pyrimidines in the dataset, 3rd positions also were RY-coded, which pools purines (adenine and guanine, R) and pyrimidines (cytosine and thymine, Y) into 2-state categories (R, Y—Phillips and Penny 2003). Maximum likelihood, parsimony, and Bayesian analyses were performed as described above for the RY-coded dataset. Sequence divergence between taxa was calculated using uncorrected *p* distances in PAUP*4.0b10. Average divergence within and between clades was calculated by hand.

Nuclear DNA analysis.—Amplification of a portion of the nuclear recombination activating gene 1 (*Rag1*) was performed using primers *Rag1*-S70 and *Rag1*-S115 (5 μM each—Steppan et al. 2004) with 1 X PCR Master Mix (Promega Corporation, Madison, Wisconsin) in a 20-μl reaction. Thermal-cycle parameters included an initial denaturation at 95°C (1 min), followed by 40 cycles of 95°C (1 min), 42°C (45 s), and 72°C (1 min), and a final extension at 72°C (10 min). When necessary to improve yield, a 2nd amplification was performed on cleaned PCR products using internal primers *Rag1*-F (5′ – GCT GGA GTT CAG AAG CCA GTC C – 3′) and *Rag1*-Rb (5′ – GGT ACT GAG ATG GAT CTT ACT GC – 3′). Conditions for this reaction differed from the initial amplification only in the number of cycles (35) and the annealing temperature (52°C). *Rag1*-F and *Rag1*-Rb were used to sequence both strands of DNA. The final *Rag1* PCR products were prepared for sequencing using the QIAquick PCR Purification Kit (QIAGEN, Inc., Valencia, California). Sequencing reactions were performed using the CEQ 2000 Dye Terminator Cycle Sequencing with Quick Start Kit and were assessed using the CEQ 8000 Genetic Analysis System (Beckman Coulter, Inc., Fullerton, California). Sequences were aligned and heterozygosity was evaluated by eye using Sequencher 4.1.2 software (Gene Codes Corporation, Ann Arbor, Michigan), and sequences were submitted to GenBank (GenBank accession nos. AY545589–AY545597). Three of 25 individuals showed evidence of heterozygosity at this locus. Each heterozygote's DNA-sequence pattern could most simply be explained by assuming a combination of alleles present in other individuals, thereby keeping the number of ''haplotypes'' necessary to explain each ''diplotype'' to a minimum (Brumfield et al. 2003).

Chromosomal analysis.—Non-preferentially stained chromosome preparations were made from 8 individuals following the postmortem field protocol described by Hafner and Sandquist (1989). Specimen localities were selected to represent the 5 major groups identified in the mtDNA analysis (1—3 individuals, at least 1 male, per group; see beyond). Karyotypes were arranged following Berry and Baker (1972) to facilitate comparison with karyotypes figured therein. Diploid number and fundamental number were determined for each individual and compared with karyotypes of *C. tylorhinus*, *C. gymnurus*, *C. fumosus*, and *C. zinseri* figured or described by Berry and Baker (1972—as *Pappogeomys*) and *C. neglectus* described by León et al. (2001).

Morphometric analysis.—For morphometric analyses, 12 mensural characters were recorded from 293 specimens (Appendix II) of the *C. gymnurus* species group. These variables included occipital-nasal length, occipital-incisor length, nasal length, rostral width, width of interorbital constriction, zygomatic breadth, cranial width, mastoid breadth, diastema length, length of maxillary tooth row, occlusal length of upper molars 1 and 2, and occlusal length of upper molar 3. This set of characters has proven useful in previous morphometric analyses of pocket gophers (Patton and Smith 1990; Smith and Patton 1988). Ninety-six of the measured specimens were juveniles (occipital-nasal length <50 mm), had missing data, or were from localities that could not be found on current maps of Mexico. These specimens were removed from the study, resulting in the morphological analysis of 197 specimens (111 females and 86 males). Univariate and multivariate statistical analyses were performed using SAS software (SAS Institute, Inc. 2000) and Systat 8.0 (SPSS 1998). The measured cranial characters for the *C. gymnurus* species group were examined for sexual dimorphism using an unpaired *t*-test. Past work has shown strong sexual dimorphism in pocket gophers (Patton and Smith 1990; Smith and Patton 1988) and our results support this finding ($P < 0.01$ for all characters except occlusal length of upper molars 1 and 2 and occlusal length of upper molar 3). Accordingly, males and females were analyzed separately.

To decrease the effect of individual size variation, all characters were transformed logarithmically and standardized (Burbrink 2001; Corruccini 1975; dos Reis et al. 1990; Gould 1966). Discriminant function analysis and size-free canonical discriminant analysis (dos Reis et al. 1990) were performed on the size-adjusted characters to determine if gophers could be separated with an a priori hypothesis of group membership to the mitochondrial clades identified by Demastes et al. 2002. Sample sizes for each clade were as follows: A = 14, B = 11, C = 20, D = 55, and E = 11 for females; A = 20, B = 7, C = 14, D = 42, and E = 3 for males. Discriminant function analysis and canonical discriminant analysis also were performed on Russell's (1968) species groups. Because of small sample sizes for the species *C. fumosus*, *C. neglectus*, and *C. zinseri*, discriminant function analysis and canonical discriminant analysis were performed only on *C. gymnurus* ($n = 44$ for females, $n = 43$ for males) and *C. tylorhinus* ($n = 52$ for females, $n = 33$ for males). Prior to discriminant function analysis, stepwise discriminant function analyses (stepwise and backward) were performed on the size-adjusted cranial characters to identify those characters most useful in discriminating among groups. Discriminant function analyses were performed using all cranial characters as well as those selected by stepwise discriminant analysis. Analyses also were performed using equal and estimated prior probabilities of group membership. The analyses generated classification matrices (jackknifed and unjackknifed) that showed the percentage of specimens correctly assigned to their a priori groupings.

RESULTS

Mitochondrial DNA analysis.—Of the 1,140 bp of cytochrome-*b* examined, 275 were potentially parsimony informa-

tive. Parsimony, maximum likelihood, and Bayesian analyses of these sequences for the 35 ingroup and 3 outgroup specimens yielded trees that differed only in minor rearrangements of terminal branches. Phylogenetic analysis of the RY-coded sequences resulted in loss of resolution at the base of the tree and, again, only minor rearrangements of terminal taxa. In the parsimony tree (Fig. 3), 4 of the 5 mtDNA clades (clades A, B, D, and E in Fig. 3) originally reported by Demastes et al. (2002) are supported by likelihood bootstrap values of 100%, and the 5th clade (clade C) received 90% likelihood bootstrap support. Posterior probabilities from the Bayesian analysis were similar to—but generally higher than—maximum likelihood bootstrap support values (Cummings et al. 2003—values available upon request).

