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Phylogeography and Systematics of the *Peromyscus eremicus* Species Group and the Historical Biogeography of North American Warm Regional Deserts

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Phylogeographic relationships among 26 populations from throughout the geographic range of the *Peromyscus eremicus* species group are described based on sequence data for a 699-bp fragment of the mitochondrial DNA COIII gene. Distance, maximum-likelihood, and maximum-parsimony analyses of phylogenetic trees generated under four separate character-weighting strategies and representing five alternative biogeographic hypotheses revealed the existence of a cryptic species (*Peromyscus fraterculus,* previously included under *P. eremicus*) on the Baja California Peninsula and adjacent southwestern California and two distinct forms of *P. eremicus,* one from the Mojave, Sonoran, and northwestern Chihuahuan regional deserts (West) and one from the remainder of the Chihuahuan Desert (East). Distinctiveness of *P. fraterculus* is supported by previous morphometric and allozyme analyses, including comparisons with neighboring *P. eremicus* and parapatric *P. eva,* with which *P. fraterculus* shares a sister taxon relationship. Divergence of the *eva* + *fraterculus,* West + East *eremicus,* and *P. merriami* haplotype lineages likely occurred in the late Neogene (3 Ma), in response to northern extension of the Sea of Cortéz and elevation of the Sierra Madre Occidental; divergence of *eva* from *fraterculus* is concordant with the existence of a trans-Peninsular seaway during the Pleistocene (1 Ma); and divergence of West from East *eremicus* occurred during the Pleistocene pluvial–interpluvial cycles, but well before the Wisconsinan glacial interval. The sequence of divergence within the *eremicus* species group and causal association of geological events of the Neogene and Holocene provide a working hypothesis against which phylogeographic patterns among other arid-adapted species of the warm regional deserts of North America may be compared. © 2000 Academic Press

Key Words: **biogeography; phylogeography; systematics; North American deserts; mitochondrial DNA; rodents; *Peromyscus eremicus; Peromyscus eva; Peromyscus merriami; Peromyscus fraterculus.***

INTRODUCTION

Knowledge of the diversification and distribution of taxa and biotas through time is fundamentally based on our understanding of the geographic distribution of and relationships among evolutionary lineages. For example, debate over the prevalence of vicariance versus dispersal will reflect the extent to which similarity among populations fails to obscure historical divergence among evolutionary lineages. Reconstructions of biogeographic history will necessarily be wrong if paraphyletic or polyphyletic lineages are erroneously interpreted to be monophyletic.

We might expect basic biogeographic patterns in the North American mammal fauna to be relatively well characterized, given a century of intensive systematic and biogeographic investigations that began with the creation of the United States Biological Survey in the late 1800s (Hoffmeister and Sterling, 1994). Instead, molecular-based studies repeatedly reveal cryptic evolutionary lineages embedded within long-recognized species of North American mammals (e.g., Riddle and Hafner, 1999). These cryptic lineages generally exhibit significant phylogeographic structure, which has profound consequences for biogeography, ecology, and conservation biology.

North American peromyscine rodents have been the subject of numerous systematic and biogeographic investigations and collectively have been called the "*Drosophila* of North American mammalogy" (Musser and Carleton, 1993, p. 728). Although several comprehensive classification schemes have been offered (Osgood, 1909; Hooper, 1968; Carleton, 1989), phylogenetic questions remain unresolved at both supraspecific and infraspecific levels. A fundamental issue yet to be evaluated robustly with molecular approaches concerns the phylogenetic diagnosis of a long-postulated basal dichotomy within the highly speciose genus *Peromyscus* into two discrete subgenera: *Haplomylomys* and *Peromyscus* (reviewed by Carleton, 1989). Of the 53 species of *Peromyscus* recognized in the most recent classifica-

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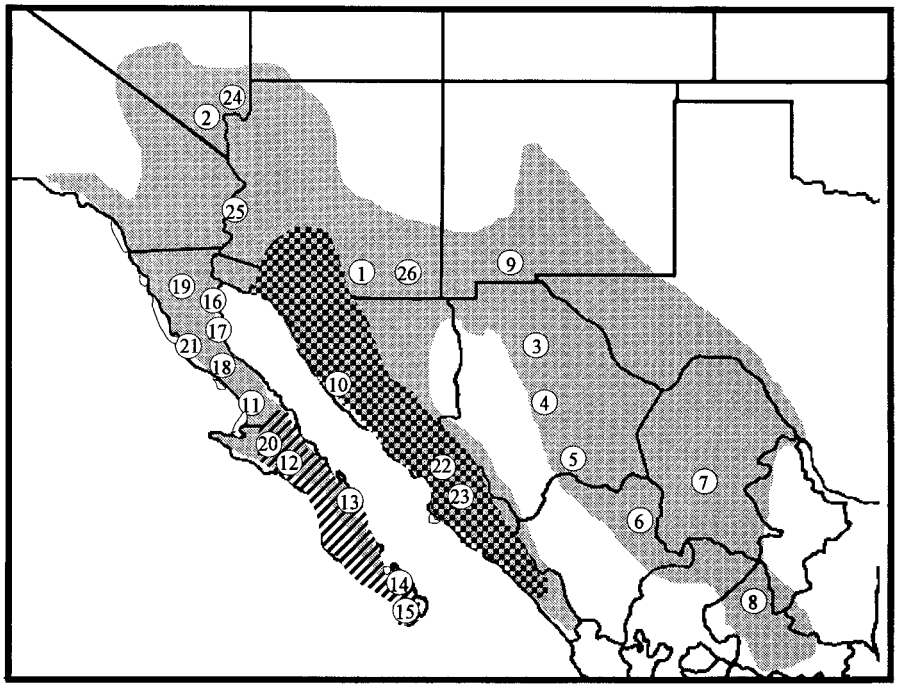

FIG. 1. Distribution of taxa in the *Peromyscus eremicus* species group (redrawn from Hall, 1981) and collecting localities (numbered as in the Appendix).

tion (Musser and Carleton, 1993), 40 species are generally included in the subgenus *Peromyscus.* Species inclusion in *Haplomylomys,* the less speciose subgenus, has been and continues to be contentious (Carleton, 1989). All taxa historically proposed as members of this clade are distributed in arid and semiarid regions of southwestern North America. *Haplomylomys* has traditionally included at least two species groups: *californicus* (a species restricted to the California chaparral) and *eremicus* (including *merriami* of the Sonoran Desert, *eva* of the Baja California Peninsular Desert, and the widespread desert species, *eremicus*). Osgood (1909) included one other desert species (*crinitus*) within *Haplomylomys,* which was later transferred to *Peromyscus* by Hooper and Musser (1964). Up to 9 species restricted to arid islands in the Sea of Cortéz have been included in the *eremicus* species group: *caniceps, collatus* (currently considered a subspecies of *eremicus*), *dickeyi, guardia, interparietalis, pembertoni, pseudocrinitus,* and possibly *stephani* and *slevini.* The failure of recent studies (e.g., Carleton, 1980; Engel *et al.,* 1998) to reach consensus on basal relationships among peromyscine genera and subgenera suggests that diagnosis and resolution of phylogenetic relationships between *Haplomylomys* and other peromyscine taxa will remain problematic.

A more immediately tractable problem concerns the radiation of a putatively monophyletic group of species within *Haplomylomys:* the *Peromyscus eremicus* species group (Carleton, 1989). Close evolutionary affinities among core mainland species in the *eremicus* species group (Fig. 1) has been generally supported, but repeated fluctuation in the proposed ranks of various taxa (reviewed in Carleton, 1989) indicates only cursory understanding of supraspecific and infraspecific evolutionary patterns within this species group (Fig. 2). Whereas morphology and allozyme electrophoresis both indicate evolutionary divergence and reproductive isolation between sympatric *merriami* and *eremicus* (Avise *et al.,* 1974), the allozyme evidence also suggests that *eremicus* is a paraphyletic species relative to *merriami.* More recently a mitochondrial DNA (mtDNA) restriction site analysis (Walpole *et al.,* 1997) revealed significant phylogeographic separation of populations of *eremicus* between the northeastern Sonoran and northern Chihuahuan deserts, suggesting the presence of two cryptic, geographically-separated species embedded within *eremicus.* Unfortunately, neither Avise *et al.* (1974) nor Walpole *et al.* (1997) sought to provide a complete phylogenetic hypothesis or depiction of biogeographic pattern across the *eremicus* species group because each was concerned with a restricted set of questions. Avise *et al.* (1974) emphasized diagnosis of species and populations on islands in the Sea of Cortéz and thus sampled no mainland populations of *eva* and had only one sample of *eremicus* from the Chihuahuan Desert and one from the Baja California Peninsular mainland, whereas Walpole *et al.* (1997) focused strictly on interpopulation variation

