

PHYLOGENETICS OF THE NEW WORLD RODENT FAMILY HETEROMYIDAE

LOIS F. ALEXANDER* AND BRETT R. RIDDLE

Department of Biological Sciences, Center for Aridlands Biodiversity Research and Education, University of Nevada Las Vegas, 4505 S Maryland Parkway, Las Vegas, NV 89154-4004, USA

The family Heteromyidae includes 6 genera of rodents traditionally placed in 3 subfamilies endemic to the Nearctic and northern Neotropical biogeographic regions. Although several of these taxa represent intensively studied members of North and Central American ecosystems (e.g., kangaroo rats and pocket mice), phylogenetic relationships within and among subfamilies, genera, and species-groups are not well understood. Here, we used maximum-likelihood, Bayesian, and maximum parsimony analyses of sequence data from 2 mitochondrial DNA genes, the cytochrome oxidase subunit 3 gene (699 base pairs [bp]) and the cytochrome-*b* gene (1,140 bp), to investigate phylogenetic relationships among 55 species-level taxa. We found robust support for monophyly of genera *Dipodomys*, *Microdipodops*, *Chaetodipus*, and *Perognathus*; sampling of *Liomys* and *Heteromys* was inadequate to evaluate their reciprocal status. All analyses converge on a phylogeny that robustly resolves several historically contentious issues, including monophyly of the subfamily Dipodomyinae (*Microdipodops* plus *Dipodomys*), and a monophyletic *Chaetodipus* that includes *C. formosus*, *C. baileyi*, *C. rudinoris*, and *C. hispidus*. However, Perognathinae (*Perognathus* plus *Chaetodipus*) is not supported, with no basal resolution among *Perognathus*, *Chaetodipus*, Dipodomyinae, and Heteromyinae. Many intrageneric clades receive strong support and are discussed herein. Although phylogenetic resolution is limited at the basal nodes of the Heteromyidae radiation, our results provide a basis for developing a provisional hypothesis regarding the historical biogeography in combination with independent information on the Neogene geological history of western North America and the fossil record of the family.

Key words: *Chaetodipus*, *Dipodomys*, Heteromyidae, *Heteromys*, historical biogeography, *Liomys*, *Microdipodops*, mitochondrial DNA, *Perognathus*, phylogenetics

The family Heteromyidae is well established within the order Rodentia as a member of the superfamily Geomyoidea, along with Geomyidae (DeBry and Sagel 2001; Montgelard et al. 2002; Patton 1993). Historically, the members of Heteromyidae and Geomyidae have been recognized as either a single family (Geomyidae) with 2 subfamilies (Geomyinae and Sacomyyinae or Heteromyinae) or more recently as 2 distinct families (Heteromyidae and Geomyidae) in the superfamily Geomyoidea (Ryan 1989; Williams et al. 1993). Examination of immunological data presented by Hafner (1982) suggested that the separation of Geomyidae and Heteromyidae may have occurred as early as the Eocene. With the use of revised molecular clock calibrations for immunological data, Hafner (1993) reinterpreted Hafner's (1982) data and placed the separation of these 2 families in the early Oligocene, which is consistent with the fossil record (Wahlert 1993).

The family Heteromyidae is a group of primarily deciduous thorn-scrub and arid-adapted rodents and is comprised of 6 genera (*Chaetodipus*, *Dipodomys*, *Heteromys*, *Liomys*, *Microdipodops*, and *Perognathus*) including approximately 57 species that are distributed as far north as British Columbia and Saskatchewan and as far south as the Pacific coast of Colombia and the northern coast of Ecuador, South America (Patton 1993; Schmidly et al. 1993; Williams et al. 1993). Genera are distributed nonrandomly across latitude (Fig. 1) and ecoregions (Table 1). *Heteromys* inhabits more mesic environments than any of the other heteromyids, and occurs primarily in lowland rainforests and tropical cloud forests of Central and northern South America, whereas *Liomys* is mostly confined to semiarid thorn-scrub habitats of Mexico and Central America (Anderson 2001; Schmidly et al. 1993). The suggestion has been made that resource partitioning between *Heteromys* and *Liomys* has resulted in *Heteromys* occurring in the higher and wetter regions of their distribution and *Liomys* remaining in the lower, drier regions (Genoways 1973). *Microdipodops* is restricted to arid regions of the central Great Basin, whereas *Dipodomys* occurs throughout the arid or semi-arid regions of western North America including both warm and cold deserts,

* Correspondent: alexandl@unlv.nevada.edu

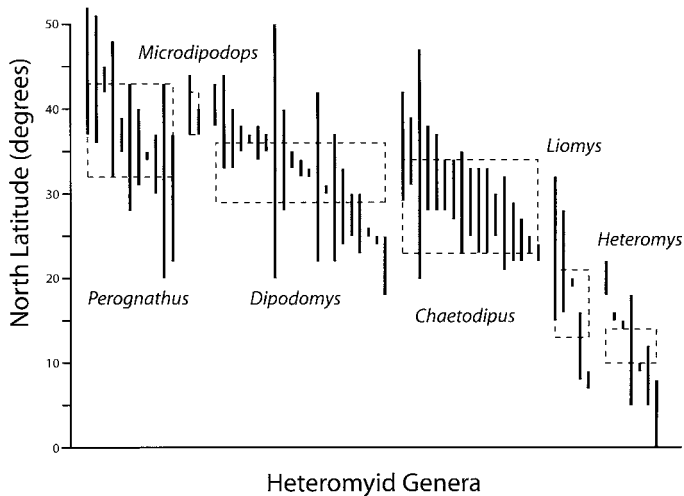


FIG. 1.—Distribution of heteromyid rodents across latitude showing nonrandom nature of the distribution.

grasslands, and chaparral. *Perognathus* occurs in desert and grassland regions that extend north to British Columbia and Saskatchewan, east to the Mississippi River, and south into Mexico; it also occurs in chaparral regions of California and the Great Basin. With 2 exceptions, *Chaetodipus* occurs in warm desert, chaparral, and subtropical thorn-scrub areas of the southern United States and northern Mexico; *C. hispidus* ranges farther north (North Dakota) and east (Louisiana) than any other species of *Chaetodipus* (Schmidly et al. 1993) and *C. formosus* inhabits intermountain sagebrush areas more typical of cold-desert microhabitats in addition to a primarily warm-desert and chaparral distribution.

Heteromyidae is currently divided into 3 subfamilies: Perognathinae containing *Perognathus* and *Chaetodipus*, Heteromyinae containing *Heteromys* and *Liomys*, and Dipodominae containing *Dipodomys* and *Microdipodops* (Hafner 1993; Patton 1993; Wahlert 1993; Williams et al. 1993). One controversial aspect of this arrangement has been the placement of *Microdipodops* within Dipodominae (Hafner 1978, 1993; Hafner and Hafner 1983; Reeder 1956; Ryan 1989; Wahlert 1985) instead of the previously accepted placement within Perognathinae (Hafner 1978; Hall 1981; Wood 1935). It is possible that this group represents an independent lineage with no close living relatives (Hafner 1978, 1993). In addition, it has been suggested that *Heteromys* is paraphyletic relative to *Liomys* (Rogers 1990). Our sampling of *Heteromys* and *Liomys* is insufficient to address this question and it is being addressed elsewhere (D. Rogers, pers. comm.).

Beyond these several examples of phylogenetic uncertainty, the relationships of subfamilies, genera, and species-groups within the family Heteromyidae are in need of comprehensive reevaluation. Our primary objectives of this study were to estimate phylogenetic relationships within and among the 6 genera in the family Heteromyidae from the perspective of mtDNA analysis, including a reevaluation of the 3 proposed subfamilies, and to evaluate the biogeographic history of the family Heteromyidae. Within that context, we summarize the Neogene earth history of western North America and the heteromyid

fossil record in order to establish the historical framework in which heteromyids evolved.

Landscape evolution.—Fossil records suggest that heteromyid rodents originated during the Oligocene in western North America and major lineages diversified within the Neogene (Wahlert 1993), during which time there was pronounced geological activity and landscape evolution. The development of the exceptional topographic complexity of western North America began with the uplift of the Rocky Mountains in the United States and the Sierra Madre Oriental in Mexico during the Eocene (Levin 1978). As large areas of the Rocky Mountain region were uplifted, enormous volumes of material eroded from the eastern slopes and filled intermontane basins to the east, thus contributing to the formation of the Great Plains (Levin 1978). These crustal movements continued throughout the remaining epochs of the Cenozoic with additional uplift and erosion creating new sedimentary layers throughout the Oligocene, Miocene, and Pliocene (Levin 1978). During the late Miocene and Pliocene, the Great Plains evolved from a woodland savanna to a grassland savanna to a grassland steppe (Riddle 1995; Webb 1977).

Also beginning in the Eocene, a continuous subduction zone off the west coast created a parallel zone of volcanic activity in the area that later became the Sierra Madre Occidental in Mexico (Ortega-Gutiérrez and Guerrero-García 1982). In the Oligocene and Miocene, hundreds of calderas and their resulting ash-flow tuff deposits, caused by the subduction of the Pacific plate, combined to form the high plateau that makes up the Sierra Madre Occidental (Mexican Plateau—Swanson and McDowell 1984). Subsequent block faulting and erosion formed isolated basins on the eastern and western aspects of the Mexican Plateau. During the Miocene, the Coast and Cascade ranges in southern Oregon began to uplift, causing a rain shadow that began to create drier climates and expanding grasslands on the east side of these ranges; this region makes up the northern Great Basin of today (Baldwin 1964).