Percentage of sequence divergence within clades was small and ranged from 0.70% to 2.19% (clade A = 2.19%, clade B = 0.76%, clade C = 1.40%, clade D = 1.89%, and clade E = 0.70%). Percentage of sequence divergence among clades A–D averaged 7.42% (A–B = 7.75%, A–C = 7.15%, A–D = 8.73%; B–C = 3.95%, B–D = 8.82%; C–D = 8.16%), and sequence divergence between clade E and all other clades was higher, averaging 11.07% (A–E = 11.23%, B–E = 11.60%, C–E = 10.66%, and D–E = 10.88%).

It is obvious that the 5 mtDNA clades (A–E; Fig. 3) do not correspond to the 5 species currently recognized in the *gymnurus* group. Neither of the 2 widespread species, *C. gymnurus* and *C. tylorhinus*, is monophyletic, and the 3 peripherally isolated monotypic species (*C. fumosus*, *C. neglectus*, and *C. zinseri*) appear to be genetically indistinct from neighboring samples. As first reported by Monterrubio et al. (2000), *C. neglectus* differs from a nearby individual of *C. tylorhinus* by only 0.2% uncorrected sequence divergence. Demastes et al. (2002) reported that *C. zinseri* differs from individuals of *C. tylorhinus* by only 0.6%, and *C. fumosus* differs from nearby individuals of *C. tylorhinus* and *C. gymnurus* by only 0.8% to 1.0%. The highest genetic divergence within the *C. gymnurus* group is approximately 11% uncorrected sequence divergence measured between clade E and the other mtDNA clades (Fig. 3).

Nuclear DNA analysis.—Of the 530 bp of *Rag1* examined, only 9 nucleotide positions were variable (Fig. 4). These sites comprised 8 alleles in *C. gymnurus*-group gophers, with the "P" allele presumed primitive because it is identical (for these 9 nucleotides) to the allele present in the outgroup, *C. castanops*. The remaining 7 alleles support the 5 clades identified in the mtDNA analysis (Fig. 3). Specifically, alleles A1, A2, and A3 are restricted to clade A and are distributed in a north-to-south pattern with the following genotype proportions: A1A1 (1 individual); A2A2 (2 individuals); A3A3 (1 individual). Allele B was found only in clade B and appeared in the homozygous state in all 5 individuals examined. Allele C was restricted to clade C with the following genotype proportions: CC (3); CP (2); PP (1). Allele D was found only in clade D, in which 6 individuals were DD homozygotes and 1 individual was a DP heterozygote. Finally, allele E was restricted to clade E and all 3 individuals examined were EE homozygotes. Alleles A1, D, and E appear to be derived directly from the presumed primitive allele (1 step each; Fig. 4), whereas alleles B and C are derived either directly from the primitive allele (3 steps each) or indirectly through alleles C and E, respectively (2 steps each; Fig. 4).

Chromosomal analysis.—In agreement with Berry and Baker (1972) and León et al. (2001), all 5 individuals karyotyped from clades A–D had the typical *gymnurus* group karyotype of 2n = 40 and FN = 76 (Fig. 5A). Two additional specimens previously karyotyped by MSH (MVZ [Museum of Vertebrate Zoology] 153889 from 6.5 km S Pátzcuaro, Michoacán [clade A], and MVZ 153894 from 1 km N, 2 km W Nahuatzén, Michaocán [clade C]) also had 2n = 40 and FN = 76. In all cases, the nondifferentially stained chromosomes were identical to those figured by Berry and Baker (1972:figures 4, 5). In contrast, all 3 individuals karyotyped from clade E had 2n = 38, FN = 72 (Fig. 5B). The contradictory report by Lee and Baker (1987) of a 2n = 38 karyotype for *C. gymnurus* (see above) is from an individual within clade A from 9.4 miles SE Pátzcuaro. As reported above, our karyotype from a nearby locality (MVZ 153889 from 6.5 km S Pátzcuaro) has 2n = 40 and FN = 76. We accept the statement by Lee and Baker (1987:3) that members of the *gymnurus* group have "indistiguishable nondifferentially stained karyotypes," and we assume (based on our karyotypes from clade A) that the 2n = 38 karyotype reported by Lee and Baker (1987) was described and figured in error.

Morphometric analysis.—Regardless of the type of multivariate analysis used (canonical discriminant analysis or discriminant function analysis), neither the mitochondrial clades A–E (Demastes et al. 2002; this study) nor species recognized by Russell (1968—*C.gymnurus* and *C. tylorhinus*) could be discriminated using the cranial characters chosen for analysis. For female pocket gophers, a posteriori rates of correct classification into the mitochondrial clades were 57–64% (clade A), 82% (clade B), 55–60% (clade C), 69–95% (clade D), and 36–82% (clade E). For male pocket gophers, rates of correct classification into mitochondrial groups were 60–65% (clade A), 43% (clade B), 79–86% (clade C), 79–93% (clade D), and 33–100% (clade E). Rates of correct classification of females into Russell's (1968) species were 75–82% and 77–83% for *C. gymnurus* and *C. tylorhinus*, respectively. Classification of males was 77–84% and 67–88% for *C. gymnurus* and *C. tylorhinus*, respectively.

Discussion

Species concepts.—Where possible, we employ the biological species concept in this study, although we realize that the small population size, patchy distribution, and genetic structure of pocket gopher populations often makes this, or any other, species concept operationally difficult to apply (Steinberg and Patton 2000). In such cases, our species concept is based on monophyly and diagnosability of lineages. In pocket gophers, reproductive barriers between species usually, but not always, are signaled by chromosomal differences and in most cases, differences in diploid number (Hafner et al. 1987; Patton 1985; but see Patton et al. 1984 and Thaeler 1968 for contrary examples). Thus, differences in diploid number, if present,