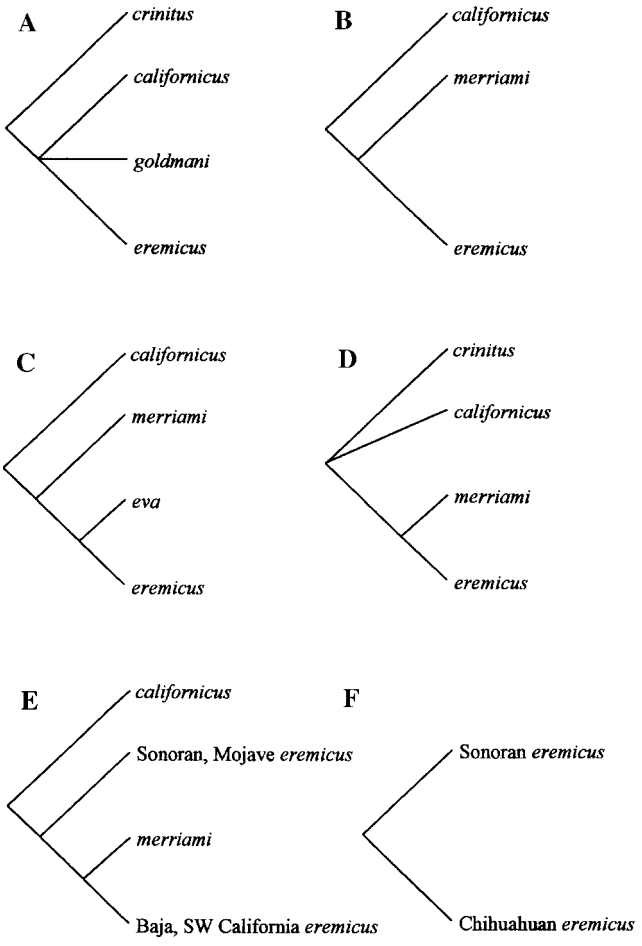

FIG. 2. Representative hypotheses of group membership and relationships within *Peromyscus* (subgenus *Haplomylomys*). (A) recognition of subgenus (Osgood, 1909); (B) recognition of *P. merriami* distinct from *P. eremicus* (Hooper, 1968); (C) recognition of *P. eva* (Lawlor, 1971); (D) *Haplomylomys* before reallocation of *P. crinitus* to subgenus *Peromyscus* (Hooper and Musser, 1964); (E) paraphyletic *P. eremicus* (Avise *et al.*, 1974); (F) distinct phylogeographic lineages within *P. eremicus* (Walpole *et al.*, 1997).

within *eremicus* from a restricted portion of the northeastern Sonoran and northern Chihuahuan deserts.

Contrary to the traditional view that the North American regional deserts have diverged only recently, during the latest Pleistocene (e.g., Wells, 1977), several investigators have suggested that there are deeper (Neogene) historical divisions among these regional deserts (Grismer, 1994; Hafner and Riddle, 1997; Morafka, 1977; Riddle, 1995). The existence of deeper-history divisions among the biotas of regional deserts would indicate some common responses across taxa to vicariant geological events. The degree to which divergent sister taxa in different regional deserts collectively reveal a general history of vicariance rather than idiosyncratic dispersal events is a question that ultimately requires analysis of codivergence across multiple, codistributed taxa. However, analysis of phylogeographic structure within a single monophyletic group of populations and species can be used to postulate areas of endemism and historical relationships among areas and, in combination with information from paleoclimatology, paleontology, and geology, may be used to develop a testable model of vicariance among specified areas of endemism. In this study, we use mtDNA sequence data to (i) reveal the number and geographic distribution of evolutionary lineages (i.e., mtDNA gene lineages) embedded within mainland populations and species of the *eremicus* species group (island forms will be addressed elsewhere), (ii) test hypotheses of phylogenetic relationship among lineages, (iii) assess alternative models of biogeographic history for the *eremicus* species group in southwestern North America, and (iv) discuss general implications for the historical biogeography of North American regional deserts, including presentation of testable hypotheses.

METHODS

Sampling Design

We included geographically representative samples from throughout the ranges of *eremicus*, *eva*, and *merriami* for a total of 73 individuals from 26 localities (Appendix; Fig. 1). Identification of individuals was verified using diagnostic morphological characters (Hoffmeister, 1986; Lawlor, 1971). Exemplar individuals representing *P. californicus* and *P. crinitus*, variously postulated to be members of the subgenus *Haplomylomys* (Fig. 2), were included to test the validity of a monophyletic *eremicus* species group. Individuals representing three species of the subgenus *Peromyscus* (*P. boylii*, *P. leucopus*, *P. maniculatus*) were included as outgroups in phylogenetic analyses.

Each individual was prepared as a standard museum skin and skeleton specimen and is housed in the permanent collections of the New Mexico Museum of Natural History (NMMNH). Soft tissues were extracted and placed in liquid nitrogen for transport to the University of Nevada, Las Vegas (UNLV); frozen tissue samples are maintained in the collections at NMMNH. Total genomic DNA was extracted from heart, liver, or kidney tissue using a lysis buffer protocol (Longmire *et al.*, 1991). A 715-bp fragment of mtDNA, including 709 bp of the COIII gene, was amplified via polymerase chain reaction (PCR) with a 1-μL aliquot of DNA and 0.25 μL of *Taq* DNA polymerase under the following reaction conditions: 95°C 1 min; 55°C 1 min; 72°C 1 min; 30 cycles. PCR fragments were extracted from a 1.0% agarose gel and purified using GeneClean (BIO 101) following manufacturers' protocols. PCR and sequencing primers were published elsewhere (Riddle, 1995). Primers H8618 and L9323 were used to sequence both strands of every individual. PCR templates were sequenced at UNLV using an ABI

310 automated sequencer and Big Dye Terminator Ready Reaction mix from PE Applied Biosystems. Sequences (699 bp) were aligned and checked for nucleotide and reading frame accuracy using The Eyeball Sequence Editor v.3.1 (Cabot and Beckenbach, 1989). GenBank accession numbers for new sequences range from AY009173 to AY009237.

Analyses

Phylogeny. We used an array of distance, maximum-likelihood (ML), and maximum-parsimony (MP) analyses to understand patterns of sequence divergence and relationship among mtDNA haplotypes. All analyses were conducted using either PAUP* v.4.0b2 (Swofford, 1999) or MEGA v.1.01 (Kumar *et al.*, 1993). We first created a neighbor-joining (NJ) tree (Saitou and Nei, 1987) among all haplotypes uncovered in this study using a Tamura–Nei (Tamura and Nei, 1993) model of sequence evolution, which assumes rate heterogeneity among each class of purine and pyrimidine substitutions and unequal base frequencies. This tree was used to establish a basic pattern of haplotype relationships and to map the geographic distributions of haplotype lineages. The complete data set was too large to rigorously evaluate phylogenetic structure among the main clades and was therefore reduced to a set of 16 exemplar haplotypes (chosen to represent the major haplotype lineages present in the initial tree) for further phylogenetic analyses.

Under a ML approach, the best model of sequence evolution for a given data set is considered to be that model with the fewest parameters that is not significantly worse than the most parameter-rich model being evaluated (Sullivan *et al.*, 1997; Swofford *et al.*, 1996). We used Modeltest 3.0 (Posada and Crandall, 1998), which utilizes a hierarchical likelihood ratio test to choose an appropriate model of sequence evolution. The resulting chosen model was subsequently used to perform a heuristic search using the maximum-likelihood criterion. The best ML tree found was employed in additional analyses described below.

Saturation plots (Fig. 3) reveal a high degree of saturation of third position transitions among more distantly related taxa. However, a large amount of phylogenetic signal supporting relationships among closely related taxa could be lost if all transversions were eliminated or down-weighted appreciably. Therefore, maximum-parsimony trees were generated using the branch-and-bound algorithm under four separate character-weighting strategies, chosen to reflect a broad range of relative weightings of transversion vs transition substitutions: all unordered characters equally, transitions down-weighted relative to transversions 2- or 10-fold, third codon position transitions removed. Bootstrap values, consistency indices, and retention indices were used to summarize and contrast performance among the sets of best trees. The Templeton (1983) nonparametric test statistic (MP criterion) and the Kishino–Hasegawa (1989) test statistic (ML criterion) were used to evaluate the significance of differences between each of the MP trees generated under each character-weighting strategy, as well as relative to the ML tree. We then evaluated four additional trees against the ML tree that represented alternative biogeographic and taxonomic hypotheses not captured by the MP or ML analyses. The range of trees produced by the MP and ML analyses and these additional trees exhausted all reasonable biogeographic and phylogenetic hypotheses available.