From the Oligocene to the late Miocene, forests and savannas were gradually replaced with steppe and semidesert habitats. This continued during the latest Miocene with expansion of regional deserts, grasslands and shrub-steppes (Axelrod 1979, 1983; Webb 1983). The remains of plants and animals in the sediments suggest that the Pliocene was cooler and drier than the Miocene (Levin 1978).

The Sierra Nevada Mountains were compressed and intruded during the Jurassic, but were steadily reduced by erosion throughout the Tertiary. The continental crust east of the Sierra Nevada began to stretch in an east–west direction in the Miocene, and as a result, the crust broke into a series of north–south–trending valleys and mountain ranges (Fiero 1986). Less than 5 million years ago (mya), through a combination of uplift of the Sierran block and down-dropping of the area to the east, the Sierra Nevada rose again. Rising far more steeply to the east than the west, the entire Sierra Nevada tilted with a gentle slope westward to California's Central Valley and a steep eastern slope (Levin 1978). During the late Pliocene, the continued continental crust expansion increased the northward extent of the Gulf of California; uplifted the Peninsular, Tehachapi, and

TABLE 1.—Heteromyid rodent species categorized by genera into 7 distinct ecoregions.

Ecoregion	Genus					
	<i>Perognathus</i>	<i>Microdipodops</i>	<i>Dipodomys</i>	<i>Chaetodipus</i>	<i>Liomys</i>	<i>Heteromys</i>
Temperate steppe (4 species)	<i>P. fasciatus</i> <i>P. flavescens</i>		<i>D. ordii</i>	<i>C. hispidus</i>		
Temperate desert (8 species)	<i>P. longimembris</i> <i>P. parvus</i> <i>P. parvus</i> (Washington)	<i>M. megacephalus</i> <i>M. pallidus</i>	<i>D. microps</i> <i>D. ordii</i>	<i>C. formosus</i>		
Mediterranean (14 species)	<i>P. alticola</i> <i>P. inornatus</i>		<i>D. agilis</i> <i>D. californicus</i> <i>D. elephantinus</i> <i>D. gravipes</i> <i>D. heermanni</i> <i>D. ingens</i> <i>D. nitratoides</i> <i>D. simulans</i> <i>D. stephensi</i> <i>D. venustus</i>	<i>C. californicus</i> <i>C. fallax</i>		
Tropical–subtropical steppe (5 species)	<i>P. apache</i> <i>P. merriami</i>		<i>D. compactus</i> <i>D. elator</i> <i>D. ordii</i>			
Tropical–subtropical desert (22 species)	<i>P. amplus</i> <i>P. flavus</i>		<i>D. deserti</i> <i>D. insularis</i> <i>D. margaritae</i> <i>D. merriami</i> <i>D. nelsoni</i> <i>D. ordii</i> <i>D. panamintinus</i> <i>D. phillipsii</i> <i>D. spectabilis</i>	<i>C. arenarius</i> <i>C. baileyi</i> <i>C. dalquesti</i> <i>C. eremicus</i> <i>C. goldmani</i> <i>C. intermedius</i> <i>C. lineatus</i> <i>C. nelsoni</i> <i>C. penicillatus</i> <i>C. rudinoris</i> <i>C. spinatus</i>		
Savanna (10 species)				<i>C. artus</i> <i>C. pernix</i>	<i>L. adpersus</i> <i>L. irroratus</i> <i>L. pictus</i> <i>L. salvini</i> <i>L. spectabilis</i>	<i>H. gaumeri</i> <i>H. goldmani</i> <i>H. nelsoni</i>
Rainforest (4 species)						<i>H. anomalus</i> <i>H. australis</i> <i>H. desmarestianus</i> <i>H. oresterus</i>

Coast ranges of Baja California and California; and drained California's Central Valley (Norris and Webb 1976).

The Cascade and Coast ranges, the Sierra Nevada, the Transverse and Peninsular ranges, and the Sierra Madre Occidental blocked the prevailing western storm tracks, whereas the Sierra Madre Oriental and the Rocky Mountains blocked the summer monsoon moisture moving north and west from the Gulf of Mexico. The combined effect of blocking the moisture from the Pacific Ocean to the west, and the summer moisture from the Gulf of Mexico, was the drying and gradual formation of the Great Basin, Mojave, Peninsular, Sonoran, and Chihuahuan deserts. The Great Basin and northern Mojave deserts changed from woodland savannas to shrub-steppe communities during the latest Miocene and early Pliocene. Similarly, the Mexican Plateau changed from a semiarid savanna to a desert–scrub-steppe woodland, and the Sonoran and southern Mojave deserts changed from semidesert and subtropical thorn-scrub to desert scrub (reviewed in Riddle 1995).

Fossil history.—The 1st heteromyid fossils (*Proheteromys*) appear in the fossil record of western North America during the Oligocene (Wahlert 1993). *Proheteromys* may be an early member of the Heteromyinae (Wood 1935), but Heteromyinae and Perognathinae are not clearly distinguishable in the fossil record in the early Miocene (Wilson 1960). The earliest identifiable fossils of *Perognathus* or *Chaetodipus* appear during the Hemingfordian North American Land Mammal Age of about 20 mya (Wahlert 1993), with representatives that are similar in size and dental morphology to extant *Perognathus* species as well as extant *Chaetodipus* species appearing in the late middle Miocene. Therefore, *Perognathus* and *Chaetodipus* possibly were differentiated as early as the late middle Miocene (Williams 1978). However, positively distinguishing between the 2 genera from fossils has not been possible thus far. Also appearing during the Hemingfordian North American Land Mammal Age of the Miocene, *Cupidinimus* previously was considered to be the earliest representative of the Dipodominae,

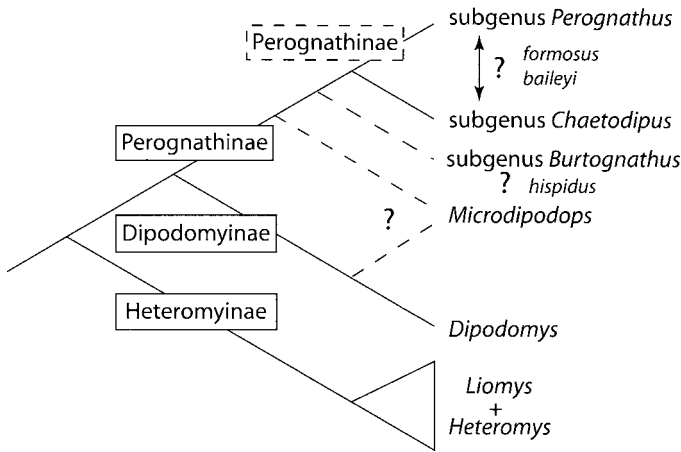


FIG. 2.—Testable hypotheses of previously or currently proposed (dashed lines and box) relationships among genera and subgenera of the 3 currently recognized subfamilies of Heteromyidae (solid lines and boxes).

but may have closer affinities with the perognathines (Wahlert 1993). The earliest recognizable fossils of *Dipodomys* appear during the early Barstovian age of the middle Miocene, whereas the earliest recognizable fossils of *Microdipodops* and *Liomys* do not appear until the Rancholabrean age of the Pleistocene (Wahlert 1993). Thus, modern genera (with the possible exception of *Microdipodops*) were in place for the majority of the tectonic development of the west including the Basin and Range expansion and the uplifts of the Rocky Mountains, Colorado Plateau, Sierra Madre Oriental, Sierra Madre Occidental, Sierra Nevada, Peninsular Mountains, Coast Range, and the Cascade Mountains. This makes the family Heteromyidae an interesting taxonomic group to use as a barometer of mammalian evolutionary development coinciding with development of a geologically dynamic and complex region.

A priori hypotheses.—The fossil record places the 1st heteromyid fossils in the Oligocene, but the subfamilies and genera are not clearly distinguishable from fossils. For example, discerning differences between *Perognathus* and *Chaetodipus* from the fossil record has not been possible; however, they have been treated as monophyletic groups, at least at the subgeneric level, based on molecular analyses of extant taxa (Patton 1993; Patton et al. 1981; Williams et al. 1993). The extent to which genera cannot be discriminated from the fossil record may be extreme. For example, *Microdipodops* does not appear in the fossil record until the Pleistocene, although it could represent a much deeper lineage split if it is indeed the sister lineage of *Dipodomys*.

The 3 currently recognized subfamilies and previously proposed relationships among them are presented as testable hypotheses in Fig. 2. Assuming monophyly of the 3 subfamilies, examples of other possible alternative hypotheses include Perognathinae as sister to Heteromyinae with Dipodomysinae basal, and Heteromyinae as sister to Dipodomysinae with Perognathinae basal. Another set of testable hypotheses of relationships involves the genera and species within the

traditional subfamilies. Notably, is *Microdipodops* related to Perognathinae (sensu stricto), some subset of Perognathinae, or Dipodomysinae? Within genera, similar testable hypotheses include evaluating the appropriateness of including *formosus*, *baileyi*, and *hispidus* within a monophyletic *Chaetodipus*. *C. formosus* and *baileyi* have been considered somewhat intermediate morphologically and ecologically between *Chaetodipus* and *Perognathus* (Patton et al. 1981). With no reference to the elevation of *Chaetodipus* to generic rank by Hafner and Hafner (1983), Hoffmeister (1986) considered all of the Perognathinae to be in the genus *Perognathus* when he placed *hispidus* into its own subgenus, *Burtognathus*, based primarily on bacular and chromosomal characteristics. Finally, we provide a provisional evaluation of previously proposed species-groups within *Chaetodipus* (Patton and Rogers 1993; Patton et al. 1981), *Dipodomys* (Best and Schnell 1974; Johnson and Selander 1971; Lidicker 1960b; Schnell et al. 1978; Stock 1974), and *Perognathus* (Williams 1978).