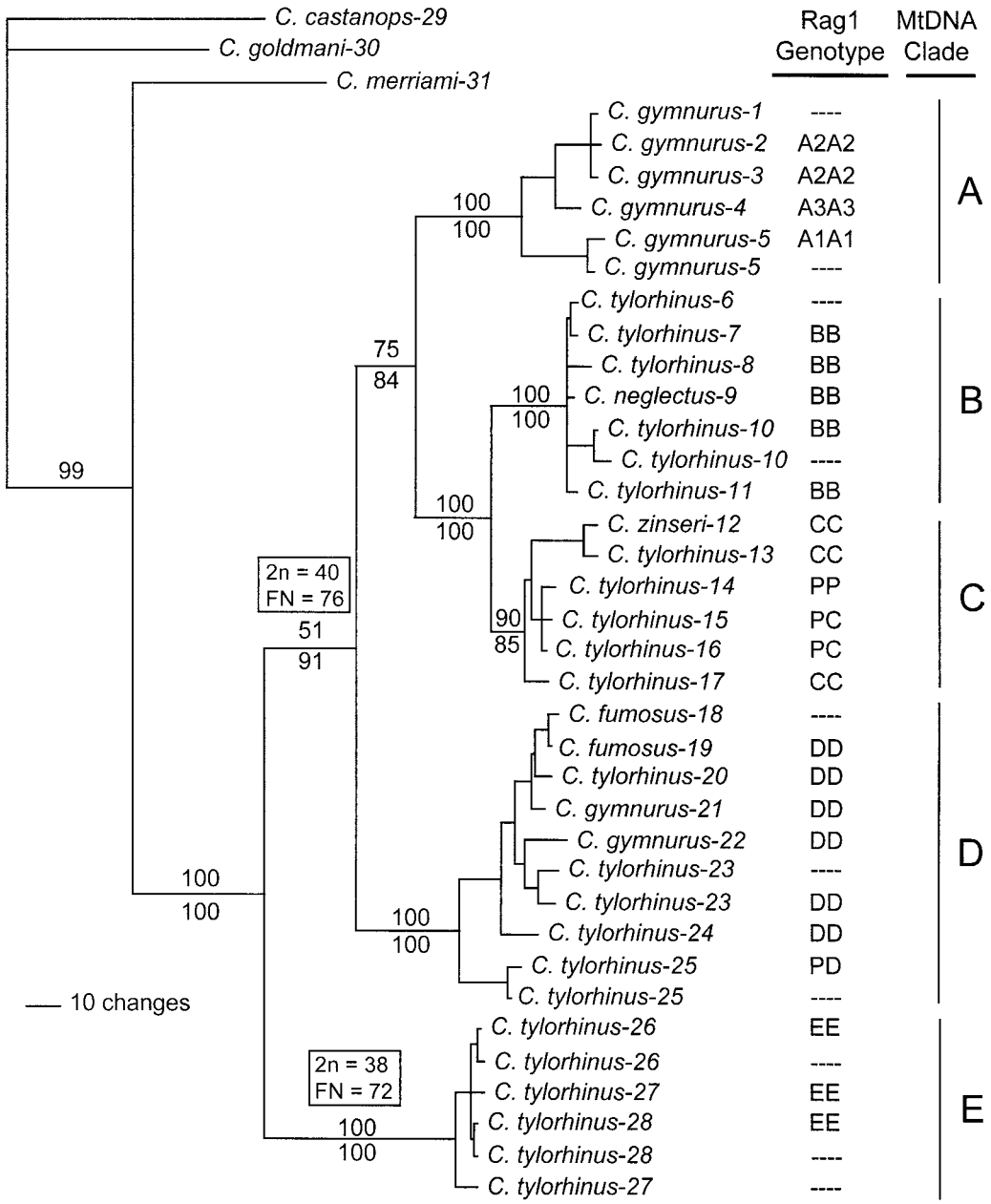

FIG. 3.—Parsimony phylogram based on the complete mtDNA cytochrome-*b* gene for 35 ingroup specimens (members of the *Cratogeomys gymnurus* species group) and 3 outgroup specimens (*C. castanops*, *C. goldmani*, and *C. merriami*). Data also were analyzed using maximum likelihood (GTR+I+Γ model) and Bayesian analyses. Bootstrap support values are indicated only for the deeper splits (maximum likelihood support values above the nodes, and maximum parsimony support values below the nodes; other support values are available upon request). Numbers next to taxon names correspond to localities (Fig. 2; Appendix I). *Rag1* genotypes as defined in text and Fig. 4 (specimens with dashed lines were not genotyped). Letters designate mtDNA clades as defined in text and Fig. 2. Diploid (2n) and fundamental numbers (FN) are indicated for the 2 major branches of the tree.

between otherwise monophyletic and diagnosable populations of pocket gophers usually lends additional support to species designations.

Relationships within the Cratogeomys gymnurus species group.—No matter how the morphometric data were treated, discriminant function analysis and canonical discriminant function analysis of 12 cranial characters failed to discriminate either Russell's (1968) species (*C. gymnurus* and *C. tylorhinus*) or Demastes et al.'s (2002) mitochondrial clades A–E. The few instances of high rate of correct classification were likely an artifact of extreme sample size differences among the groups, which ranged from as few as 3 to as many as 55 individuals. It is important to note that these same cranial characters were able to discriminate among gopher genetic units in California (Patton and Smith 1990; Smith and Patton 1988) as well as other gopher genetic units in Mexico (*C. merriami*—M. S. Hafner in litt.). Considering that the specimens measured in this study were collected over a time span >100 years, it is possible

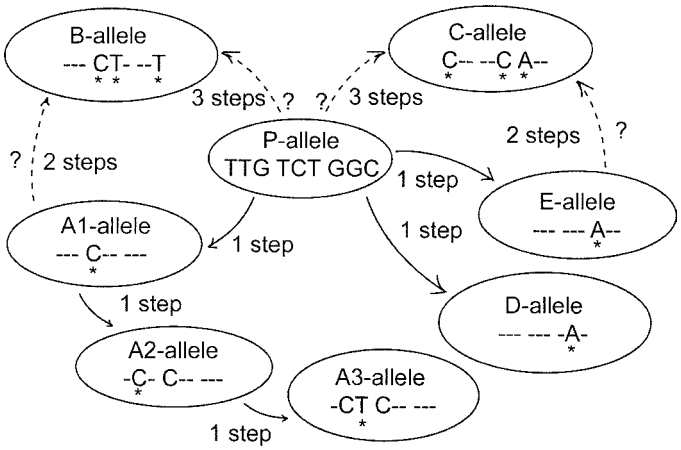

FIG. 4.—Network of 8 *Rag1* alleles found in *Cratogeomys gymnurus*-group gophers. The C allele can be derived directly from the primitive, P, allele (3 steps) or indirectly through the E allele (2 steps). Similarly, the B allele could be derived directly from the primitive allele (3 steps) or indirectly through the A1 allele.

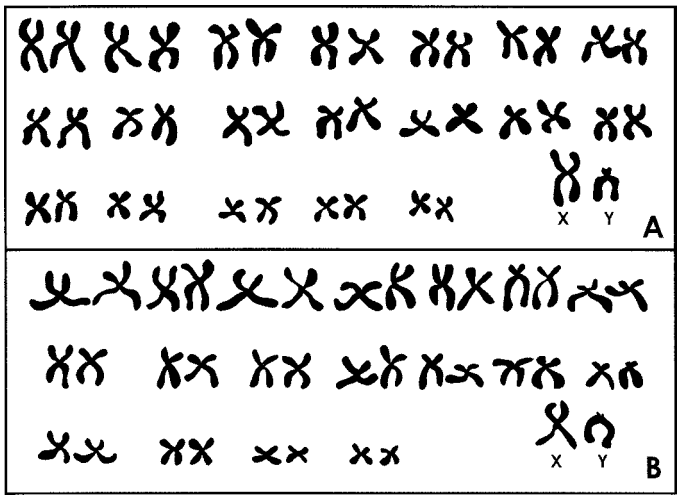

FIG. 5.—Nondifferentially stained karyotypes representing A) *Cratogeomys fumosus* (clades A—D), 2n = 40, FN = 76 (CNMA 41816); and B) *C. planiceps* (clade E), 2n = 38, FN = 72 (LSUMZ 36303).

that temporal variation has masked the geographic variation that our analyses are designed to detect. Unfortunately, the number of available specimens is too low to subdivide the data set into temporal strata.