Biogeography and divergence times. Two complementary approaches were used to evaluate biogeographic hypotheses. First, a variety of phylogenetic trees (described above) were tested against the ML tree to provide an objective criterion for rejecting alternative biogeographic hypotheses. Second, we evaluated the potential association of nodes in unrejected trees with postulated biogeographic events after estimating times of divergence among the major haplotype lineages. Divergence times were estimated by calibrating rates of divergence based on the assumption of a near-simultaneous origination of extant peromyscine genera and subgenera 6.5 Ma. All previous analyses of phylogenetic relationships have failed to resolve a polychotomous bush among genera and subgenera of peromyscine rodents, indicating an explosive radiation (reviewed by Engel *et al.*, 1998). This was exemplified by an extensive phylogenetic analysis of 1340 bp of mtDNA sequence data (Engel *et al.*, 1998) that failed to provide a robust resolution between nine genera or subgenera of peromyscines. One of these genera, *Onychomys*, is morphologically diagnostic in the fossil record and first appears during the Hemphillian North American Land Mammal Age, around 6.5 Ma (Jacobs and Lindsay, 1984). If the basal peromyscine polychotomy indicates a near-simultaneous origination of extant genera and subgenera, then the split between *Peromyscus* and *Haplomylomys* was approximately coincident with the origination of *Onychomys* and we can use 6.5 Ma as a minimum estimate of divergence time between genera and thus a calibration point for subsequent calculation of times of divergence of various clades in this study. Before estimating times of divergence using this calibration, we first evaluated whether significant rate heterogeneity existed among lineages on the ML tree by using a likelihood ratio test to compare trees generated with and without a clock constraint (Huelsenbeck and Rannala, 1997). A measure of nucleotide diversity (π; Nei, 1987, Eq. 10.5; calculated with REAP, v.1.0, McElroy *et al.*, 1991) was used to summarize and compare nucleotide heterozygosity values within species and major haplotype lineages.

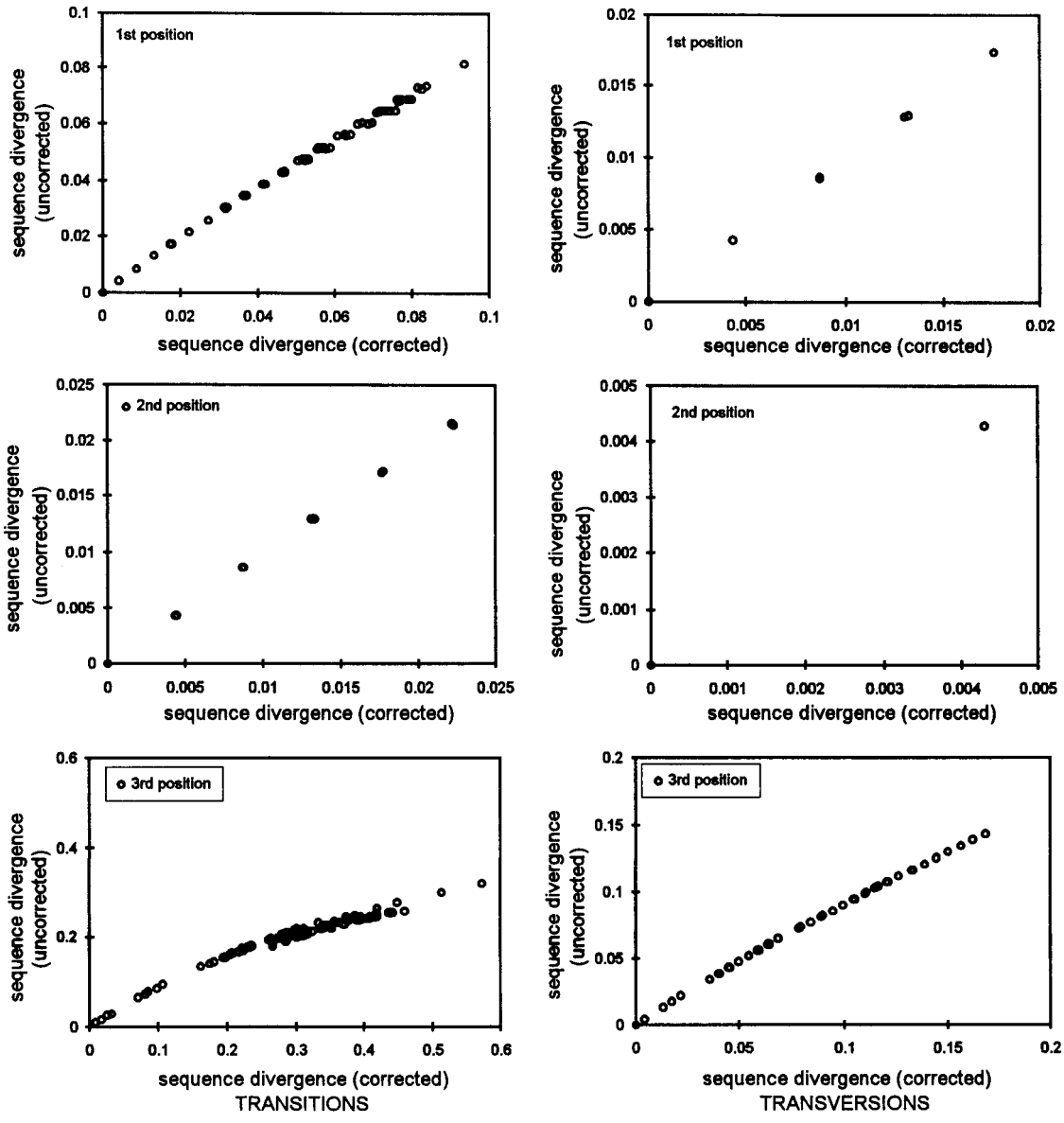

FIG. 3. Saturation plots of corrected (Tamura–Nei, 1993) vs. uncorrected estimates of sequence divergence for transition and transversion substitutions at 1st, 2nd, and 3rd codon positions.

RESULTS

Nucleotide Sequence Structure and Haplotype Diversity

Sequence data from 699 bp of COIII revealed a total of 65 distinct haplotypes among 75 ingroup (including the *eremicus* species group, *crinitus,* and *californicus*) and three outgroup individuals (Appendix). Numbers of haplotypes, sample size (individuals, localities), and nucleotide diversity (π) within each nominate species of the *eremicus* species group are *eremicus,* 47 haplotypes, n = (57, 21), π = 0.04; *eva,* 7 haplotypes, n = (7, 3), π = 0.009; *merriami,* 6 haplotypes, n = (9, 2), π = 0.029. Twenty-three of 26 localities were represented by more than 1 individual (n = 2 to 6); 21 of these localities included at least 2 and as many as 5 different haplotypes.

The overall frequency distribution of nucleotides at 1st, 2nd, and 3rd codon positions (in percentages: A = 24.5, 22.0, 49.0; C = 25.1, 25.2, 24.1; G = 24.1, 15.9, 1.3; T = 26.4, 36.9, 25.6) was similar to the cytochrome *b* mtDNA protein-coding gene in mammals (Irwin *et al.,* 1991). Compositional bias at each codon position (1st = 0.019, 2nd = 0.161, 3rd = 0.328; calculated as in Irwin *et al.,* 1991) was slightly less than that for mammalian cytochrome *b,* but was similar in pattern of variation among codon positions. Overall base frequency composition was unequal at close to the 5%