MATERIALS AND METHODS

We applied maximum parsimony (MP), maximum-likelihood (ML), and Bayesian methods by using PAUP 4.0b (Swofford 1999) and MrBayes 2.01 (Huelsenbeck and Ronquist 2001) to analyze mitochondrial DNA (mtDNA) sequences from nearly all species of Heteromyidae from the United States and Mexico as well as exemplars of neotropical genera. Throughout this paper, we refer to “species-level” taxa where preliminary evidence exists for distinction but taxonomic changes have not been published. Within *Dipodomys*, *Microdipodops*, *Chaetodipus*, and *Perognathus*, all species except for 1 of questionable taxonomic status (*Chaetodipus lineatus*—Williams et al. 1993) were sampled. We included 16 species-level taxa from the genus *Chaetodipus*; *C. lineatus* was not included, and *C. arenarius* was split into 2 species (*arenarius*1 and *arenarius*2) based on preliminary evidence indicating presence of a cryptic species (*arenarius*2) that is provisionally assignable to *C. dalquesti* (Riddle et al. 2000b; Roth 1976; but see Best 1993). We included 11 species-level taxa from the genus *Perognathus*; *parvus* was split into 2 species (*parvus* Utah and *parvus* Columbia Plateau) based on the preliminary evidence of Riddle (1995). We included 22 previously described taxa of *Dipodomys*, including 20 species-level taxa; *D. venustus* and *D. elephantinus* are now considered to be conspecific (Best et al. 1996) and preliminary evidence suggests that *D. insularis*, *D. margaritae*, and *D. merriami* from the southern Baja California peninsula also might be conspecific (Alexander et al., in litt.; Riddle et al. 2000b). We included both species of *Microdipodops*, 1 representative of *Heteromys* (*H. desmarestianus*), and 2 representative species of *Liomys* (*L. pictus* and *L. irroratus*). *Geomys breviceps*, which belongs to the sister family Geomyidae, served as the outgroup taxon (Appendix I).

Total genomic DNA was extracted from frozen tissue by following a lysis buffer protocol (Longmire et al. 1991). A 705-base pair (bp) fragment of mtDNA including the cytochrome oxidase subunit 3 gene (*COIII*) was amplified via polymerase chain reaction (PCR) with primers L8618 and H9323 (Riddle 1995). The mtDNA cytochrome-*b* region (*Cytb*) was amplified via PCR with primers MVZ05 and MVZ14 (Smith and Patton 1993). PCR reaction conditions were as follows: 95°C for 1 min, 55°C for 1 min, and 72°C for 1 min, for 30 cycles. PCR fragments were gel purified with a QBiogene Gene Clean kit (Q Biogene, Carlsbad, California) by following manufacturer protocols. The same primers that were used for PCR amplification of

COIII and *Cytb* were used to sequence both strands of every individual. In addition to the primers used for PCR, 1 additional primer (L15162) was used for sequencing *Cytb* (Taberlet et al. 1992). A total of 699 bp of *COIII* and 1,140 bp of *Cytb* were aligned with BioEdit (Hall 1999) and used in all analyses.

These gene regions are not independent estimates of phylogeny, but are evolving at a similar rate (Xia 1998) and therefore are being used in combination to increase numbers of informative characters available for analysis. A homogeneity partition test was performed to confirm that these gene regions could be combined for analyses ($P = 0.07$; PAUP 4.0b—Swofford 1999). Maximum-parsimony analyses (heuristic search, random addition sequence, and tree bisection and reconnection [TBR] branch swapping, for 20 repetitions) were performed with equal weights, and because of differential probability of saturation relative to site positions in a coding sequence, we also weighted characters by site-specific transition–transversion ratios. Both of these analyses were repeated with 500 bootstrap repetitions. With the assistance of Modeltest 3.06 (Posada and Crandall 1998), we chose the Tamura–Nei model (Tamura and Nei 1993), with a gamma distribution of rate heterogeneity among sites (0.6593) and an assumption of some invariant sites (proportion = 0.4634), as the best evolutionary model for the full, 2-gene set, and used the resulting likelihood settings in the maximum-likelihood analyses of the entire family Heteromyidae. A maximum-likelihood log-likelihood ratio test was used to address whether the best maximum-likelihood tree is significantly more likely than various alternative trees of interest.

For the Bayesian analyses, independent analyses were run twice; stationarity levels were compared and determined to be equivalent (Huelsenbeck and Bollback 2001). With each analysis, we ran 4 Markov chain Monte Carlo iterations simultaneously by using MrBayes for 1,000,000 generations sampling every 100 generations, resulting in 10,000 trees. The point at which likelihood scores stabilized (stationarity) was noted and trees recorded before that point (1,000 trees) were discarded as the “burn-in.” Topologies from the remaining 9,000 trees were used to generate a 50% majority-rule consensus tree, with clade support indicated as posterior probabilities. Because posterior probabilities reflect actual statistical significance, all nodes representing probability values less than 0.95 were collapsed.

We compared pruned Bayesian trees from each of the 3 primary clades for which we had good taxon sampling (*Chaetodipus*, *Dipodomys*, and *Perognathus*) to phylogenetic hypotheses of previous studies with Kishino–Hasegawa (K-H) tests (which are more appropriate if a priori hypotheses are available), as well as parallel-likelihood tests in the form of Shimodaira–Hasegawa (S-H) tests (which are more appropriate without a priori hypotheses—Goldman et al. 2000; Shimodaira and Hasegawa 1999) in PAUP 4.0b (Swofford 1999).

This research was conducted in accordance with the guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists (Animal Care and Use Committee 1998).

TABLE 2.—Total variable and parsimony informative sites by codon for each gene region.

	1st position	2nd position	3rd position	Total
<i>COIII</i>				
Total variable	85	43	232	360
Parsimony informative	75	34	231	340
<i>Cytb</i>				
Total variable	139	58	375	572
Parsimony informative	112	36	366	514

RESULTS

The number of total variable and parsimony informative sites by codon for each gene region are presented in Table 2. Regardless of method used for analysis (Figs. 3–5), we found robust support for the monophyly of genera *Dipodomys*, *Microdipodops*, *Chaetodipus*, and *Perognathus*; for a clade that includes *Microdipodops* and *Dipodomys* (i.e., Dipodomyinae); and for a clade that includes exemplars representing *Liomys* and *Heteromys* (i.e., Heteromyinae). Gamma-corrected distances among the genera are provided in Table 3. The parsimony analysis (Fig. 3) offers weak support for a clade comprised of *Chaetodipus* and *Perognathus*, which is unsupported otherwise (Bayesian posterior probability = 0.54; Figs. 4 and 5). Generally, we found very little support for sister-group relationships at the base of the tree. Although the maximum-likelihood analysis shows a fully resolved tree with a basal *Perognathus*, grouped next with *Chaetodipus*, then Heteromyinae, then Dipodomyinae (Fig. 5; $-\ln$ likelihood [$-\ln L$] = 36,026.84165), this tree is not significantly better than one showing the traditional subfamilial topology ($-\ln L$ = 36,027.25254; S-H test, $P = 0.459$).

Dipodomys.—Kangaroo rats have been divided into 6–9 different species-groups primarily based on morphology (Best and Schnell 1974; Blair 1954; Davis 1942; Grinnell 1921; Lidicker 1960a, 1960b; Schnell et al. 1978; Setzer 1949) and chromosomes (Johnson and Selander 1971; Stock 1974). Our analyses of the *Cytb* and *COIII* regions of the mtDNA are consistent with many of the previous groupings, at least in terms of group membership (Figs. 3–5). We found support in all analyses for a *Dipodomys agilis* species-group with an *agilis* plus *simulans* clade grouping with an *elephantinus* plus *venustus* clade. *Dipodomys heermanni*, *panamintinus*, and *stephensi* consistently group together with strong support in all analyses. *Dipodomys gravipes*, *ingens*, and *microps* exhibit affinities to the *heermanni* group, but do not have any support in their

→

FIG. 3.—Heteromyid maximum-parsimony (MP) tree with unweighted characters (tree length = 9,047, consistency index [CI] = 0.1896, and retention index [RI] = 0.1823, number of parsimony informative characters = 854, total number of characters = 1,839). Numbers along branches summarize results of 500 bootstrap repetitions. All nodes with bootstrap support < 50 have been collapsed. The topology of the weighted (site-specific transition–transversion ratios) maximum-parsimony tree was the same except for a weak association between *Dipodomys ordii* and *D. compactus*: CI = 0.1795, RI = 0.4915, tree length = 10,130.3. Abbreviations for genera are as follows: *Chaetodipus* (C), *Perognathus* (P), *Dipodomys* (D), *Microdipodops* (M), *Liomys* (L), *Heteromys* (H), and *Geomys* (G).

specific relationships. All of these taxa together form a clade that is moderately well supported and joins *D. californicus*.