Each of the 5 clades (A–E) recognized in the analysis of the mtDNA data (Fig. 3) coincides exactly with a unique *Rag1* nuclear allele or set of alleles (Fig. 4) not present in other clades. However, the *Rag1* and mitochondrial data suggest a different set of relationships among the clades. The *Rag1* data (Fig. 4) suggest a sister relationship between clades A and B and between clades C and E, whereas the mitochondrial data support a B+C clade within an A+B+C+D clade (Fig. 3). We favor the mitochondrial tree for several reasons. First, the mtDNA tree is supported by many characters with good bootstrap support, whereas *Rag1* relationships are based on only 9 characters with only 2 potential synapomorphies. Second, we favor the mtDNA tree because a tree based on mitochondrial haplotypes has a substantially higher probability of accurately tracking a short internode than does a tree based on nuclear autosomal genes (Moore 1995). Presence of the P allele in these clades suggests that there has not been ample time (or sufficient coalescence) for a nuclear gene to track population histories accurately. Third, biogeographical considerations argue against A+B and C+E sister relationships (note the geographic distribution of these clades in Fig. 2). Clades B and C, whose sister status is strongly supported in the mtDNA tree, share the eastern and western portions, respectively, of the Rio Lerma watershed, which drains the Mesa Central to the northwest. The other 3 *C. gymnurus* clades identified in the mtDNA analysis (clades A, D, and E) are associated more directly with the Rio Grande and Rio Balsas watersheds, which drain the Mesa Central to the southwest. Fourth, the distribution of chewing lice (*Geomydoecus*) that parasitize these pocket gophers supports the mtDNA tree. For example, clades A–D host 2 species of the *Geomydoecus mcgregori* complex not found in clade E, and clade E hosts 2 species of lice (*G. merriami* and *G. traubi*) not found on clades A–D (Price and Hellenthal 1989). Finally, chromosomal evidence contradicts the C+E clade suggested by the *Rag1* data, in that clade E has a karyotype different from that shared by clades A–D (Fig. 5). Merriam (1895) recognized specimens from the vicinity of Volcán de Toluca (our locality number 28 [clade E] in Fig. 3) as a species, *Platygeomys* [*Cratogeomys*] *planiceps*, distinguishable from other *gymnurus*-group gophers based on morphological criteria, including 2 of the characters (width of jugal and occipital breadth) used in our morphological key (below).

TAXONOMIC CONCLUSIONS

The 5 species that comprise Russell's (1968) *C. gymnurus* species group (*fumosus*, *gymnurus*, *neglectus*, *tylorhinus*, and *zinseri*) were described based largely on differences in body size and fur coloration, characters that are either ecophenotypic (Patton and Brylski 1987) or under strong directional selection (Ingles 1950; Patton and Smith 1990) and are therefore generally unreliable for use in geomyid taxonomy. Perhaps not surprisingly, none of Russell's (1968) 5 species was distinguishable based on the molecular, chromosomal, or morphological data analyzed in this study. Rather, 5 different clades were identified in the mitochondrial (Fig. 3) and nuclear (Fig. 4) DNA analyses, and 2 clades were distinguished in the chromosomal analysis (Fig. 5). These findings warrant major taxonomic changes within the *C. gymnurus* species group.

Mitochondrial clades A–D are chromosomally homogeneous and show levels of sequence divergence ranging from 4 to 9% (uncorrected). Although these levels of sequence divergence are relatively high by typical mammalian standards, conspecific populations of pocket gophers and other subterranean mammals often show unusually high levels of genetic differentiation (Hafner et al. 1987; Patton and Yang 1977; Steinberg and Patton 2000). Numerous studies of pocket gophers have

suggested that speciation in the family is unrelated to levels of genetic differentiation (Hafner et al. 1983; Hafner et al. 1987; Patton 1981; Patton and Yang 1977). Rather, genetic differentiation appears to be more a function of time and degree of separation of populations (Soulé 1976) than a reflection of degree of reproductive compatibility among them. None of the clades A–D can be diagnosed based on morphology, chromosomes, or parasite fauna. Accordingly, we consider them conspecific, and the name *C. fumosus* has priority over all other available names. Because clades A–D represent distinct mtDNA clades (Fig. 3) and each of these clades possesses a unique *Rag1* genotype (Fig. 4), we will treat them as subspecies of *C. fumosus* (see below), pending further study of possible contact zones between these clades.

Unlike clades A–D, clade E is diagnosable based on multiple characters, including *Rag1* genotype, chromosomal diploid number, parasite fauna, and qualitative morphological characters (see key below). Accordingly, clade E fits our operational definition of species discussed earlier, and we herein resurrect Merriam's (1895) species *planiceps* to represent members of the genus *Cratogeomys* from the Volcán de Toluca and Valle de Bravo regions of central Mexico (clade E in Fig. 2). The relatively large genetic divergence between *C. planiceps* and *C. fumosus* (approximately 11% uncorrected mtDNA sequence divergence) suggests relatively long-term isolation of these species. Patton (1981) argued that a major mode of speciation in the pocket gopher genus *Thomomys* is the fixation of structural chromosomal rearrangements, such as reciprocol translocations, that lead to meiotic imbalance and hybrid sterility. Because structural chromosomal rearrangements in pocket gophers are usually evident as differences in diploid number (Patton 1973; Patton and Sherwood 1982), we suggest that the difference in diploid number between *C. planiceps* and *C. fumosus* likely would render them reproductively incompatible.

Cratogeomys Merriam, 1895

Cratogeomys Merriam, 1895:150. Type species *Geomys merriami* Thomas. *Cratogeomys* was regarded as a subgenus of *Pappogeomys* by Russell, 1968:592, but was returned to generic status by Honeycutt and Williams, 1982:212.

Platygeomys Merriam, 1895:162. Type species *Geomys gymnurus* Merriam. Regarded as inseparable from *Cratogeomys* by Hooper, 1946:397.

The genus *Cratogeomys* Merriam includes 8 species divided into 2 species groups. The *castanops* species group includes the species *castanops*, *goldmani* (sensu Lee and Baker 1987), and *merriami*. The taxonomic status of these taxa is not evaluated in this study. The *gymnurus* species group contains the species *fumosus*, *gymnurus*, *neglectus*, *tylorhinus*, and *zinseri*. Based on the findings of this study, we revise this group to contain only 2 species, *C. fumosus* and *C. planiceps*, and we refer to this group as the "*C. fumosus* species group."

Cratogeomys fumosus (Synonymy under subspecies)

Geographic range.—Patchily distributed over widespread regions of the TMVB and Mesa Central of Mexico; range extending from northeastern Querétero southward to southern edges of the Valle de México, and from eastern regions of the state of México westward to the eastern slopes of the Sierra Madre del Sur in Jalisco and Colima. Elevational range approximately 30–2,900 m.

Description.—Extremely variable in body size and fur coloration, but most individuals large for genus and fur usually brownish (not blackish) dorsally; occipital region of skull flattened; paraoccipital processes usually flat and broad when viewed from ventral perspective. See key for additional characters.