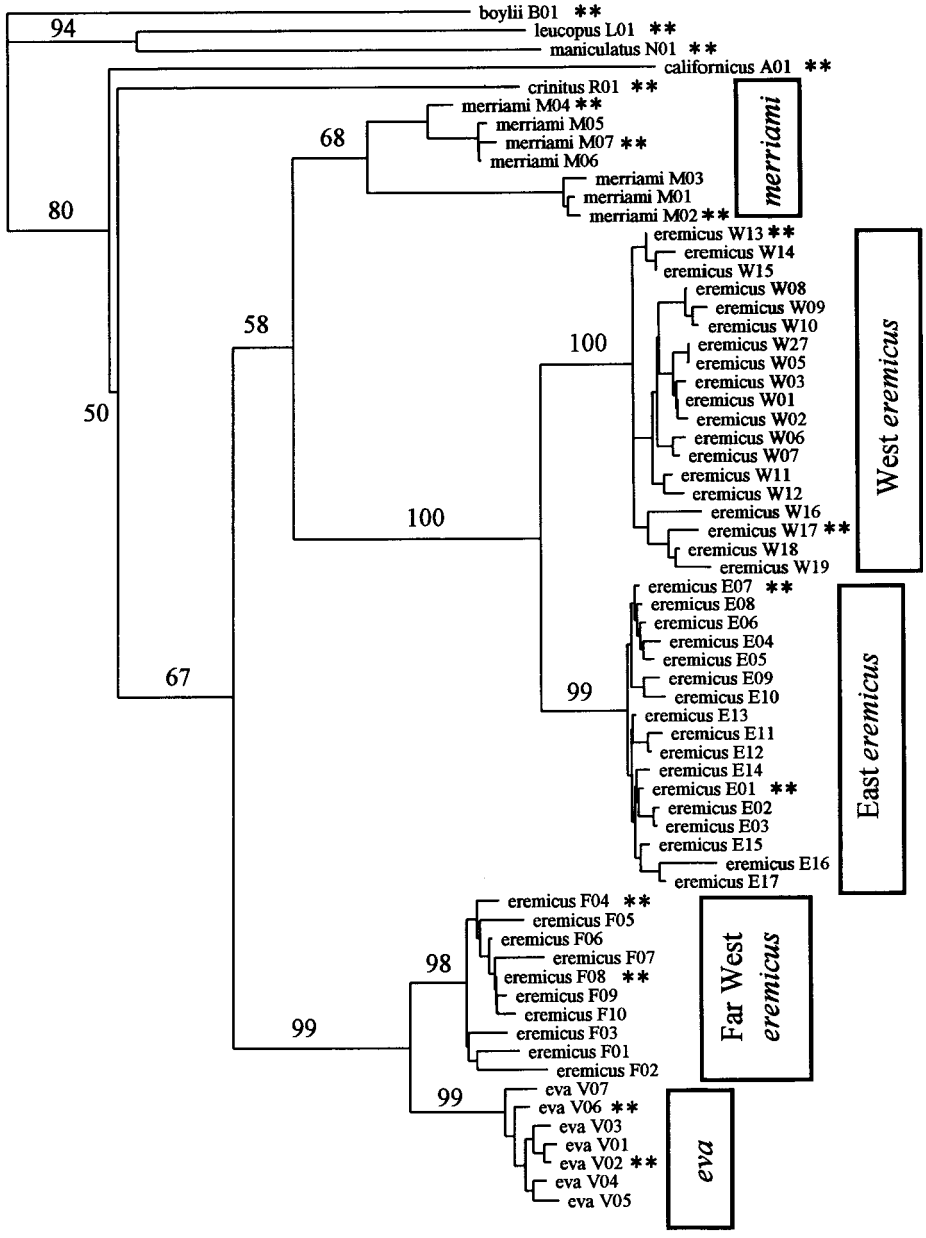

FIG. 4. Neighbor-joining tree using corrected (Tamura–Nei, 1993) estimates of sequence divergence among all variable haplotypes (specimen and locality distributions summarized in Appendix); numbers along branches represent 1000 bootstrap replications. Double asterisks represent those haplotypes used in subsequent analyses.

level ($\chi^2 = 7.74$; $P < 0.1$). The pairwise distribution of nucleotide sequence variation among haplotypes from *californicus*, *crinitus*, and the *eremicus* species group varies from 1 bp difference up to 108 bp differences. A total of 152 sites (107 ingroup) were parsimony informative. Although most variation (78%) occurs among third position characters, transition substitutions are likely to be phylogenetically very noisy among more distantly related taxa based on saturation plots (Fig. 3). All other substitution categories appear to be relatively nonsaturated.

Phylogenetic Analyses

All haplotypes. The NJ tree constructed among all 65 haplotypes (Fig. 4) revealed strong bootstrap support for the presence of three distinct haplotype lineages within *eremicus* and one lineage representing *eva;* a lineage composed of the two localities of *merriami* received lower bootstrap support. Mapping (Fig. 5) reveals no known geographic overlap between three lineages of *eremicus,* with a distinct clade occupying the Chihuahuan Desert, another in the Mojave, Sono-

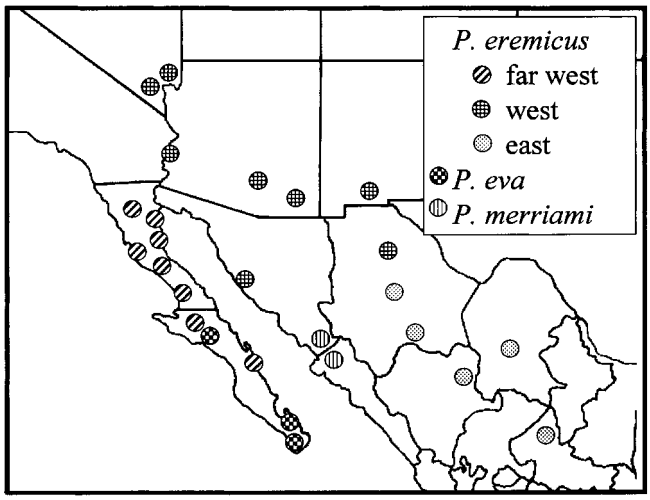

FIG. 5. Distribution across localities (Fig. 1; Appendix) of haplotype lineages (Fig. 4) in the *Peromyscus eremicus* species group.

ran, and northwestern Chihuahuan deserts, and another on the Baja California Peninsula. The latter clade and *eva* overlap geographically in Baja California Sur. Only four geographic regions are left unsampled (Fig. 1): *eremicus* in southwestern California, the Trans-Pecos region of the Chihuahuan Desert, and southernmost Sonora or Sinaloa, and *merriami* from northern Sonora or southern Arizona.

Two of the *eremicus* lineages (hereafter referred to as "West" and "East") were joined as a clade with strong bootstrap support at about 3.5% sequence divergence (s.d.), distinct from a separate, strongly supported clade that grouped the Baja California lineage of *eremicus* (hereafter, "Far West") with *eva*, also at 3.5% s.d. Numbers of haplotypes, sample size (individuals, localities), and nucleotide diversity within each clade within *eremicus* are East, 17 haplotypes, $n = (19, 5)$, $\pi = 0.008$; West, 19 haplotypes, $n = (21, 8)$, $\pi = 0.011$; Far West, 10 haplotypes, $n = (17, 8)$, $\pi = 0.009$. A clade including the West and East groups of *eremicus* plus *merriami* joined at 9% s.d., but was weakly supported by bootstrap values. Further down the tree, weak support was indicated for a monophyletic *eremicus* species group coalescing at 9.5% s.d. Finally, the positions of *crinitus* and *californicus* were left uncertain, but there is moderate support from bootstrap values for inclusion of both species with the *eremicus* species group in the subgenus *Haplomylomys*, apart from the three species representing the subgenus *Peromyscus*. Based on this analysis, we chose 16 haplotypes (Fig. 4), representative of all taxa and each of the major haplotype lineages, to further explore phylogenetic relationships within the *eremicus* species group.

ML analyses. Using the 16 haplotypes represented in the reduced data set, Modeltest 3.0 chose the Tamura–Nei model (Tamura and Nei, 1993), with gamma-distributed rate heterogeneity, as the best model of sequence evolution for these data. Therefore, the ML tree (Fig. 6) was produced through a heuristic search (random addition, one replication, tbr branch swapping) using this model (2314 rearrangements evaluated, -lnL score = 2917.46826, estimated value of the alpha shape parameter for the gamma distribution = 0.182084). Conspicuous features of this tree include a polyphyletic *eremicus*, with the Far West clade joining *eva* and the West + East clade joining *merriami*, and a monophyletic *eremicus* species group, joined next by *californicus* and finally *crinitus*. Using the likelihood ratio test statistic, this tree was not significantly different from a tree produced using the same model plus enforcing a molecular clock (-lnL = 2928.37910; LRT = 21.82; $\chi^2 = 23.69$, $P < 0.05$). Total divergence from the root of a tree produced under a molecular clock to any of the tips is estimated at 1.9476×10^{-1} substitutions/base, and using the calibration of 6.5 Ma for this point, average rate of divergence is 2.996×10^{-2} substitutions/base/million years.

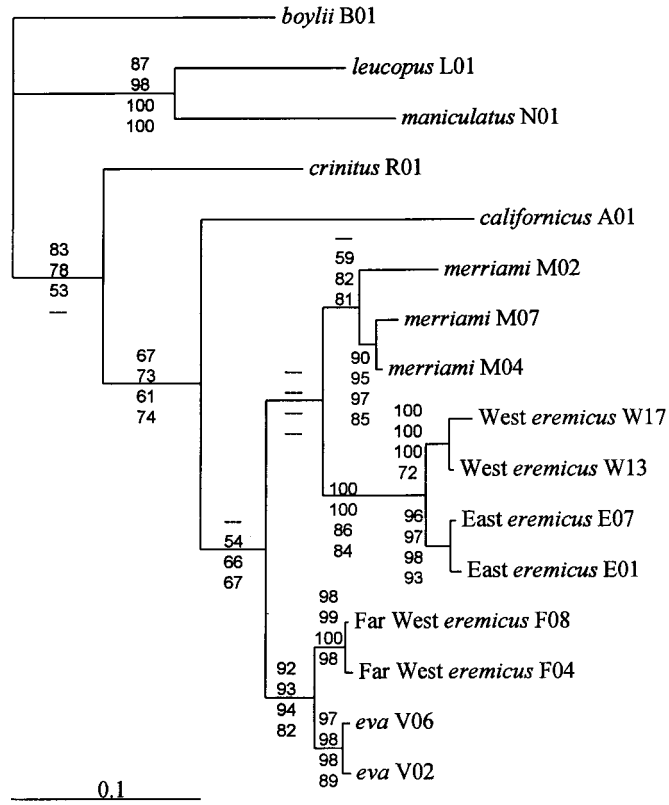

FIG. 6. Maximum-likelihood tree among 16 representative haplotypes (Tamura–Nei + gamma model). Numbers represent bootstrap support (branch and bound, 1000 replications) for each node on the ML tree under each of four MP character weightings (from top to bottom; equal, transitions down-weighted 2 or 10 times, and no 3rd position transitions).