We found robust support in all analyses for a *Dipodomys merriami* species-group comprised of *merriami*, *insularis*, *margaritae*, and *nitratoides* that is sister to an *elator* plus *phillipsii* clade (*D. phillipsii* species-group). A *spectabilis* plus *nelsoni* clade (*D. spectabilis* species-group) is strongly supported in all analyses, as is the basal position of *D. deserti*. Only in the Bayesian analysis did we find any support (weak in the weighted MP analysis; bootstrap = 57) for a *compactus* plus *ordii* clade. We found very little resolution for the relationships among species-groups. The maximum-parsimony analyses resulted in an unresolved polytomy among the *heermanni* plus *agilis* plus *californicus* clade, the *merriami* plus *phillipsii* clade, *ordii*, *compactus*, and a *spectabilis* plus *nelsoni* clade. Kishino–Hasegawa and Shimodaira–Hasegawa tests were performed to compare the mtDNA *Dipodomys* clade based on MrBayes with that generated from chromosomal data by Patton and Rogers (1993); the mtDNA tree generated in this study was significantly better than the chromosomal tree (K-H = $P < 0.0001$, mtDNA tree length = 2,891, chromosome tree length = 3,165; S-H = $P < 0.0001$; $-\ln L = 14,113.069$).

Chaetodipus.—Sixteen species-level taxa were included in the analysis of *Chaetodipus*. Several convincing lines of evidence now have placed *C. formosus* solidly within the genus *Chaetodipus* rather than *Perognathus* (Patton et al. 1981). Previously described species-groups for this genus were based primarily on general morphologic similarities rather than actual relationship; the taxonomic breakdown has included a species-group with moderately well-developed rump spines (including *intermedius*, *nelsoni*, *fallax*, *artus*, and *goldmani*) and a species-group without defined rump spines (including *penicillatus* [plus *eremicus*], *pernix*, and *arenarius*). Most of the remaining taxa (*californicus*, *spinatus*, *baileyi* [plus *rudinoris*], *hispidus*, and *formosus*) were placed in monotypic species-groups (Hafner and Hafner 1983; Patton and Rogers 1993; Patton et al. 1981).

Based on chromosome research summarized by Patton and Rogers (1993), *C. penicillatus*, *C. baileyi*, and *C. pernix* each have significant karyotypic variation that may reflect cryptic species. In the cases of *C. penicillatus* and *C. baileyi*, the previously embedded cryptic species are now recognized as *C. eremicus* and *C. rudinoris*, respectively (Lee et al. 1996; Riddle et al. 2000a).

Chaetodipus formosus and *C. baileyi* (plus *rudinoris*) traditionally have been described as somewhat intermediate in morphology between *Chaetodipus* and *Perognathus*. We consistently found robust support for a *baileyi* plus *rudinoris* group and strong (Bayesian; Fig. 4) to very weak support (MP; Fig. 3) for uniting this group with *formosus* before uniting with

all of the rest of the *Chaetodipus*. They are clearly basal lineages, but our results support their inclusion within a monophyletic *Chaetodipus*.

Morphologic and chromosomal characteristics traditionally have been used to separate *C. hispidus* from the rest of the genus; it has been placed into its own subgenus of *Chaetodipus*, *Burtognathus* (Hoffmeister 1986). In each of our analyses, *C. hispidus* consistently groups within the monophyletic *Chaetodipus* and is 1 step inside the basal *formosus*–*baileyi*–*rudinoris* subclade (Figs. 3–5).

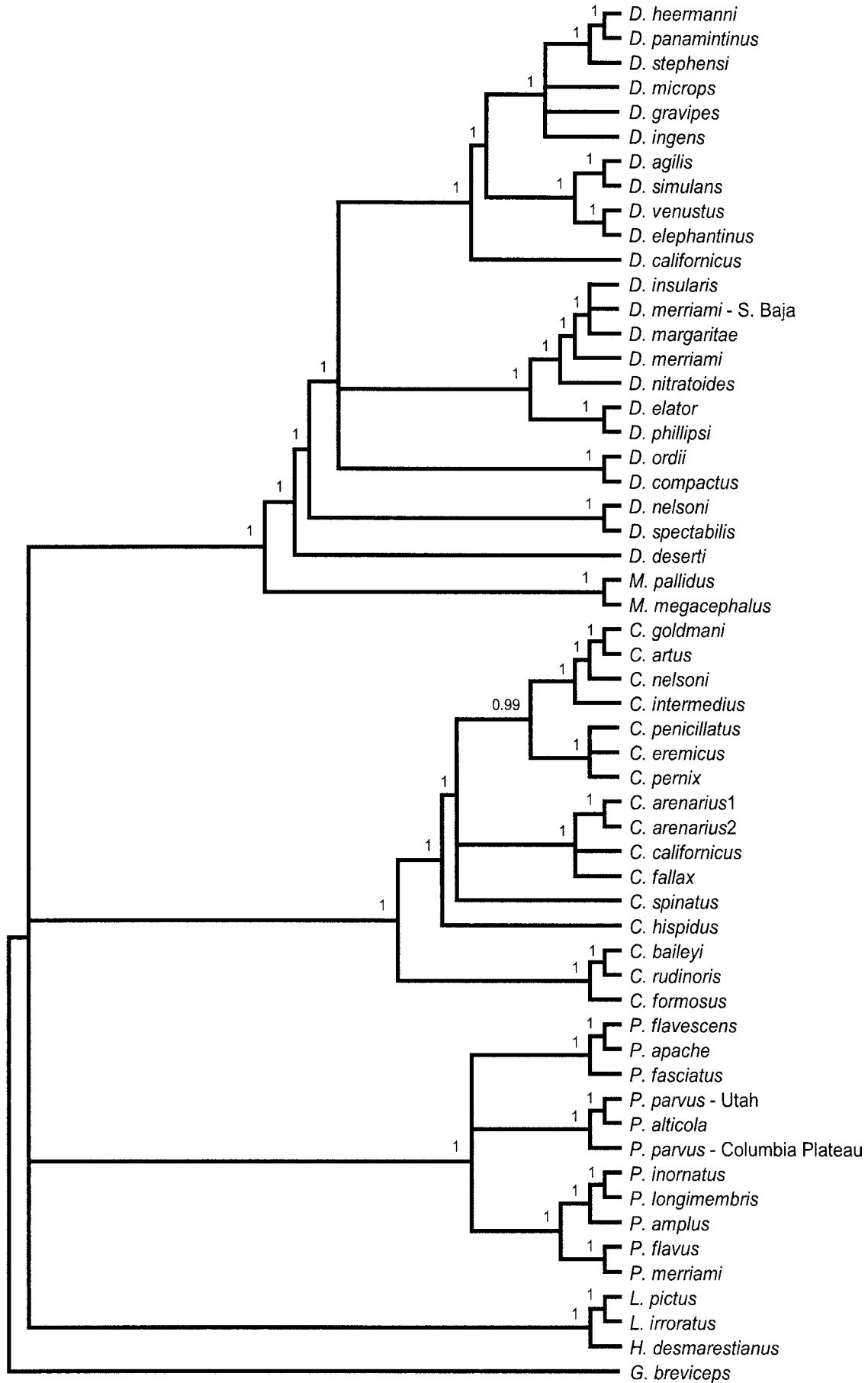
We found some agreement with the 2 traditional, morphology-based species-groups (Figs. 3–5). In all analyses, we found robust support for a *goldmani*, *artus*, *nelsoni* group and support (weak in the MP; Fig. 3) for the subsequent addition of *intermedius* to that group (but no support for the traditional inclusion of *fallax*). We found robust support for an *eremicus*, *pernix*, *penicillatus* group (but no support for the traditional inclusion of *arenarius*); the relationships at the tips differ slightly in the various analyses. We found solid Bayesian support (Fig. 4) that 1st unites these 2 groups (with maximum-likelihood agreement and concurrence with Riddle et al. [2000a]), followed by an unresolved trichotomy with an *arenarius*1, *arenarius*2, *californicus*, *fallax* group and *spinatus* (all 5 taxa are grouped in the ML; Fig. 5). However, the maximum parsimony analyses result in an unresolved polytomy of these initial 2 groups along with *spinatus*, *fallax*, *californicus*, and a solidly supported *arenarius*1 plus *arenarius*2 group (Fig. 3).

Kishino–Hasegawa and Shimodaira–Hasegawa tests were performed to compare the mtDNA *Chaetodipus* clade generated by MrBayes with a tree generated from chromosomal data by Patton and Rogers (1993) and a tree that was generated from allozyme data (Patton et al. 1981). The mtDNA tree generated in this study was significantly better than both the chromosomal tree (K-H = $P < 0.0001$, mtDNA tree length = 3,181, chromosome tree length = 3,508; S-H = $P < 0.0001$, $-\ln L = 14,122.431$) and the allozyme tree (K-H = $P < 0.0001$, mtDNA tree length = 3,181, chromosome tree length = 3,374; S-H = $P < 0.0001$, $-\ln L = 14,126.147$).