Cratogeomys fumosus angustirostris (Merriam, 1903)

Pappogeomys tylorhinus angustirostris (Merriam, 1903:81). Type locality "Cerro Patambán, 10,000 ft., Michoacán."

Platygeomys varius (Goldman, 1939:90). Type locality "Uruapan, about 6000 ft., Michoacán."

Pappogeomys zinseri (Goldman, 1939:91). Type locality "Lagos, 6150 ft., Jalisco, México."

Pappogeomys tylorhinus brevirostris Russell, 1968:733. Type locality "2 mi. E Celaya, 5800 ft., Guanajuato."

Geographic range.—Patchily distributed over the southwestern portion of the Central Mexican Plateau (see distribution of clade C in Fig. 2).

Cratogeomys fumosus fumosus (Merriam, 1892)

Geomys fumosus Merriam, 1892:165. Type locality "Colima City, México" (restricted to 3 miles W Colima, 1,700 feet, Colima, México; Hall and Kelson 1959:471). Type specimen adult male, skin and skull, U.S. National Museum number 33202/45207. Collected 27 March 1892 by E. W. Nelson, original number 2338.

Pappogeomys gymnurus gymnurus (Merriam, 1892:166). Type locality Zapotlán (= Ciudad Guzmán), 4,000 feet Jalisco, México.

Platygeomys gymnurus inclarus Goldman, 1939:88. Type locality "North slope Sierra Nevada de Colima, 10,000 ft., Jalisco."

Cratogeomys fumosus Hooper, 1948:302. First use of current name combination.

Cratogeomys zinseri morulus Russell, 1953:541. Type locality "N end Lago de Sayula, 4400 ft., 9 mi. N and 2 mi. E Atoyac, Jalisco."

Pappogeomys tylorhinus atratus (Russell, 1968:731). Type locality "Top of Cerro Viejo de Cuyutlán, 9700 ft., 19 mi. S and 9 mi. W Guadalajara, Jalisco."

Pappogeomys tylorhinus zodius (Russell, 1968:742). Type locality "13 mi. S and 15 mi. W Guadalajara, about 4500 ft., Jalisco."

Pappogeomys gymnurus tellus (Russell, 1968:756). Type locality "3 mi. W Tala, 4300 ft., Jalisco."

Geographic range.—Patchily distributed over western Michoacán (generally west of longitude 102°30′W) and the eastern slopes of the Sierra Madre del Sur in Jalisco and Colima (see distribution of clade D in Fig. 2).

Cratogeomys fumosus imparilis (Goldman, 1939)

Pappogeomys gymnurus imparilis (Goldman, 1939:89). Type locality "Pátzcuaro, Michoacán."

Geographic range.—Patchily distributed over mostly wooded regions of central Michoacán in the vicinities of Morelia and Pátzcuaro (see distribution of clade A in Fig. 2).

Cratogeomys fumosus tylorhinus (Merriam, 1903)

Pappogeomys tylorhinus tylorhinus (Merriam, 1895:167). Type locality "Tula, [6800 ft.,] Hidalgo, México."

Pappogeomys neglectus (Merriam, 1902:68). Type locality Cerro de la Calentura, about 8 miles NW of Pinal de Amoles, Querétaro, México, elevation 9,000 feet.

Cratogeomys tylorhinus arvalis Hooper, 1947:45. Type from "México, Distrito Federal, México City, Colonia del Valle, 2275 m."

Geographic range.—Patchily distributed over southeastern portions of the Central Mexican Plateau, generally east of longitude 100°W (see distribution of clade B in Fig. 2).

Cratogeomys planiceps (Merriam, 1895)

Platygeomys planiceps Merriam, 1895:168. Type locality "North slope Volcan Toluca, México." Type specimen adult male, skin and skull, U.S. National Museum number 55906 collected 12 September 1893 by E. W. Nelson, original number 5466.

Cratogeomys planiceps (this study). First use of current name combination.

Geographic range.—Known from the northern slopes of Volcán de Toluca, southeastern slopes of Valle de Bravo, and forested hills north of Valle de Bravo. Elevational range approximately 2,500–3,500 m.

Description.—Medium to large body size for genus; dorsal pelage usually dark (approaching black in some individuals), with light-brown wash laterally; occipital region of skull flattened, but less so than in *C. fumosus*. See key for additional characters.

Key to the *Cratogeomys fumosus* Species Group

This key is based on examination of 18 adult specimens in the *C. castanops* species group and 27 adult specimens in the *C. fumosus* species group housed in the Museum of Natural Science, Louisiana State University (LSUMZ). All 45 of these specimens were correctly assigned to species group using the morphological characters in step 1 of this key. Similarly, all 27 specimens in the *C. fumosus* species group were assigned to the correct species (as determined genetically) using only the morphological characters in steps 2 and 3 of this key. Reliability of each morphological character (i.e., percentage of specimens correctly identified using this character alone) is indicated following the character description. This key is for adult specimens only, with adulthood determined by fusion of the basioccipital-basisphenoid suture.

1 Mastoid process not extending laterally beyond auditory meatus (Fig. 6A; 96% reliable for the 45 specimens examined); breadth across angular processes of mandible usually less than greatest length of mandible, including incisors (87.5% reliable); chromosomes not 2n = 40, FN = 76 or 2n = 38, FN = 72 . . . . . *C. castanops* species group
Mastoid process extending laterally beyond auditory meatus (Fig. 6B; 96% reliable); breadth across angular processes of mandible usually greater than greatest length of mandible, including incisors (87.5% reliable); chromosomes 2n = 40, FN = 76 or 2n = 38, FN = 72 . . . . . *C. fumosus* species group; 2

2 Paraoccipital processes usually broad (≥3 mm wide at midpoint) when viewed from ventral perspective (Fig. 6C; 85.2% reliable); dorsal pelage usually brown or reddish brown (77.8% reliable); chromosomes 2n = 40, FN = 76 . . . . . *C. fumosus* (part)
Paraoccipital processes usually narrow (<3 mm wide at midpoint) when viewed from ventral perspective (Fig. 6D; 85.2% reliable) 3

3 Anterior edge of jugal broad (Fig. 6E; 88.9% reliable); depth of skull at occipital plate usually less than 90% of least width of occipital plate (Fig. 6G; 81.5% reliable); dorsal pelage usually brown or reddish brown (77.8% reliable); chromosomes 2n = 40, FN = 76 . . . . . *C. fumosus* (part)
Anterior edge of jugal narrow (Fig. 6F; 88.9% reliable); depth of skull at occipital plate usually greater than 90% of least width of occipital plate (Fig. 6G; 81.5% reliable); dorsal pelage usually dark (approaching black) with light-brown wash laterally (77.8% reliable); chromosomes 2n = 38, FN = 72 . . . . . *C. planiceps*

Geomyid diversity in the TMVB.—This revision of the *C. fumosus* (formerly *C. gymnurus*) species group, plus the study of *Pappogeomys alcorni* by Demastes et al. (2003), reduces the number of geomyid species in the TMVB region (latitude 18°–22°N) from 14 to 10 species, indicating that approximately 30% of the apparent geomyid diversity in the TMVB was the result of taxonomic oversplitting. Nevertheless, with 10 species, the TMVB remains high in pocket gopher species diversity and is still the pinnacle of genus-level diversity in the Geomyidae (Fig. 1). Ongoing study of another geomyid species of the TMVB, *C. merriami*, likely will result in recognition of additional species (M. S. Hafner, in litt.).