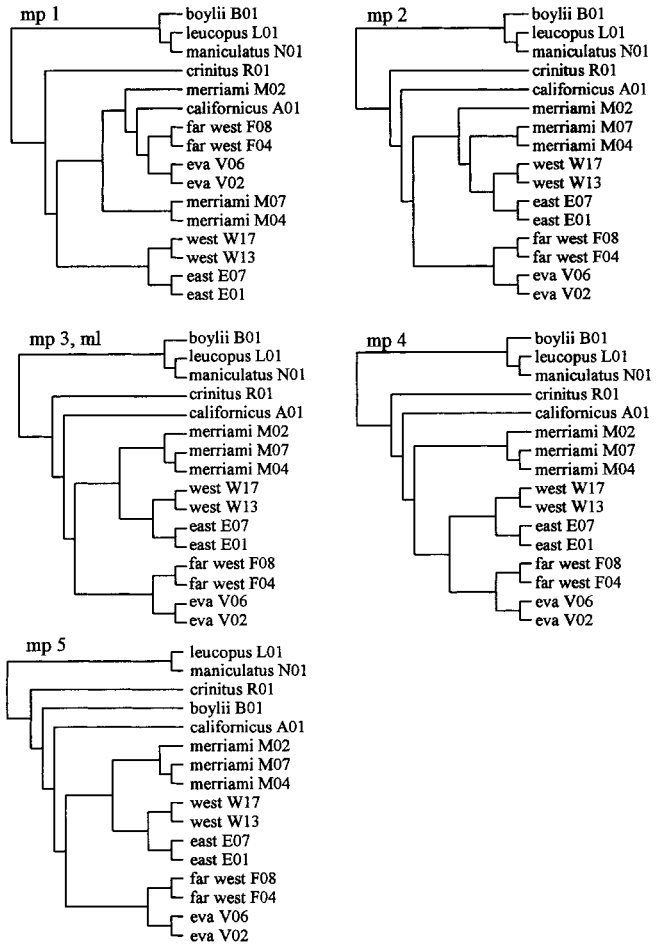

FIG. 7. Five maximum-parsimony trees found using four different character-weighting strategies (discussed in text): equal, trees mp1, mp2; transitions down-weighted 2-fold (mp3) or 10-fold (mp4); no 3rd position transitions, tree mp5.

MP analyses. With all characters weighted equally, two MP trees (mp1, mp2; Fig. 7) were recovered using the branch and bound search option in PAUP* (length = 462; CI = 0.49; RI = 0.64). Down-weighting transitions 2-fold produced the ML tree (mp3; Fig. 7; CI = 0.52; RI = 0.64), and 10-fold produced tree mp4 (Fig. 7; CI = 0.57; RI = 0.67). One final tree (mp5; Fig. 7) was recovered following removal of 3rd position transitions (length = 175; CI = 0.52; RI = 0.68). No trees in this analysis indicated a monophyletic *eremicus* relative to *eva*. A Far West *eremicus* + *eva* and a separate West + East *eremicus* clade, each supported by high bootstrap numbers (Fig. 6), occurred in all MP trees. Slightly weaker support was found for a West + East *eremicus* clade joined next by *merriami*, an *eremicus* species group, or a monophyletic *merriami*. When evaluated under each character weighting, the Templeton test revealed no significant differences between the best MP tree and any of the others. This result was also true when a Kishino–Hasegawa test

TABLE 1

***P* Values (Kishino and Hasegawa, 1989) and Likelihood Scores for the Set of Maximum-Parsimony (Fig. 7) and Additional (Fig. 8) Trees Relative to the Best ML Tree**

Tree	-1nL	*P* Value
ml, mp 3	2917.46826	Best
mp 1	2924.04363	0.44
mp 2	2922.64047	0.21
mp 4	2919.70797	0.61
mp 5	2919.70508	0.60
tree 6	2935.35991	0.04*
tree 7	2923.19995	0.26
tree 8	2935.19744	0.06
tree 9	2934.52593	0.01*

Note. Asterisks denote significantly worse trees ($P < 0.05$).

was employed to evaluate likelihood scores for the three MP trees that differed from the best ML tree (Table 1).

Evaluation of other trees against the ML tree. The set of MP trees did not include several additional alternative trees worth considering for phylogenetic and biogeographic reasons (Fig. 8). Tree 6 is similar to mp4, but makes *eremicus* monophyletic and considers *eva* its sister group. Tree 7 places *crinitus* rather than *californicus* as sister group to a monophyletic *eremicus* species group. Tree 8 splits the Far West *eremicus* + *eva* and considers as monophyletic the Far West *eremi-*

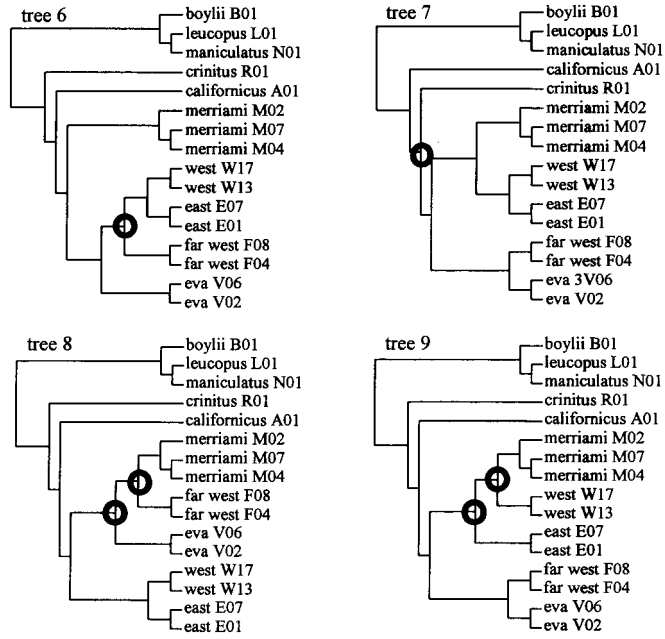

FIG. 8. Four biogeographically and phylogenetically viable user-specified trees, evaluated relative to the maximum-likelihood tree (Fig. 6; see text and Tables 1 and 2). Circled nodes are discussed in the text.

TABLE 2

***P* Values (Templeton, 1983) for the Set of Trees Shown in Fig. 8, as Evaluated under Each of the Seven Different Character-Weighting Strategies Employed against the ML Tree**

	Character weighting			
Tree	Equal	tv2	tv10	no3ts
ml	Best	Best	Best	Best
tree 6	0.06	0.04*	0.03*	0.25
tree 7	0.68	0.49	0.41	0.64
tree 8	0.02*	0.04*	0.04*	0.41
tree 9	0.0002*	0.0002*	0.0002*	0.32

Note. Asterisks denote trees that are significantly worse than the best tree ($P < 0.05$).

cus + *merriami*. Tree 9 splits the West + East *eremicus* clade and considers as monophyletic West *eremicus* + *merriami*. Using the Kishino–Hasegawa test of likelihood scores (Table 1), trees 6 and 9 were rejected as being significantly worse than the ML tree, tree 8 was nearly significantly worse, but tree 7 was not rejected. Using the Templeton test statistic (Table 2), trees 6, 8, and 9 were uniformly rejected relative to the best ML tree under all weighting strategies except removal of 3rd position transitions, whereas tree 7 could not be rejected under any weighting.

DISCUSSION

Phylogeny of the Peromyscus eremicus Species Group

The P. eremicus species group is tentatively supported. With the exception of one tree (mp1) that placed *californicus* as sister group to the Far West + *eva* clade (and produced a paraphyletic *merriami*), all other trees generated in this study indicate that *eremicus* (all three lineages), *eva*, and *merriami* form a monophyletic group relative to the other putative members of *Haplomylomys*, *californicus*, and *crinitus*. The tree mp1 was generated through equal weighting of all characters and thus is likely to be phylogenetically very noisy at deeper nodes, given the high number of saturated characters (third codon position transitions) in this data set. Even so, a monophyletic *eremicus* species group did not receive particularly strong bootstrap support, nor was tree mp1 rejected as significantly worse than the best MP trees or ML tree in respective analyses. Several other hypotheses, which placed *californicus* variously as sister group to clades within the *eremicus* species group (not shown), also generally failed to reject those trees over the best ML tree. We therefore conclude that, whereas a monophyletic *eremicus* species group is generally supported, more data will be required at basal nodes in *Haplomylomys* to be able to robustly support or reject this hypothesis.