Perognathus.—Eleven species-level taxa were included in this analysis, including 2 species-level taxa within *P. parvus* (based on the preliminary evidence of Riddle [1995]). Previously described species-groups (Williams 1978) include a *longimembris* group (*longimembris*, *amplus*, and *inornatus*), a *parvus* group (*parvus* and *alticolus*), a *fasciatus* group (*fasciatus*, *flavescens*, and *apache*), and a *flavus* group (*flavus* and *merriami*). These species-groups were supported with high levels of bootstrap support in the analyses of Riddle (1995) and in the current study. We found strong parsimony bootstrap

→

FIG. 4.—Heteromyid 50% majority-rule consensus Bayesian tree generated from running 4 Markov chain Monte Carlo iterations simultaneously for 1×10^6 generations and sampling every 100 generations. Numbers along branches summarize results of 95% posterior probability values from 9,000 trees after discarding the first 1,000 trees as the burn-in. All nodes with support < 95 have been collapsed. Abbreviations for genera as in Fig. 3.



support (Fig. 3) and high Bayesian probabilities (Fig. 4) for these species-groups as well as identical relationships within species-groups, regardless of analysis method. In the maximum-parsimony, Bayesian, and maximum-likelihood analyses (Figs. 3, 4, and 5, respectively), the only differences in the resulting phylogenetic hypotheses are the relationships among the species-groups. All 3 methods support a *longimembris* plus *flavus* arrangement. The differences arise in the relationships between this *longimembris* plus *flavus* clade and the remaining 2 species-groups. Both the parsimony (Fig. 3) and Bayesian analyses (Fig. 4) resulted in an unresolved trichotomy of the *parvus*, *fasciatus*, and *longimembris* plus *flavus* species-groups, although there is nonsignificant indication ($P = 0.88$) of a *fasciatus* plus *parvus* grouping in the Bayesian analysis, which agrees with that found by Williams (1978). The maximum-likelihood analysis (Fig. 5) arranged *longimembris* plus *flavus* with *fasciatus* and then the entire clade with *parvus*. The specific relationships among the 4 species-groups remain unresolved.

Kishino–Hasegawa and Shimodaira–Hasegawa tests were performed to compare the mtDNA *Perognathus* clade generated by MrBayes to previously suggested relationships based on chromosomal data (Williams 1978) and mtDNA data from *Cytb* and *COIII* (Riddle 1995). The MrBayes tree generated in this study was identical to the relationships described by Williams (1978) and by Riddle (1995) except for the placement of the *parvus* group. Williams (1978) placed the *parvus* group with the *fasciatus* group, whereas Riddle (1995) placed the *parvus* group with the *longimembris* plus *flavus* groups. Because the current Bayesian analysis placed these groups in an unresolved trichotomy, both of the previously published trees were somewhat better than our Bayesian tree, but neither of them was significant in the Shimodaira–Hasegawa tests. The mtDNA tree generated by Riddle (1995) was better than the Bayesian tree (K-H = $P < 0.0001$, Riddle mtDNA tree length = 2,186, Bayesian mtDNA tree length = 2,210; S-H = $P < 0.093$, $-\ln L = 10,933.630$); the tree generated from chromosomal data by Williams (1978) also resulted in a somewhat better tree (K-H = $P < 0.0001$, chromosome tree length = 2,192, mtDNA tree length = 2,210; S-H = $P < 0.272$, $-\ln L = 10,941.316$). If the 2 previously published studies are compared, the mtDNA tree of Riddle (1995) is shorter, but not significantly better (K-H = $P < 0.3547$, Riddle mtDNA tree = 2,186, chromosome tree length = 2,192; S-H = $P < 0.117$, $-\ln L = 10,933.631$) than that provided by Williams (1978).

DISCUSSION

In all analyses we found robust support for the monophyly of all genera as well as for clades that support Dipodominae and Heteromyinae. The lack of resolution for the basal nodes within the family Heteromyidae is most likely caused by the use of

mitochondrial genes that saturate fairly quickly (Simon et al. 1994). More conservative genes might offer better resolution of the deeper nodes on this tree; we are currently evaluating a suite of nuclear genes to address this problem.

Dipodominae.—One significant finding of these phylogenetic analyses is corroboration of the position of *Microdipodops* within the subfamily Dipodominae rather than within the Perognathinae. Based primarily on fossil dental characteristics, Reeder (1956) suggested that *Microdipodops* is more closely related to *Dipodomys* than any other extant taxa. He stated “although it is not recently derived from similar stock, it is probably the remnant of the flourishing *Cupidinimus*–*Perognathoides* complex of the late Tertiary” (Reeder 1956:416). In the extent of hypsodonty and the pattern of cusps, the dentition of *Microdipodops* is nearly identical to that of *Cupidinimus* and very similar to that of *Perognathoides* (Reeder 1956).

The deep divergence between *Dipodomys* and *Microdipodops* in our data indicates that *Microdipodops* diverged at least 10 million years earlier than its 1st appearance in the fossil record (Pleistocene). *Dipodomys* 1st appears in the fossil record during the Barstovian age of the middle Miocene and radiated thereafter. The phylogenetic split between the ancestors of the *Dipodomys* and *Microdipodops* lineages must therefore have occurred no later than the early–middle Miocene. Early *Microdipodops* tooth-only fossils may have been misidentified as *Cupidinimus* or *Perognathoides*. *Microdipodops* tends to occur along shorelines of pluvial lakes, but *M. megacephalus* also occupies somewhat gravelly soils; the xeric, sandy habitat to which *Microdipodops* is specifically adapted may not have assumed its current distribution until the interpluvial periods of the Pleistocene.

Perognathinae.—These analyses corroborate the phylogenetic separation of *Chaetodipus* and *Perognathus*. In fact, we have found no support for the historical inclusion of both genera (*Perognathus* and *Chaetodipus*) in the subfamily Perognathinae (MP bootstrap = 79; Bayesian posterior probability = 0.54). Levels of interspecific divergence in both *Chaetodipus* and *Perognathus* within *Cytb* are considerably higher than in other genera of rodents (Johns and Avise 1998). The conservative nature of the morphology of both genera is in stark contrast to their molecular divergence (Modi 2003). Even though paleontologists have been unable to distinguish the 2 genera based on fossils, these genera are highly divergent lineages within the family Heteromyidae. It would be interesting to revisit the fossil specimens now that this generic dichotomy is robustly established and ask whether they can be assigned to genus with confidence. Morphometric data presented by Hafner (Hafner 1978:357, figure 3) demonstrated that *Chaetodipus* and *Perognathus* are not particularly similar in morphometric space. Hafner presented phenograms representing phenetic relationships (Hafner 1978:356, figure 2) that place *Microdipodops* in

→

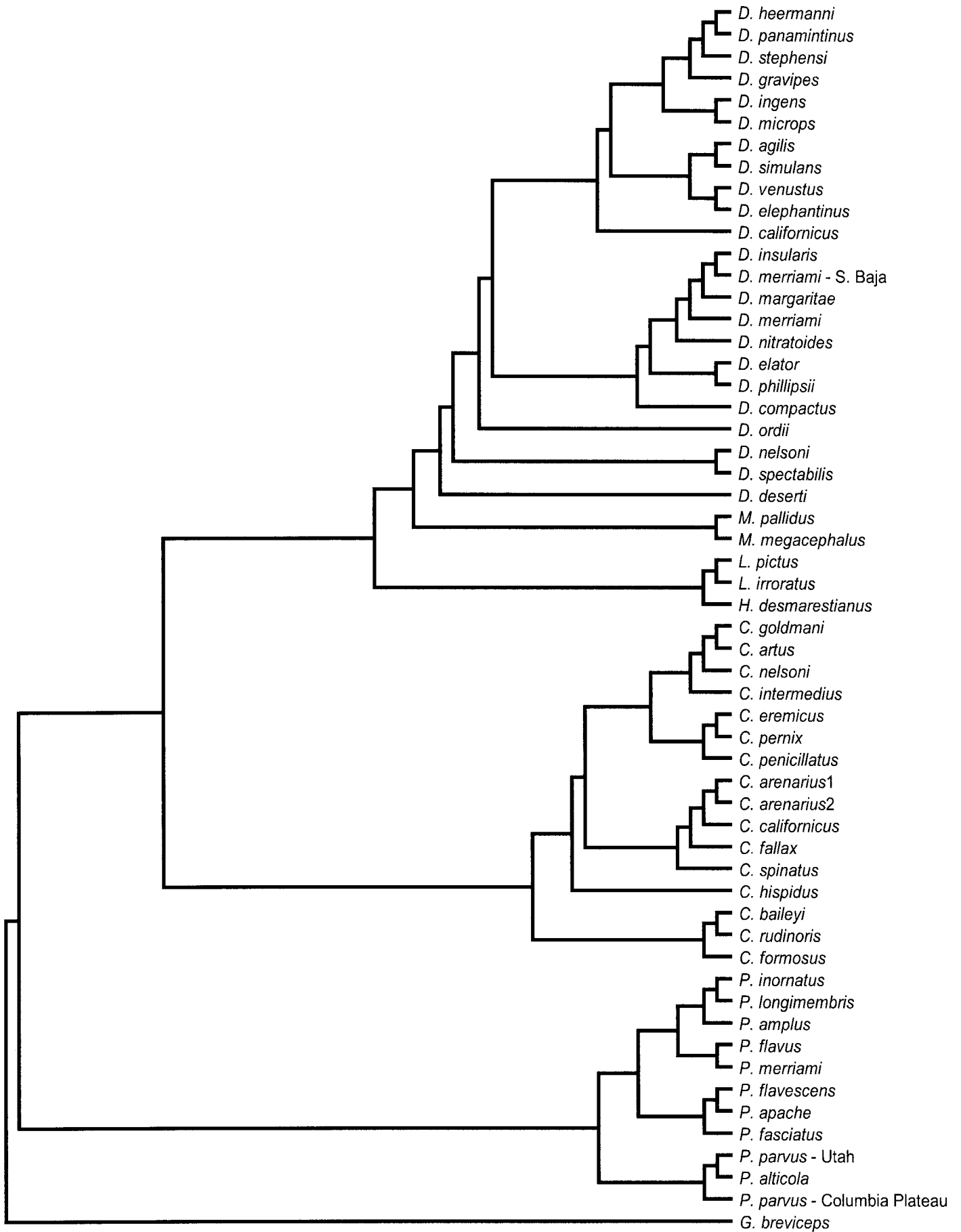


TABLE 3.—Gamma-corrected mean distance within genera (bold diagonal), gamma-corrected mean distance between genera (above diagonal), and corresponding standard error (below diagonal).