Resumen

El género *Cratogeomys*, particularmente las especies del grupo *C. gymnurus*, aportan en gran medida a la alta diversidad de especies de Tuzas en el Eje Neovolcánico Transversal Mexicano. Estudios moleculares recientes de este grupo de especies han revelado una fuerte discordancia entre clados

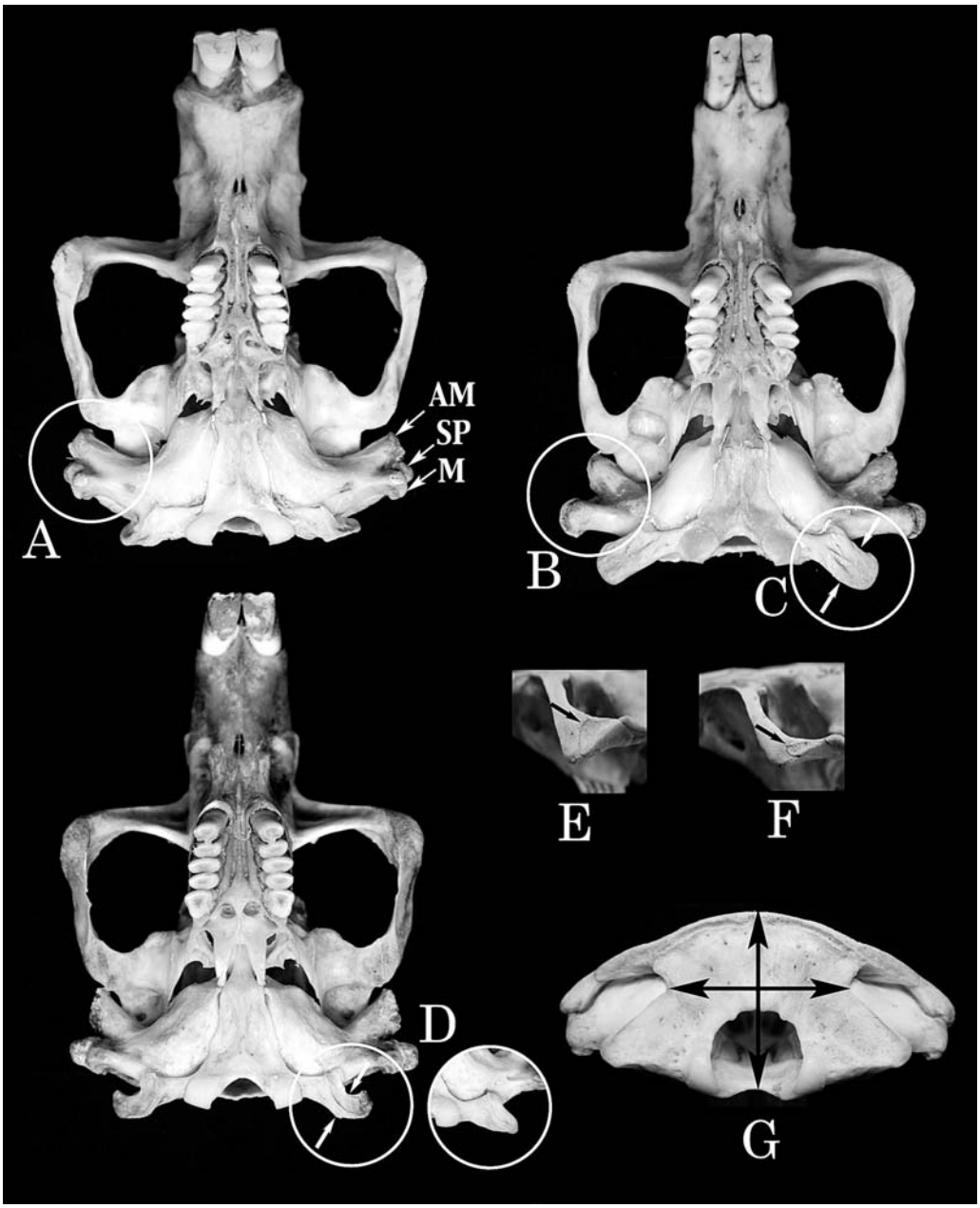

Fig. 6.—A) Ventral view of cranium of *Cratogeomys merriami* (LSUMZ 36068), which is a member of the *C. castanops* species group; in members of this species group, the mastoid process, M, does not extend laterally beyond the external auditory meatus, AM (note that the supraoccipital process, SP, is visible just below the mastoid process). B) *C. fumosus* (LSUMZ 36081); in members of the *C. fumosus* species group, the mastoid process extends laterally well beyond the external auditory meatus and obscures most of the supraoccipital process when viewed from the ventral perspective. C) Specimens of *C. fumosus* usually have flat, broad paraoccipital processes. The measurement mentioned in the key is taken approximately at the midpoint of the paraoccipital process (indicated by arrows); D) *C. planiceps* (LSUMZ 36075 and 36122 [inset]); in *C. planiceps*, the paraoccipital processes usually are not flat and broad when viewed from the ventral perspective, but are curved anteriorly (left) or tapered distally (inset). E) Lateral view of left zygomatic arch of *C. fumosus* (LSUMZ 34339); note the broad anterior edge of the jugal bone. F) Lateral view of left zygomatic arch of *C. planiceps* (LSUMZ 36122); note the narrow anterior edge of the jugal bone. G) Posterior view of cranium of *C. planiceps* (LSUMZ 36075); arrows show dimensions of the occipital plate referred to in the key.

genéticamente definidos y la taxonomía actual de las especies. Por lo tanto, investigamos las relaciones entre las 5 especies en el grupo *C. gymnurus* utilizando DNA mitocondrial y nuclear, cromosomas, y caracteres morfológicos. Aunque los análisis morfométricos cuantitativos no mostraron discriminación entre especies o clados dentro de este grupo, los datos moleculares fueron consistentes en identificar 5 clados alopátricos, ninguno de los cuales corresponde a cualquiera de las 5 especies actualmente reconocidas. Cuatro de estos 5 clados genéticamente definidos carecen de una clara diagnosis, por lo que son agrupados dentro de la especie politípica *C. fumosus*. El quinto clado es diagnosticable basado en mùltiples caracteres,

incluyendo genotipo nuclear, nùmero cromosómico diploide, fauna parasitaria y caracteres morfológicos cualitativos. En consecuencia, resucitamos a la especie *planiceps* de Merriam (1895) para representar miembros de este clado, el cual ocurre en el Volcán de Toluca y la región de Valle de Bravo en el centro de México. Basados en la observación de que diferencias en el nùmero diploide usualmente señalan aislamiento reproductivo entre poblaciones de Tuzas, planteamos la hipótesis que *C. fumosus* y *C. planiceps* son incompatibles reproductivamente. Proveemos sinonimias y descripciones para estas dos especies, junto con una clave para el grupo de especies *Cratogeomys fumosus*.