P. eremicus is a paraphyletic or polyphyletic species. These analyses provide consistently strong rejection of one of the fundamental taxonomic statements within the subgenus *Haplomylomys:* that widespread populations extending from the Baja California Peninsular Desert in the west to the southernmost reaches of the Chihuahuan Desert in the east form a single monophyletic species, *P. eremicus*. This statement has been challenged only once before, in an allozyme electrophoresis study (Avise *et al.*, 1974) that aligned populations within the range of the Far West *eremicus* lineage with *merriami*. That study did not sample mainland populations of *eva* and did not identify populations clearly within the range of our East *eremicus* clade. We believe that the three main mtDNA haplotype lineages of *eremicus* identified in this study likely represent the major patterns of divergence and geographic structure across extant populations within the nominal species *eremicus*. Regardless of previous sampling limitations, mtDNA and allozyme data are congruent in recognizing the paraphyletic or polyphyletic nature of *eremicus*. Our initial NJ tree among all haplotypes (Fig. 4) and the best ML tree among 16 exemplar haplotypes differ from the allozyme study in placing *merriami* as sister clade to the West + East *eremicus* clade. However, we find little support for this topology over alternative trees that would place *merriami* elsewhere within the *eremicus* species group.

Legg (1978) described multivariate morphological separation between a group composed of Peninsular and southwestern California populations relative to all other populations of *eremicus*. If we provisionally consider the Far West *eremicus* clade to geographically include southwestern California (not yet sampled), then our results are congruent with morphological (Legg, 1978) and allozyme (Avise *et al.*, 1974) indications of historical divergence between Far West and all other populations of *eremicus*. As such, available evidence strongly supports recognition of the Far West lineage as a species (*P. fraterculus*) separate from the remainder of *eremicus* under phylogenetic (Cracraft, 1989) and concordance (Avise and Ball, 1990) species concepts.

Peromyscus fraterculus (Miller, 1892)

Vesperimus fraterculus Miller, 1892, *Am. Nat.* **26:** 261. Type locality "Dalzura, San Diego Co., California."

P[*eromyscus*]. *eremicus fraterculus*, J. A. Miller, 1898, *Bull. Amer. Mus. Nat. Hist.* **10:** 154.

Sitomys herronii Rhodes, 1893, *Am. Nat.* **27:** 832. Type locality "Reche Canyon, San Bernardino Co., California."

Sitomys herroni nigellus Rhodes, 1894, *Proc. Acad. Nat. Sci. Philadelphia* **46:** 257. Type locality "West Cajon Pass, San Bernardino Co., California."

Peromyscus eremicus propinquus J. A. Allen, 1898, *Bull. Amer. Mus. Nat. Hist.* **10:** 154. Type locality "San Pablo Point, Baja California."

Peromyscus homochroia Elliot, 1903, *Field Columb. Mus. Publ. 74 Zool. Ser.* **3**(10): 158. Type locality "San Quintín, Baja California."

Distribution. Southwestern California, Baja California, and Baja California Sur; continuously distributed from Nordhoff, Ventura Co., California into Baja California (exclusive of the northeastern corner of Baja California), then south from San Felipe to the Viscaino Desert of Baja California Sur, along the west coast to the Santa Clara Mountains, and along the east coast to Punta Pulpito (Lawlor, 1971). A disjunct population from Las Cruces, Baja California Sur, was identified as *P. eremicus* by Lawlor (1971), and presumably represents *P. fraterculus.* Species designation of populations of the *eremicus* species group that occur on islands surrounding the Baja California Peninsula awaits mtDNA sequence analysis of those populations.

Remarks. This species includes specimens from San Felipe and south on the Baja California Peninsula previously assigned to *P. eremicus eremicus.* Morphometric comparisons between *P. fraterculus* and adjacent *P. eremicus* are provided by Legg (1978). Osgood (1909) included *P. eremicus propinquus* under *P. eremicus eva* (elevated to *P. eva* by Lawlor, 1971) and included *P. homochroia* and *Sitomys herronii* under *P. eremicus fraterculus.* Hall (1981) included *P. propinquus* under *P. eremicus fraterculus* based on Lawlor (1971).

P. eva is distinct from, but a sister-taxon to P. fraterculus. *P. eva* was recognized as a species distinct from adjacent and sympatric *eremicus* (= *fraterculus*) using morphological criteria (Lawlor, 1971), and its evolutionary relationship to *eremicus* has not previously been assessed using molecular evidence. This study clearly reveals that two geographically separate and reciprocally monophyletic mtDNA lineages of the *eremicus* species group occur on the Baja California Peninsula (*eva* and *fraterculus*). Further, these two species are sister taxa, with substantial genetic divergence between this sister group, the other two lineages of *eremicus,* and *merriami. Peromyscus eva* occurs from the Cape Region in the southernmost portion of the Peninsula northward nearly to the mid-Peninsular Vizcaino Desert. *P. fraterculus* has a generally northern Peninsular distribution, but extends south along the eastern coast at least to 26°N latitude. These distributions closely resemble original descriptions provided by Lawlor (1971) and thus indicate a congruence between mtDNA and morphological criteria in the diagnosis of two separate species of cactus mice on the Peninsula. Lawlor (1971) reported five localities of sympatry between *eva* and *eremicus* (= *fraterculus*): Calmallí, Baja California; San Ignacio, 20 km W San Ignacio, Aguaje de Santana (= Santa Ana); and Las Cruces, Baja California Sur.

Mainland P. eremicus includes two phylogeographic units. Recently, Walpole *et al.* (1997) postulated that Chihuahuan and Sonoran populations of *eremicus* were subdivided into eastern and western mtDNA lineages based on restriction fragment length polymorphism analysis of a geographically limited set of samples (three northeastern populations from the transition zone between the Sonoran and the Chihuahuan deserts, and six populations from Trans-Pecos and Rio Grande Valley portions of the Chihuahuan Desert). Through extensive sampling of populations from the Chihuahuan, Sonoran, and Mojave deserts (Fig. 1), we conclude that reciprocally monophyletic eastern and western mtDNA lineages do indeed exist as predicted by Walpole *et al.* (1997). Additionally, by sampling throughout the combined ranges of species in the *eremicus* species group, we conclude that the eastern and western mtDNA lineages originally identified by Walpole *et al.* (1997) are sister lineages and relatively closely related to one another within the overall context of genetic diversity in the *eremicus* species group (Figs. 4 and 6). Interestingly, the West *eremicus* lineage extends well into the northwestern Chihuahuan Desert, and we postulate that a contact zone between West and East *eremicus* occurs north of Ciudad Chihuahua to the south (probably along the Rio Conchos) and coincides with the Rio Grande to the east.

Nearby populations of P. merriami are genetically divergent. It is of interest that the two geographically close populations of *merriami* represented in this study are more divergent from one another than are Far West *eremicus* from *eva,* or East from West *eremicus* (Figs. 4 and 6). Additional geographic and character sampling is necessary to better characterize the nature of variation within *merriami.*

Historical Biogeography of the Peromyscus eremicus Species Group

Estimated times of lineage divergence. The use of molecular data to generate estimates of divergence times is often fraught with uncontrollable and large sources of error (Hillis *et al.,* 1996), including calculations of sequence divergence, lineage-specific rate heterogeneity, lack of diagnostic fossils, and underestimation of actual divergence times based on fossils that postdate lineage divergence. Thus, we offer the following estimates of divergence times as only rough approximations, but suggest that they are appropriate for differentiating between alternative biogeographic hypotheses. Specifically, it is reasonable to divide classes of biogeographic models that bear on the evolution of North American desert biotas into three separate time

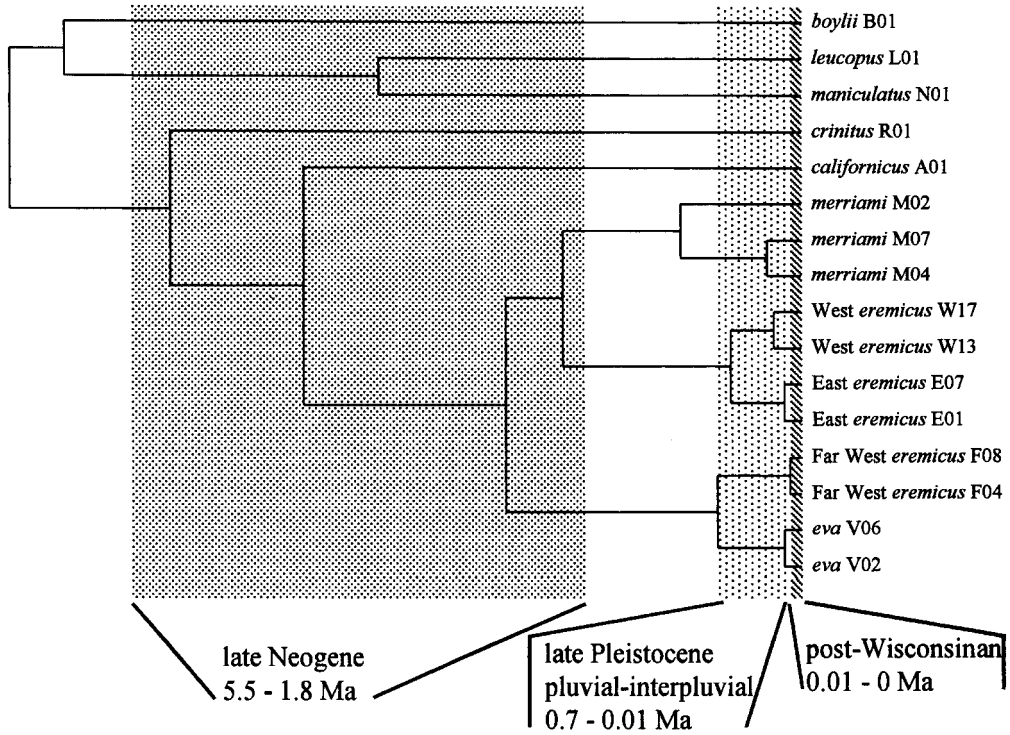

FIG. 9. ML tree under a molecular clock constraint. The time frame is calibrated using an estimate of 6.5 Ma for divergence between the subgenera *Peromyscus* and *Haplomylomys* (rationale discussed in text).