	<i>Dipodomys</i>	<i>Microdipodops</i>	<i>Liomys</i>	<i>Heteromys</i>	<i>Chaetodipus</i>	<i>Perognathus</i>
<i>Dipodomys</i>	0.198	0.294	0.354	0.339	0.353	0.362
<i>Microdipodops</i>	0.016	0.207	0.354	0.288	0.361	0.370
<i>Liomys</i>	0.020	0.021	0.218	0.257	0.359	0.366
<i>Heteromys</i>	0.020	0.018	0.018		0.366	0.340
<i>Chaetodipus</i>	0.018	0.020	0.018	0.020	0.275	0.361
<i>Perognathus</i>	0.019	0.019	0.019	0.017	0.018	0.293

a position that implies paraphyly of the genus *Perognathus*; this paraphyletic arrangement is removed when we realize that the “*Perognathus*” that Hafner (1978) referred to now includes both *Perognathus* and *Chaetodipus*. Interestingly, if we consider modern taxonomy, Hafner (1978) found that *Microdipodops* is morphologically more similar to *Perognathus* than *Perognathus* is to *Chaetodipus*. Our analyses show no evidence for a subfamily Perognathinae containing *Perognathus* and *Chaetodipus*.

Historical biogeography.—From the Oligocene to the late Miocene, subtropical thorn forests and woodland savannas were gradually replaced with steppe and semidesert habitats. This continued during the latest Miocene with expansion of regional deserts, grasslands and shrub-steppes. The early to middle Miocene experienced a tremendous radiation of heteromyid rodents (Korth 1994; Savage and Russell 1983). *Perognathus* (including *Chaetodipus*) and *Dipodomys* were well established by the middle Miocene (Wahlert 1993). The remaining 3 genera (*Microdipodops*, *Liomys*, and *Heteromys*) have such poor fossil records that we are unable to identify their initial appearance from fossils. However, examination of our data suggests that the 4 primary clades (Dipodominae [including *Dipodomys* and *Microdipodops*], *Perognathus*, *Chaetodipus*, and Heteromyinae [including *Heteromys* and *Liomys*]) all have had a similar amount of time since lineage divergence. The initial diversification of all of these groups probably coincided with the middle Miocene formation and expansion of steppe and semidesert habitats into at least 3 provinces (Riddle et al. 2000a): eastern grasslands and savannas (occupied by *Chaetodipus hispidus*, and the ancestors of the *Perognathus fasciatus*, *Dipodomys spectabilis*, and *D. ordii* species-groups), semideserts and woodlands of the Basin and Range (occupied by *D. deserti*, *D. microps*, *Microdipodops*, and the ancestors of the *C. formosus* and *P. parvus* species-groups), and semideserts and subtropical thorn-scrub in western Mexico (occupied by the ancestors of the *C. baileyi* and *D. merriami* species-groups). Subsequent diversification events within each genus took place in response to continuing isolation of the regional deserts throughout the late Miocene, early Pliocene, and into the recent glacial–interglacial cycles of the Pleistocene.

The subtropical Heteromyinae has the most primitive morphology within the family Heteromyidae. The genus *Liomys* is restricted to the arid and semiarid thorn-scrub regions of Central and South America and is apparently limited in its distribution by extreme aridity and high moisture (Genoways 1973; Schmidly et al. 1993). *Liomys* has an apparent requirement of

at least 250 mm of rainfall per year, but is replaced by *Heteromys* in more mesic tropical habitats (Schmidly et al. 1993). If the subfamily Heteromyinae is approximately as old as the Dipodominae, *Perognathus*, and *Chaetodipus* as it appears in these analyses, this group of rodents could have evolved in southern North America, moved south into Central America, and then on into South America after the rejoining of Panama and Colombia as part of the great American biotic interchange (Anderson 2001; Webb 1985) during the Pliocene (~3 mya). These taxa probably were restricted to several refugia in Central America during the glacial periods of the late Pleistocene when climatic conditions became colder and drier. The Pleistocene refugia may have provided the isolation necessary for speciation within each of these genera.

Two mitochondrial gene regions were evaluated for this study. Even though they are not independent estimates of phylogeny, they are evolving at a similar rate, and therefore, combining the 2 increased the numbers of informative characters available for analysis. Even though these relatively rapidly evolving genes did lose phylogenetic signal at the base of the family-level and generic-level trees, they provide a robust hypothesis for subfamilial monophyly and for a number of species-groups and sister-species relationships within each genus, allowing us to work toward a phylogenetically based assessment of diversification and biogeographic history in this endemic New World family of rodents. Additional nuclear loci will need to be examined to provide additional resolution to phylogenetic relationships within and among genera within Heteromyidae.

ACKNOWLEDGMENTS

We thank T. L. Best (Department of Biological Sciences, Auburn University, Alabama) and D. J. Hafner (New Mexico Museum of Natural History, Albuquerque) for many tissue samples without which this project would not have been possible. D. J. Hafner contributed the latitude and ecoregion figures as well as many valuable discussions and editorial reviews. His involvement in this project is very much appreciated. We thank J. Demastes (Department of Biology, University of Northern Iowa), M. D. Engstrom (Royal Ontario Museum, Toronto, Ontario, Canada), J. L. Patton (Museum of Vertebrate Zoology, University of California), and P. Sudman (Biological Sciences, Tarleton State University, Stephenville, Texas) for additional tissue samples. We thank F. A. Cervantes (Instituto de Biología, Universidad Nacional Autónoma de México), S. T. Alvarez-Castañeda and P. Cortés-Calva (Centro de Investigaciones Biológicas del Noroeste), and their students for assistance in the field and for arranging collecting

permits in Mexico. This work represents a portion of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree in the Department of Biological Sciences, University of Nevada Las Vegas, for LFA. Financial support for this project was provided from Grants-in-aid of Research from the American Society of Mammalogists, Sigma Xi, and the American Museum, Theodore Roosevelt Fund to LFA; several Graduate Student Association Research Grants from the University of Nevada Las Vegas to LFA; and grants from the National Science Foundation to BRR (DEB-9629787) and D. J. Hafner (DEB 9629840).