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APPENDIX I

List of 31 localities from which 35 ingroup and 3 outgroup specimens of *Cratogeomys* were examined in the molecular and chromosomal analyses. Specimens are grouped into the 5 clades identified in the molecular analyses (Figs. 3 and 4). GenBank numbers are from the study by DeWalt et al. (1993). Collection acronyms are defined in Appendix II. Localities (except outgroups) are mapped by locality number in Fig. 2. All localities are in Mexico.

Clade A.—1. MICHOACÁN, Cerro del Burro, 20 km SE Pátzcuaro, originally recognized as *C. gymnurus*, GenBank L11905; 2. MICHOACÁN, 6.5 km S Pátzcuaro, 2,200 m, *C. gymnurus*, LSUMZ 34425; 3. MICHOACÁN, San Gregorio, 8 km E Opopeo, 9,000 feet, C. *gymnurus*, LSUMZ 36136; 4. MICHOACÁN, 1 km S Tacambaro, 5,100 feet, *C. gymnurus*, LSUMZ 36129; 5. MICHOACÁN, 5 km S, 20 km E Morelia, 6,850 feet, *C. gymnurus*, LSUMZ 36130 and CNMA 41816.

Clade B.—6. MÉXICO, Puebla Nuevo de Morelos (MPIO-Zumpango), *C. tylorhinus*, GenBank L11909; 7. MÉXICO, 1 km S Tepexpan, 7,300 feet, *C. tylorhinus*, LSUMZ 36066; 8. MÉXICO, 20 km NW Toluca, 9,000 feet, *C. tylorhinus*, LSUMZ 36071; 9. QUERÉTERO, La Cañada, 9 km by road SW Pinal de Amoles, 9,000 feet, *C. neglectus*, LSUMZ 36091; 10. MÉXICO, 26 km W Toluca, 2,970 m, *C. tylorhinus*, LSUMZ 36162 and 36163; 11. MÉXICO, 1 km N La Isla, 2,612 m, *C. tylorhinus*, LSUMZ 34902.

Clade C.—12. JALISCO, 3 km NE Lagos de Moreno, 6,150 feet, *C. zinseri*, LSUMZ 36084; 13. GUANAJUATO, 1 km E Celaya, 5,800 feet, *C. tylorhinus*, LSUMZ 36092; 14. MICHOACÁN, 2 km N Uruapan, 5,500 feet, *C. tylorhinus*, LSUMZ 36133; 15. MICHOACÁN, Tangancícuaro, 5,700 feet, *C. tylorhinus*, LSUMZ 36124; 16. MICHOACÁN, 2 km NW Patambán, 2,342 m, *C. tylorhinus*, LSUMZ 36292; 17. MICHOACÁN, 3 km E Zacapù, 2,030 m, *C. tylorhinus*, LSUMZ 36166.

Clade D.—18. COLIMA, Colima, *C. fumosus*, GenBank L11903; 19. COLIMA, 5 km S Colima, 1,000 feet, *C. fumosus*, LSUMZ 36080; 20. JALISCO, 6 km NE Atemajac, 8,000 feet, *C. tylorhinus*, LSUMZ 36083; 21. JALISCO, 15 km N Ciudad Guzman, 1,600 m, *C. gymnurus*, LSUMZ 34339; 22. JALISCO, 16 km E Ameca, 4,200 feet, *C. gymnurus*, LSUMZ 36081; 23. MICHOACÁN, 5 km N Tinguindin, 1,700 m, *C. tylorhinus*, LSUMZ 36164 and CNMA 41817; 24. JALISCO, 5 km SW Mazamitla, 7,000 feet, *C. tylorhinus*, LSUMZ 36077; 25. MICHOACÁN, 2 km N, 5 km W Apo, 1,720 m, *C. tylorhinus*, LSUMZ 36165 and CNMA 39673.

Clade E.—26. MÉXICO, 25 km N Valle de Bravo, 8,000 feet, *C. tylorhinus*, LSUMZ 36075 and 36303; 27. MÉXICO, 3 km S, 20 km E Valle de Bravo, 8,600 feet, *C. tylorhinus*, LSUMZ 36123 and 36291; 28. MÉXICO, 10 km S, 16 km W Toluca, 3,000 m, *C. tylorhinus*, LSUMZ 36121 and 34901.

Outgroups.—29. TAMAULIPAS, Matamoros, *C. castanops*, GenBank L11908; 30. ZACATECAS, 20 km E, 2 km N Río Grande, *C. goldmani*, GenBank L11904; 31. MÉXICO, 34 km S México City, *C. merriami*, GenBank L11906.

APPENDIX II

Specimens examined in the morphometric analysis (all localities are in Mexico). Museum acronyms are as follows: Colección Nacional de Mamíferos, Universidad Nacional Autónoma de México (CNMA), University of Kansas Natural History Museum (KU); Louisiana State University Museum of Natural Science (LSUMZ); University of California Museum of Vertebrate Zoology (MVZ); The Museum, Texas Tech University (TTU); University of Michigan Museum of Zoology (UMMZ); and U.S. National Museum of Natural History (USNM).