frames. First, we recognize a late Neogene (5.5–1.8 Ma) period of geomorphological evolution of the western North American landscape, during which time (1) the Baja California Peninsula was torn away from the Mexican mainland through rifting and development of the Gulf of California (reviewed by Grismer, 1994); (2) the Sierra Nevada mountains were developing an increasingly strong rain shadow to the east (Ruddiman *et al.*, 1989); (3) the Sierra Madre Occidental mountains were forming between the uplifting Mexican Plateau and the thorn-scrub lowlands of northwestern Mexico, developing yet another rain shadow (Coney, 1983); and (4) marine waters from the Gulf of California underwent episodes of northward extension, forming marine embayments in low elevations in California northwesterly to the San Gorgonio Pass, and northward along the Colorado River at least to Lake Mojave (reviewed by Grismer, 1994). Second, we recognize a period of Pleistocene pluvial–interpluvial cycles (700–11 Ka) during which 100,000-year climatic oscillations occurred in concert with cycles of polar ice accumulation and recession (Webb and Bartlein, 1992), resulting in changes in the distributions of habitats and species in western North America (e.g., FAUNMAP Working Group, 1996). Third, we recognize a post-Wisconsinan (11 Ka–present) period of possible range shifting following recession of the latest (Wisconsinan) pluvial period.

An estimated time frame for divergence of the *eremicus* species group (Fig. 9) indicates that separations of *fraterculus* + *eva*, East + West *eremicus*, and *merriami* are likely to have occurred within the late Neogene and are unlikely to have been associated with pluvial–interpluvial cycles of the Pleistocene. (This estimate is based on the calibration point of 6.5 Ma for divergence of extant genera and subgenera of peromyscine rodents, as argued above.) Divergence of *fraterculus* from *eva* (on the Baja California Peninsula) and of West from East *eremicus* probably occurred within a Pleistocene pluvial–interpluvial time frame, possibly in response to repeated cycles of sea level changes and elevational–latitudinal climatic shifts. Finally, it appears that population-level differences within each phylogeographic unit have evolved subsequent to the last pluvial interval.

General biogeographic implications. Results of this study provide a basis for evaluating more general models underlying the historical development of desert biotas in North America. Shreve (1942) originally provided a floristic definition of three regional warm deserts in North America: Chihuahuan, Mojave, and Sonoran. Importantly, his delineation of the Sonoran Desert included the Baja California Peninsula. Hafner (1981) proposed recognition of the Peninsular Desert based on a faunal analysis of arid-adapted mammals and reptiles. Grismer (1994) summarized evidence for the timing of the opening of the Sea of Cortéz (forming

the Baja California Peninsula) and subsequent episodes of marine embayments that provided the geomorphological foundation for a model of Peninsular herpetofaunal origins and evolution within a latest Neogene (5.5–1.8 Ma) time frame. Hafner and Riddle (1997) presented evidence from fossil records and phylogeographic patterns in arid-adapted mammals that indicated both Neogene and Pleistocene periods of isolation of the Peninsular fauna and summarized the characteristics of the Peninsular complement of plants, mammals, reptiles, birds, insects, and scorpions that supported distinctiveness of the Peninsular Desert.

We provide clear evidence for a distinct Peninsular and southwestern California lineage (*fraterculus* + *eva*), and an estimated time frame for its divergence from mainland lineages (Fig. 9), that is consistent with Grismers' (1994) "northern Pliocene vicariant complex" of 10 reptilian genera. As envisioned by Grismer (1994, p. 76), ". . . the lineages of this complex . . . had a pre-Pliocene circum-gulf distribution ranging throughout northern Baja California, around the head of the Gulf of California, and in most cases into northwestern Mexico. This distribution was in place before the northernmost extension of the Gulf of California, approximately 3 mya during the late Pliocene. This northerly extension divided the ranges of these circum-gulf taxa and promoted the formation of sister lineages on opposite sides of the northern limit of the gulf regions. The subsequent regression of the Gulf of California to its current position around 1 mya allowed the divergent allopatric sister lineages to regain contact in the vicinity of the head of the current Gulf of California." To the extent that this pattern is strongly predicted in reptiles (Grismer, 1994) and a variety of mammals (Hafner and Riddle, 1997), and already has been demonstrated in the *Neotoma lepida* species group of woodrats (Planz, 1992) and the *eremicus* species group (this study), it appears to be an important and general historical vicariant event in the diversification of North American desert biotas.

At least two vicariant events have been proposed that could account for a pattern of north–south lineage divergence on the Baja California Peninsula: the Isthmus of La Paz (Grismer, 1994) and a midpeninsular seaway (Upton and Murphy, 1997). Grismer (1994) proposed a Pliocene (>3 Ma) isolation of populations in the Cape Region from northern lineages, resulting from inundation of the Isthmus of La Paz by a shallow seaway. Because this event preceded the northernmost extension of the Gulf of California discussed above, members of any northern Pliocene vicariant group of taxa with separate northern and southern Peninsular lineages, such as the *eremicus* species group, should exhibit higher within-Peninsular differentiation than Peninsular vs mainland differentiation. Upton and Murphy (1997) argued that mtDNA sequence data for the lizard *Uta stansburiana* and close relatives provided circumstantial support for the existence of a midpeninsular seaway in the vicinity of the present Vizcaino Desert at about 1 Ma. The concept of such a seaway was originally proposed based on low midpeninsular elevations and subsequently has been supported by the distribution of marine organisms on the Pacific and Gulf sides of the Peninsula. Our estimates of divergence times (Fig. 9) and geographic distributions of *fraterculus* and *eva* are largely consistent with this model. Further sampling of phylogeographic structure in other reptiles and mammals with northern and southern Peninsular distributions will be required to evaluate the generality of either postulated model. Interestingly, *U. stansburiana* is yet another species in which molecular analyses revealed biogeographic subdivision of Peninsular populations not predicted from morphology and, as a result, Grismer (1994) did not include this species as a candidate for subdivision into northern and southern Peninsular lineages.

If divergence between Peninsular and mainland clades within the *eremicus* species group was initiated around 3 Ma as argued above, then divergence between *merriami* and the West + East *eremicus* lineage either was postdated somewhat (best ML and initial NJ trees) or was approximately coincident with that split. We consider the most likely scenario for this event to be isolation of populations between the western lowland deserts and thorn-scrub forests (*merriami*) and the uplifted Mexican Plateau to the east (*eremicus*), which was becoming increasingly xeric as a result of the growing double rain shadow forming from rising cordilleras to the west (Sierra Madre Occidental) and east (Sierra Madre Oriental). Alternatively, divergence could have been initiated through ecological separation of ancestrally sympatric or parapatric populations along the developing thorn-scrub to desert-scrub continuum in the western lowlands. However, ecological separation between modern populations of each species is subtle (Hoffmeister, 1986) and does not suggest a history of isolation and divergence based solely on ecological criteria. It is otherwise difficult to identify physiographic features within the western lowlands that could be historically associated with biogeographic barriers. Further support for a trans-Sierra Madre Occidental vicariant model would come from demonstration of other sister lineages of mammals and reptiles that exhibit a western thorn-scrub forest form and an eastern desert-scrub form.

Finally, we suggest that divergence between West and East lineages of *eremicus* was initiated during the time frame of Pleistocene pluvial–interpluvial cycles (Fig. 9). However, we note that this event considerably precedes the Wisconsinan pluvial period, so that even among these most-similar sister lineages within the *eremicus* species group, the latest Pleistocene glacial period does not appear to have been a factor in the origination of extant lineage diversity or among-lin-

eage geographic distribution, contra traditional views for mammals (Findley, 1969; Schmidly *et al.*, 1993), reptiles (Morafka, 1977), and birds (Hubbard, 1973) of the Sonoran and Chihuahuan regional deserts. Whether pluvial–interpluvial cycles formed the driving mechanisms underlying isolation is problematic, because isolation could have been accomplished through a final separation of desert-scrub habitats west and east of the uplifting Sierra Madre Occidental and may have had little to do directly with climatic oscillations. That phylogeographic separation between eastern and western desert-scrub terrestrial vertebrates appears to be a general pattern (e.g., Lee *et al.*, 1995; Orange, 1997; Riddle, 1995) suggests a model of barrier formation more durable through time than would be predicted by pluvial–interpluvial climatic cycles. Otherwise, periodic contact between populations or sister species should have led to a more complex pattern of gene lineage distributions among the eastern and western deserts than what appears to be the case in those vertebrates that exhibit eastern and western sister lineages.