LITERATURE CITED

- ANDERSON, R. P. 2001. Systematics and biogeographic modeling of spiny pocket mice (Rodentia: Heteromyidae: *Heteromys*) in South America. Ph.D. dissertation, University of Kansas, Lawrence.
- ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. *Journal of Mammalogy* 79:1416–1431.
- AXELROD, D. I. 1979. Age and origin of Sonoran Desert vegetation. *Occasional Papers of the California Academy of Sciences* 132:1–74.
- AXELROD, D. I. 1983. Paleobotanical history of the western deserts. Pp. 113–129 in *Origin and evolution of deserts* (S. G. Wells and D. R. Haragan, eds.). University of New Mexico Press, Albuquerque.
- BALDWIN, E. M. 1964. *Geology of Oregon*. University of Oregon, Eugene.
- BEST, T. L. 1993. Patterns of morphologic and morphometric variation in heteromyid rodents. Pp. 197–235 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists 10:1–719.
- BEST, T. L., R. K. CHESSER, D. A. McCULLOUGH, AND G. D. BAUMGARDNER. 1996. Genic and morphometric variation in kangaroo rats, genus *Dipodomys*, from coastal California. *Journal of Mammalogy* 77:785–800.
- BEST, T. L., AND G. D. SCHNELL. 1974. Bacular variation in kangaroo rats (genus *Dipodomys*). *American Midland Naturalist* 91:257–270.
- BLAIR, W. F. 1954. Mammals of the mesquite plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. *Texas Journal of Science* 6:235–264.
- DAVIS, W. B. 1942. The systematic status of four kangaroo rats. *Journal of Mammalogy* 23:328–333.
- DEBRY, R. W., AND R. M. SAGEL. 2001. Phylogeny of Rodentia (Mammalia) inferred from the nuclear-encoded gene IRBP. *Molecular Phylogenetics and Evolution* 19:290–301.
- FIERO, B. 1986. *Geology of the Great Basin*. University of Nevada Press, Reno.
- GENOWAYS, H. H. 1973. Systematics and evolutionary relationships of spiny pocket mice, genus *Liomys*. *Special Publications, The Museum, Texas Tech University* 5:1–368.
- GOLDMAN, N., J. P. ANDERSON, AND A. G. RODRIGO. 2000. Likelihood-based tests of topologies in phylogenetics. *Systematic Biology* 49:652–670.
- GRINNELL, J. 1921. Revised list of the species in the genus *Dipodomys*. *Journal of Mammalogy* 2:94–97.
- HAFNER, J. C. 1978. Evolutionary relationships of kangaroo mice, genus *Microdipodops*. *Journal of Mammalogy* 59:354–366.
- HAFNER, J. C. 1993. Macroevolutionary diversification in heteromyid rodents: heterochrony and adaptation in phylogeny. Pp. 291–318 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists 10:1–719.
- HAFNER, J. C., AND M. S. HAFNER. 1983. Evolutionary relationships of heteromyid rodents. *Great Basin Naturalist Memoirs* 7:3–29.
- HAFNER, M. S. 1982. A biochemical investigation of geomyoid systematics (Mammalia: Rodentia). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 20:118–130.
- HALL, E. R. 1981. *The mammals of North America*. Wiley, New York 1:1–600 + 90.
- HALL, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41:95–98.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. The University of Arizona Press and The Arizona Game and Fish Department, Tucson.
- HUELSENBECK, J. P., AND J. P. BOLLBACK. 2001. Empirical and hierarchical Bayesian estimation of ancestral states. *Systematic Biology* 50:351–366.
- HUELSENBECK, J. P., AND F. RONQUIST. 2001. MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17:754.
- JOHNS, G. C., AND J. C. AVISE. 1998. A comparative summary of genetic distances in the vertebrates from the cytochrome *b* gene. *Molecular Biology and Evolution* 15:1481–1490.
- JOHNSON, W. E., AND R. K. SELANDER. 1971. Protein variation and systematics in kangaroo rats (genus *Dipodomys*). *Systematic Zoology* 20:377–405.
- KORTH, W. W. 1994. *The Tertiary record of rodents in North America*. Plenum Press, New York.
- LEE, T. E., B. R. RIDDLE, AND P. L. LEE. 1996. Speciation in the desert pocket mouse (*Chaetodipus penicillatus* Woodhouse). *Journal of Mammalogy* 77:58–68.
- LEVIN, H. L. 1978. *The earth through time*. W. B. Saunders Company, Philadelphia, Pennsylvania.
- LIDICKER, W. Z., JR. 1960a. An analysis of intraspecific variation in the kangaroo rat *Dipodomys merriami*. *University of California Publications in Zoology* 67:125–218.
- LIDICKER, W. Z., JR. 1960b. The baculum of *Dipodomys ornatus* and its implication for superspecific groupings of kangaroo rats. *Journal of Mammalogy* 41:495–499.
- LONGMIRE, J. L., ET AL. 1991. Use of sex-linked minisatellite fragments to investigate genetic differentiation and migration of North American populations of the peregrine falcon (*Falco peregrinus*). Pp. 217–229 in *DNA fingerprinting: approaches and applications* (T. Burke, G. Dolf, A. Jeffreys and R. Wolff, eds.). Birkhauser Publishing Ltd., Basel, Switzerland.
- MODI, W. S. 2003. Morphological, chromosomal, and molecular evolution are uncoupled in pocket mice. *Cytogenetic and Genome Research* 103:150–154.
- MONTGELARD, C., S. BENTZ, C. TIRARD, O. VERNEAU, AND F. M. CATZEFELIS. 2002. Molecular systematics of Sciurognathi (Rodentia): The mitochondrial cytochrome *b* and 12S rRNA genes support the Anomaluroidea (Pedetidae and Anomaluridae). *Molecular Phylogenetics and Evolution* 22:220–233.
- NORRIS, R. M., AND R. W. WEBB. 1976. *Geology of California*. John Wiley and Sons, New York.
- ORTEGA-GUTIÉRREZ, F., AND J. C. GUERRERO-GARCIA. 1982. The geologic regions of Mexico. Pp. 99–104 in *Perspectives in regional geological synthesis. D-NAG Special Publication 1* (A. R. Palmer, ed.). Geological Society of America 1:1–176.
- PATTON, J. L. 1993. Family Heteromyidae. Pp. 477–486 in *Mammal species of the World* (D. E. Wilson and D. M. Reeder, eds.). 2nd ed. Smithsonian Institution Press, Washington, D.C.
- PATTON, J. L., AND D. S. ROGERS. 1993. Biochemical genetics. Pp. 259–269 in *Biology of the Heteromyidae* (H. H. Genoways and

- J. H. Brown, eds.). Special Publication, American Society of Mammalogists 10:1–719.
- PATTON, J. L., S. W. SHERWOOD, AND S. Y. YANG. 1981. Biochemical systematics of chaetodipine pocket mice, genus *Perognathus*. *Journal of Mammalogy* 62:477–492.
- POSADA, D., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14:817–818.
- REEDER, W. G. 1956. A review of Tertiary rodents of the family Heteromyidae. Ph.D. dissertation, University of Michigan, Ann Arbor.
- RIDDLE, B. R. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the late Cenozoic development of a North American aridlands rodent guild. *Journal of Mammalogy* 76:283–301.
- RIDDLE, B. R., D. J. HAFNER, AND L. F. ALEXANDER. 2000a. Comparative phylogeography of Baileys' pocket mouse (*Chaetodipus baileyi*) and the *Peromyscus eremicus* species-group: historical vicariance of the peninsular and continental deserts. *Molecular Phylogenetics and Evolution* 17:161–172.
- RIDDLE, B. R., D. J. HAFNER, L. F. ALEXANDER, AND J. JAEGER. 2000b. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceedings of the National Academy of Sciences* 97:14438–14443.
- ROGERS, D. S. 1990. Genic evolution, historical biogeography, and systematic relationships among spiny pocket mice (subfamily Heteromyinae). *Journal of Mammalogy* 71:668–685.
- ROTH, E. L. 1976. A new species of pocket mouse (*Perognathus*: Heteromyidae) from the Cape Region of Baja California Sur, Mexico. *Journal of Mammalogy* 57:562–566.
- RYAN, J. M. 1989. Comparative myology and phylogenetic systematics of the Heteromyidae (Mammalia, Rodentia). *Miscellaneous Publications of Museum of Zoology, University of Michigan* 176:1–103.
- SAVAGE, D. E., AND D. E. RUSSELL. 1983. *Mammalian paleofaunas of the world*. Addison-Wesley, New York.
- SCHMIDLY, D. J., K. T. WILKINS, AND J. N. DERR. 1993. Biogeography. Pp. 319–356 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists 10:1–719.
- SCHNELL, G. D., T. L. BEST, AND M. L. KENNEDY. 1978. Interspecific morphologic variation in kangaroo rats (*Dipodomys*): degree of concordance with genic variation. *Systematic Zoology* 27:34–48.
- SETZER, H. W. 1949. *Subspeciation in the kangaroo rat, Dipodomys ordii*. University of Kansas Publications, Museum of Natural History 1:473–573.
- SHIMODAIRA, H., AND M. HASEGAWA. 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution* 16:1114–1116.
- SIMON, C., F. FRATI, A. BECKENBACH, B. CRESPI, H. LIU, AND P. FLOOK. 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America* 87:651–701.
- SMITH, M. F., AND J. L. PATTON. 1993. The diversification of South American murid rodents: evidence from mitochondrial sequence data for the akodontine tribe. *Biological Journal of the Linnean Society* 50:149–177.
- STOCK, A. D. 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. *Journal of Mammalogy* 55:505–526.
- SWANSON, E. R., AND F. W. MCDOWELL. 1984. Calderas of the Sierra Madre Occidental volcanic field, western Mexico. *Journal of Geophysical Research* 89:8787–8799.
- SWOFFORD, D. L. 1999. PAUP*: phylogenetic analysis using parsimony (* and other methods) 4.0 beta version. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- TABERLET, P., A. MEYER, AND J. BOUVET. 1992. Unusual mitochondrial DNA polymorphism in two local populations of blue tit (*Parus caeruleus*). *Molecular Ecology* 1:27–36.
- TAMURA, K., AND M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* 10:512–526.
- WAHLERT, J. H. 1985. Skull morphology and relationships of geomyoid rodents. *American Museum Novitates* 2812:1–20.
- WAHLERT, J. H. 1993. The fossil record. Pp. 1–37 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication, American Society of Mammalogists 10:1–719.
- WEBB, S. D. 1977. A history of savanna vertebrates in the New World. Part 1: North America. *Annual Review of Ecology and Systematics* 8:355–380.
- WEBB, S. D. 1983. The rise and fall of the late Miocene ungulate fauna in North America. Pp. 267–306 in *Coevolution* (M. H. Nitecki, ed.). University of Chicago Press, Chicago, Illinois.
- WEBB, S. D. 1985. Late Cenozoic mammal dispersals between the Americas. Pp. 357–386 in *The great American biotic interchange* (F. G. Stehli and S. D. Webb, ed.). Plenum Press, New York.
- WILLIAMS, D. F. 1978. Karyological affinities of the species groups of silky pocket mice (Rodentia, Heteromyidae). *Journal of Mammalogy* 59:599–612.
- WILLIAMS, D. F., H. H. GENOWAYS, AND J. K. BRAUN. 1993. Taxonomy. Pp. 38–196 in *Biology of the Heteromyidae* (H. H. Genoways and J. H. Brown, eds.). Special Publication, The American Society of Mammalogists 10:1–719.
- WILSON, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. *The University of Kansas, Paleontological Contributions, Vertebrata* 7:1–92.
- WOOD, A. E. 1935. Evolution and relationship of the heteromyid rodents with new forms from the Tertiary of western North America. *Annals of Carnegie Museum* 24:73–262.
- XIA, X. 1998. The rate heterogeneity of nonsynonymous substitutions in mammalian mitochondrial genes. *Molecular Biology and Evolution* 15:336–344.