Cratogeomys fumosus (n = 275).—COLIMA: Colima (TTU, 1); W Colima (TTU, 2); Colima City (KU, 1); Colima City, 1,700 feet (USNM, 8); Colima, 2 miles W by RR [railroad] (TTU, 4); Colima, 4 miles SW, 1,400 feet (KU, 2); Colima, 5 km S, 1,000 feet (LSUMZ, 1). DISTRITO FEDERAL: Colonia del Valle (KU, 1; UMMZ, 8); Coyoacan, 2,350 m (UMMZ, 3). GUANAJUATO: Celaya, 1 km E, 5,800 feet (LSUMZ, 1); Celaya, 5 miles E, 6,000 feet (KU, 2); Celaya, 2 miles E, 5,800 feet (KU, 6 [includes holotype of *C. t. brevirostris*]). HIDALGO: Marques, 8,000 feet (USNM, 5); Pachuca, circa 6 miles S (TTU, 1); Tula, 6,800 feet (USNM, 3); Tula, 1 km E, 1 km N (TTU, 1). JALISCO: Ameca, 15 miles E (TTU, 3); Ameca, 16 km E (LSUMZ, 1); Atemajac, 6 km NE, 8,000 feet (LSUMZ, 1); Atemajac de Brizuela, 4 miles E, 8,000 feet (KU, 1); Atoyac, 9 miles N, 2 miles E, Lago de Sayula, 4,400 feet (KU, 4 [includes holotype of *C. g. gymnurus*]); Ciudad Guzman, 2 miles N (KU, 4); Ciudad Guzman, 3 miles W, 5,100 feet (KU, 1); Ciudad Guzman, 5 miles S, 5,000 feet (USNM, 2); Ciudad Guzman, 9 miles W, 2 miles S, 7,000 feet (KU, 1); Ciudad Guzman, 15 km N, 1,600 m (LSUMZ, 1); Ciudad Guzman, 18 miles W, on road to Venustiano Carrarza (TTU, 6); Guadalajara, 13 miles S, 15 miles W (KU, 8 [includes holotype of *C. tylorhinus zodius*]); Guadalajara, 19 miles S, 9 miles W, Top of Cerro Viejo de Cuyutlan, 9,700 feet (KU, 6 [includes holotype of *C. tylorhinus atratus*]); Jazmin, 2.5 miles ENE, 6,800 feet (KU, 7); Jazmin, 4 miles ENE, 7,700 feet (KU, 1); Jilotlán de los Dolores, 2,400 feet (KU, 3); Jilotlán de los Dolores, 8 miles E, 2,000 feet (KU, 4); Lagos de Moreno, 6,150 feet, (USNM, 7); Lagos de Moreno, 6300 feet (KU, 2); Lagos de Moreno, near RR [railroad] in city (TTU, 3); Lagos de Moreno, 0.5 miles NE, 6,370 feet (KU, 2); Lagos de Moreno, 3 km NE, 6,150 feet (LSUMZ, 1); Mazamitla, 5 km SW, 7,000 feet (LSUMZ, 1); Mazamitla, 3 miles WSW (KU, 3); Mazamitla, 4 miles W, 6,600 feet (KU, 3); Mazamitla, 5 miles SW by road (TTU, 6); Mazamitla, 6 miles S, 6,200 feet (KU, 1). Sierra Nevada de Colima, (USNM, 1); Sierra Nevada de Colima, 5,000 feet (USNM, 1); Tala, 1 mile NE, 4,400 feet (KU, 3); Tala, 2.5 miles W, 1 mile S El Refugio (KU, 2); Tala, 3 miles W, 4,300 feet (KU, 5 [includes holotype of *C. gymnurus tellus*]); Toliman, 12 miles S, 7,700 feet (KU, 15 [includes

holotype of *C. gymnurus russelli*]); Toluca, 26 km W, 2,970 feet (LSUMZ, 2); Zapoltitic, 3 miles WNW, 5,100 feet (KU, 1); Zapotlan, 4,000 feet (USNM, 4). MÉXICO: La Isla, 1 km N, 2,612 m (LSUMZ, 1); San Jose Allende, 7 miles W, 3 miles N (KU, 2); Templo de Sol Piramide de San Juan, Teotihuacán (KU, 1); Tenango Isla, 3 miles NNW (KU, 2); Tepexan, 1 km S, 7,300 feet (LSUMZ, 1); Toluca, 20 km NW, 9,000 feet (LSUMZ, 1); Toluca, 14 miles NW, El Rio San Bernabe (KU, 3); Zumpango, Pueblo Nuevo de Moreles (TTU, 1). MICHOACÁN: Apo, 2 km N, 5 km W, 1,720 feet (LSUMZ, 1); Ciudad Hidalgo, 15 miles W, 3 miles S (KU, 1); Corupo, 1 mile S, Sta. [Station] 162 (UMMZ, 2); Michoacán (TTU, 1); Morelia, 5 km S, 20 km E, 6,850 feet (CNMA, 1; LSUMZ, 2); Nahuatzén, 1 km N, 2 km W, 2,200 m (MVZ, 1); Nuevo San Juan, 10 miles SE (by road), 2,200 m (MVZ, 1), Opopeo, 6 miles E (TTU, 1); Opopeo, 8 miles E (TTU, 1); Patambán, 2 km NW, 342 m (LSUMZ, 1); Pátzcuaro (TTU, 1); Pátzcuaro, 7,000 feet (USNM, 4); Pátzcuaro, 2 miles W, 7,800 feet (MVZ, 3); Pátzcuaro, 4 miles S, 7,800 feet (MVZ, 1); Pátzcuaro, 5 miles S (MVZ, 6); Pátzcuaro, 6.5 km S, 2,200 m (MVZ, 4); Pátzcuaro, 7 miles S (MVZ, 1); Pátzcuaro, 9 miles SE, 8,000 feet (MVZ, 1); Pátzcuaro, 15 km SE (TTU, 2); Pátzcuaro, 20 km SE (TTU, 1); Pueblo Nuevo, 2 miles SW (TTU, 1); San Gregorio, 2 miles E (KU, 2); San Gregorio, 8 km E Opopeo, 9,000 feet (LSUMZ, 1); Sierra Potamba [= Patambán], W Slope, Jesùs Diaz, 7,500 feet (KU, 6); Tacámbaro, 1 km S, 5,100 feet (LSUMZ, 1); Tacámbaro, 1.5 miles S, 5,700 feet (MVZ, 2); Tacámbaro, 1.75 miles S, 5,700 feet (MVZ, 1); Tacámbaro, 4 km N on Hwy 41 (TTU, 1); Tangancíquaro, 5,500 feet (KU, 3); Tangancícuaro, 5,700 feet (LSUMZ, 1); Tarecuato, 2 miles N, 7,200 feet (KU, 3); Tarecuato, 4.5 miles NE, 6,600 feet (KU, 3); Tingüindin, 1 mile N, 6,300 feet (KU, 3); Tingüindin, 5 km N, 1,700 feet (CNMA, 1; LSUMZ, 1); Uruápan Airfield (UMMZ, 2); Uruápan Airfield, 2.5 miles E (UMMZ, 1); Uruápan, 0.5 miles E (UMMZ, 1); Uruápan, 2 km N, 5,500 feet (LSUMZ, 1); Uruápan, 5 miles SW, Nuevo San Juan (UMMZ, 8); Uruápan, 6 miles SE, road to Tzararocua Falls (UMMZ, 2); Uruápan, 11.2 miles E (TTU, 1); Uruápan, 15 miles NW, 2 miles S Corupo, 2,350 m (UMMZ, 1); Uruápan, Cupatitzio National Park (UMMZ, 2); Zacapu, 6,600 feet (KU, 2); Zacapu, 2 miles SW, 6,600 feet (KU, 3); Zacapu, 3 km E, 2,030 feet (LSUMZ, 1). QUERETARO: Pinal de Amoles, 9,500 feet (USNM, 4).

Cratogeomys planiceps (n = 18).—MÉXICO: Bosencheve, 3 miles S, Refugio San Cayetano (UMMZ, 3); Raices, 4 miles S, Nevada de Toluca (USNM, 1); Toluca, 10 km S, 16 km W, 3,000 m (LSUMZ, 4); Toluca Volcano, N Slope (USNM, 1); Valle de Bravo, 3 km S, 20 km E, 8,600 feet (LSUMZ, 3); Valle de Bravo, 25 km N, 2,500 m (LSUMZ, 2); Valle de Bravo, 10 miles N, 6 miles E, 7,640 feet (KU, 4).