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APPENDIX

Scientific names	Country	State	County	Locality	LVT Number	Haplotype number	Locality Number
Peromyscus eremicus	MX	Chihuahua		5 km NNW Chihuahua	LVT-01069	E 04	4
Peromyscus eremicus	MX	Chihuahua		5 km NNW Chihuahua	LVT-01073	E 05	4
Peromyscus eremicus	MX	Chihuahua		3 mi NE Parral	LVT-01086	E 07	5
Peromyscus eremicus	MX	Chihuahua		3 mi NE Parral	LVT-01087	E 06	5
Peromyscus eremicus	MX	Chihuahua		3 mi NE Parral	LVT-01088	E 13	5
Peromyscus eremicus	MX	Chihuahua		3 mi NE Parral	LVT-01089	E 09	5
Peromyscus eremicus	MX	Chihuahua		3 mi NE Parral	LVT-01090	E 10	5
Peromyscus eremicus	MX	Durango		5 km SW Lerdo	LVT-01124	E 14	6
Peromyscus eremicus	MX	Durango		7 km SW Lerdo	LVT-01140	E 15	6
Peromyscus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-01150	E 08	7
Peromyscus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-01151	E 11	7
Peromyscus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-01152	E 02	7
Peromyscus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-01153	E 03	7
Peromyscus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-01154	E 12	7
Peromyscus eremicus	MX	San Luis Potosi		10 mi S Matehuala	LVT-01180	E 01	8
Peromyscus eremicus	MX	San Luis Potosi		10 mi S Matehuala	LVT-01181	E 16	8
Peromyscus eremicus	MX	San Luis Potosi		3 mi S, 0.5 mi W Matehuala	LVT-01193	E 01	8
Peromyscus eremicus	MX	San Luis Potosi		3 mi S, 0.5 mi W Matehuala	LVT-01194	E 01	8
Peromyscus eremicus	MX	San Luis Potosi		3 mi S, 0.5 mi W Matehuala	LVT-01195	E 17	8
Peromyscus eremicus	USA	AZ	Pinal	Picacho State Park	LVT-00326	W 14	1
Peromyscus eremicus	MX	Chihuahua		4 km SW Parrita	LVT-01048	W 06	3
Peromyscus eremicus	MX	Chihuahua		4 km SW Parrita	LVT-01049	W 07	3
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01223	W 16	10
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01224	W 17	10
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01225	W 27	10
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01226	W 19	10
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01227	W 16	10
Peromyscus eremicus	MX	Sonora		2 km N Puerto de la Libertad	LVT-01228	W 18	10
Peromyscus eremicus	USA	NV	Clark	1.5 mi S, 1.5 mi E Mountain Springs	LVT-01594	W 11	2
Peromyscus eremicus	USA	NM	Doña Ana	Afton Lava Flow	LVT-01595	W 12	9
Peromyscus eremicus	USA	NV	Clark	Valley of Fire State Park	LVT-01769	W 08	24
Peromyscus eremicus	USA	NV	Clark	0.5 mi S Blue Diamond Hwy; Cottonwood Valley	LVT-02079	W 09	2

APPENDIX—*Continued*

Scientific names	Country	State	County	Locality	LVT Number	Haplotype number	Locality Number
Peromyscus eremicus	USA	NV	Clark	0.5 mi S Blue Diamond Hwy; Cottonwood Valley	LVT-02080	W 10	2
Peromyscus eremicus	USA	AZ	La Paz	3 mi E Ehrenberg	LVT-02499	W 01	25
Peromyscus eremicus	USA	AZ	La Paz	3 mi E Ehrenberg	LVT-02500	W 02	25
Peromyscus eremicus	USA	AZ	La Paz	3 mi E Ehrenberg	LVT-02501	W 05	25
Peromyscus eremicus	USA	AZ	Cochise	9.5 mi SE Willcox	LVT-04728	W 13	26
Peromyscus eremicus	USA	AZ	Cochise	9.5 mi SE Willcox	LVT-04729	W 13	26
Peromyscus eremicus	USA	AZ	Pinal	5 mi S, 5 mi E Picacho	LVT-04741	W 15	1
Peromyscus eremicus	USA	AZ	Pinal	5 mi S, 5 mi E Picacho	LVT-04742	W 03	1
Peromyscus fraterculus	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-02097	F 08	16
Peromyscus fraterculus	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-02163	F 08	17
Peromyscus fraterculus	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-02165	F 04	17
Peromyscus fraterculus	MX	Baja California		27 km S Punta Prieta	LVT-03661	F 08	11
Peromyscus fraterculus	MX	Baja California		27 km S Punta Prieta	LVT-03662	F 04	11
Peromyscus fraterculus	MX	Baja California		27 km S Punta Prieta	LVT-03663	F 08	11
Peromyscus fraterculus	MX	Baja California		27 km S Punta Prieta	LVT-03664	F 06	11
Peromyscus fraterculus	MX	Baja California		1 km W Cataviña	LVT-03711	F 08	18
Peromyscus fraterculus	MX	Baja California		1 km W Cataviña	LVT-03713	F 02	18
Peromyscus fraterculus	MX	Baja California		Misión San Fernando	LVT-03753	F 05	21
Peromyscus fraterculus	MX	Baja California		Misión San Fernando	LVT-03754	F 10	21
Peromyscus fraterculus	MX	Baja California		10 mi S, 10 mi E Valle de Trinidad	LVT-03789	F 04	19
Peromyscus fraterculus	MX	Baja California		10 mi S, 10 mi E Valle de Trinidad	LVT-03792	F 04	19
Peromyscus fraterculus	MX	Baja California Sur		San Francisco de la Sierra	LVT-02172	F 07	20
Peromyscus fraterculus	MX	Baja California Sur		San Francisco de la Sierra	LVT-02174	F 09	20
Peromyscus fraterculus	MX	Baja California Sur		10 km SW Loreto	LVT-03595	F 03	13
Peromyscus fraterculus	MX	Baja California Sur		10 km SW Loreto	LVT-03597	F 01	13
Peromyscus eva	MX	Baja California Sur		20 mi. W San Ignacio	LVT-03583	V 07	12
Peromyscus eva	MX	Baja California Sur		30 km N Todos Santos	LVT-03612	V 05	14
Peromyscus eva	MX	Baja California Sur		30 km N Todos Santos	LVT-03615	V 03	14
Peromyscus eva	MX	Baja California Sur		30 km N Todos Santos	LVT-03616	V 01	14
Peromyscus eva	MX	Baja California Sur		11 km S Todos Santos	LVT-03635	V 06	15
Peromyscus eva	MX	Baja California Sur		11 km S Todos Santos	LVT-03637	V 02	15
Peromyscus eva	MX	Baja California Sur		11 km S Todos Santos	VLT-03638	V 04	15
Peromyscus merriami	MX	Sonora		10 km SSE Alamos	LVT-01241	M 07	22
Peromyscus merriami	MX	Sonora		10 km SSE Alamos	LVT-01242	M 07	22
Peromyscus merriami	MX	Sonora		10 km SSE Alamos	LVT-01243	M 04	22
Peromyscus merriami	MX	Sonora		10 km SSE Alamos	LVT-01244	M 07	22
Peromyscus merriami	MX	Sonora		10 km SSE Alamos	LVT-01245	M 05	22
Peromyscus merriami	MX	Sinaloa		5 km SW El Fuerte	LVT-01280	M 01	23
Peromyscus merriami	MX	Sinaloa		3 km E El Fuerte	LVT-01281	M 03	23
Peromyscus merriami	MX	Sinaloa		5 km SW El Fuerte	LVT-01282	M 02	23
Peromyscus merriami	MX	Sonora		15 km S Navojoa	LVT-01298	M 06	22
Peromyscus californicus	MX	Baja California		2 mi SW Laguna Hanson	LVT-03695	A 01	
Peromyscus crinitus	USA	CA	Riverside	9 mi W, 1 mi S Quien Sabe Point	LVT-00985	R 01	

APPENDIX—*Continued*

Scientific names	Country	State	County	Locality	LVT Number	Haplotype number	Locality Number
Peromyscus boylii	USA	NV	Clark	1.5 mi S, 1.5 mi E Mountain Springs	LVT-01585	B 01	
Peromyscus leucopus	MX	Chihuahua		4 km SW Parrita	LVT-01045	L 01	
Peromyscus maniculatus	MX	Baja California Sur		11 km S Todos Santos	LVT-03634	N 01	

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