Submitted 20 January 2004. Accepted 14 July 2004.

Associate Editor was Eric A. Rickart.

APPENDIX I

Specimens examined.—Taxa, catalog numbers (LVT = Las Vegas Tissue Collection, MVZ = Museum of Vertebrate Zoology), localities, and GenBank accession numbers (*COIII*, *Cytb*) for all specimens included in these analyses. Tissue samples received from Troy L. Best are listed with the Las Vegas Tissue number (LVT) and a collection number (as either TLB or NK) separated by a slash; (mi = miles).

*Chaetodipus arenarius*1.—LVT 2128; 7 miles S, 7 miles E San Felipe, Baja California, Mexico; AY009265, AY926399.

*Chaetodipus arenarius*2.—LVT 3645; 11 km S Todos Santos, Baja California, Mexico; AY010230, AY926400.

Chaetodipus artus.—LVT 1270; Presa Hidalgo, 10 km NE El Fuerte, Sinaloa Mexico; AY009260, AY926396.

Chaetodipus baileyi.—LVT 1210; 2 km N Puerto de la Libertad, Sonora Mexico; AY009310, AY926393.

- Chaetodipus californicus*.—LVT 3682; 2 mi SW Laguna Hanson, Baja California, Mexico; AY009259, AY926401.
- Chaetodipus eremicus*.—LVT 1160; 1 mi SE Hundido, Coahuila, Mexico; AY009256, AY926392.
- Chaetodipus fallax*.—LVT 3741; Misión San Fernando, Baja California, Mexico; AY009262, AY926402.
- Chaetodipus formosus*.—LVT 987; 9 mi W, 1 mi S Quien Sabe Point, Riverside County, California; AY926424, AY926387.
- Chaetodipus goldmani*.—LVT 1264; 4 km N Navojoa, Sonora, Mexico; AY009261, AY926394.
- Chaetodipus hispidus*.—LVT 1099; 7 mi NNW La Zarca, Durango, Mexico; AY009254, AY926391.
- Chaetodipus intermedius*.—LVT 1063; 5 km NNW Chihuahua, Chihuahua, Mexico; AY009264, AY926389.
- Chaetodipus nelsoni*.—LVT 1075; 3 mi NE Parral, Chihuahua, Mexico; AY009255, AY926390.
- Chaetodipus penicillatus*.—LVT 1016; 1.5 mi S, 6.5 mi W Glamis, Imperial County, California; AY009257, AY926388.
- Chaetodipus pernix*.—LVT 1267; 4 km N Navojoa, Sonora, Mexico; AY009258, AY926395.
- Chaetodipus rudinoris*.—LVT 2114; 7 mi S, 7 mi E San Felipe, Baja California, Mexico; AY009267, AY926397.
- Chaetodipus spinatus*.—LVT 2119; 7 mi S, 7 mi E San Felipe, Baja California, Mexico; AY009263, AY926398.
- Dipodomys agilis*.—LVT 2035/TLB 11237; near Wrightwood, Los Angeles County, California; AY926433, AY926366.
- Dipodomys californicus*.—LVT 2037/TLB 10357; 6 mi NE Dales, Tehama County, California; AY926435, AY926368.
- Dipodomys compactus*.—LVT 2060/TLB 11476; Padre Island National Seashore, Kleberg County, Texas; AY926446, AY926379.
- Dipodomys deserti*.—LVT 2083; St. Thomas Gap, Clark County, Nevada; AY926448, AY926381.
- Dipodomys elator*.—LVT 2059/TLB 10566; 2 mi W Harrold, Wilbarger County, Texas; AY926445, AY926378.
- Dipodomys elephantinus*.—LVT 2047/TLB 10068; 1 mi N Pinnacles, San Benito County, California; AY926441, AY926374.
- Dipodomys gravipes*.—LVT 2048/TLB 11048; 12 km NE El Rosario, Baja California, Mexico; AY926442, AY926375.
- Dipodomys heermanni*.—LVT 2041/TLB 10045; 1 mi N Pinnacles, San Benito County, California; AY926436, AY926369.
- Dipodomys ingens*.—LVT 2057/TLB 10825; Naval Petroleum Reserve No. 2, Kern County, California; AY926444, AY926377.
- Dipodomys insularis*.—LVT 2043/TLB 11018; Isla San Jose, Baja California Sur, Mexico; AY926438, AY926371.
- Dipodomys margaritae*.—LVT 2042/NK 2158; Isla Santa Margarita, Baja California Sur, Mexico; AY926437, AY926370.
- Dipodomys merriami*.—LVT 1023; Kelso Dunes, San Bernadino County, California; AY926430, AY926363.
- Dipodomys merriami*.—LVT 3610; 30 km N Todos Santos, Baja California Sur, Mexico; AY926450, AY926383.
- Dipodomys microps*.—LVT 4935; 9 mi N Beatty, Oasis Valley, Nye County, Nevada; AY926452, AY926385.
- Dipodomys nelsoni*.—LVT 1107; 7 mi NNW La Zarca, Durango, Mexico; AY926431, AY926364.
- Dipodomys nitratoides*.—LVT 2045/TLB 10241; 6 mi W Buttonwillow, Kern County, California; AY926439, AY926372.
- Dipodomys ordii*.—LVT 1108; 7 mi NNW La Zarca, Durango, Mexico; AY926432, AY926365.
- Dipodomys panamintinus*.—LVT 4672; 9 mi NNE Johannesburg, San Bernadino County, California; AY926451, AY926384.
- Dipodomys phillipsii*.—LVT 2056/NK 16072; Las Cabras, 4.6 mi NW Bledos, San Luis Potosi, Mexico; AY926443, AY926376.
- Dipodomys simulans*.—LVT 2036/TLB 10993; 3 km SE Colonia Vicente Guerrero, Baja California, Mexico; AY926434, AY926367.
- Dipodomys spectabilis*.—LVT 2470; San Mateo Mountains, Nogal Canyon, Socorro County, New Mexico; AY926449, AY926382.
- Dipodomys stephensi*.—LVT 2061/TLB 10775; 2 mi W, 2 mi S Moreno, Riverside County, California; AY926447, AY926380.
- Dipodomys venustus*.—LVT 2046/TLB 10292; 14 mi SE Carmel Valley, Monterey County, California; AY926440, AY926373.
- Heteromys desmarestianus*.—LVT 5499; Tikal, El Peten, Guatemala; AY926425, AY926358.
- Liomys irroratus*.—LVT 2064/NK 7500; 5 mi N, 7.5 mi E Villa de Cos, Zacatecas, Mexico; AY926427, AY926360.
- Liomys pictus*.—LVT 1253; 10 km SSE Alamos, Sonora, Mexico; AY926426, AY926359.
- Microdipodops megacephalus*.—LVT 5155; 6 mi N, 31 mi W Hiko, Lincoln County, Nevada; AY926429, AY926362.
- Microdipodops pallidus*.—LVT 1573; 7 mi N, 6.45 mi W Tempiute, Lincoln County, Nevada; AY926428, AY926361.
- Perognathus alticola*.—MVZ 197329; Cameron Creek, Tehachapi Mountains, Kern County, California; AY926454, AY926413.
- Perognathus amplus*.—LVT 403; 0.5 mi N Organ Pipe Cactus National Monument, Pima County, Arizona; AY926414, AY926403.
- Perognathus apache*.—LVT 3703; Rio Solado, Socorro County, New Mexico; AY926423, AY926412.
- Perognathus fasciatus*.—LVT 2525; 10 mi S Seminoe, Carbon County, Wyoming; AY926421, AY926410.
- Perognathus flavescens*.—LVT 2527; 27 mi N Lakeside, Sheridan County, Nebraska; AY926422, AY926411.
- Perognathus flavus*.—LVT 702; 3 mi S Keyenta, Navajo County, Arizona; AY926417, AY926405.
- Perognathus inornatus*.—LVT 601; Madera County, California; AY926415, AY926404.
- Perognathus longimembris*.—LVT 2191; 27 km S Punta Prieta, Baja California, Mexico; AY926420, AY926408.
- Perognathus merriami*.—LVT 603; Val Verde County, Texas; AY926416, AY926409.
- Perognathus parvus*.—LVT 1816; 9 mi S, 2 mi W Hanksville, Wayne County, Utah; AY926418, AY926406.
- Perognathus parvus*.—LVT 1920; 4 mi S, 6 mi E Ritzville, Adams County, Washington; AY926419, AY926407.
- Geomys breviceps*.—LVT 5500; 3 miles NW Alleene, Little River County, Arkansas; AY926453, AY926386.