



Molecular Biogeography in the Pocket Mice (*Perognathus* and *Chaetodipus*) and Grasshopper Mice (*Onychomys*): The Late Cenozoic Development of a North American Aridlands Rodent Guild

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MOLECULAR BIOGEOGRAPHY IN THE POCKET MICE
(*PEROGNATHUS* AND *CHAETODIPUS*) AND GRASSHOPPER MICE
(*ONYCHOMYS*): THE LATE CENOZOIC DEVELOPMENT OF A
NORTH AMERICAN ARIDLANDS RODENT GUILD

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Paleoecological and geological evidence previously have been used to infer a sequential development of arid landscapes in western North America composed of: a gradual Miocene development of savanna and semidesert habitats; a rapid late-Miocene expansion of regional deserts, grasslands, and shrubsteppes; cyclical late Pliocene-Pleistocene changes in the distribution and composition of aridlands biotas. Rodents that characterize aridlands regions in western North America include lineages detectable in the fossil record back to the late Oligocene as well as mid-Miocene immigrants from Asia. In this study, nucleotide-sequence data from the mitochondrial DNA genes COIII and cytochrome *b* were used to analyze phylogeny, genetic divergence, and geographic structure within the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*). Molecular phylogenies, estimates of divergence times, and geographic distributions suggest that middle to late Pleistocene glacial cycles appear to have had little influence on lineage divergence in aridlands rodents. Rather, a correspondence between molecular, distributional, paleoecological, and geological evidence suggests that divergence and current distributions of most extant lineages can be attributed to late Tertiary-early Quaternary development of the western North American cordillera. These data are used to produce a predictive generalized model of late Cenozoic area relationships among arid regions in western North America.

Key words: biogeography, rodents, North American aridlands, mitochondrial DNA, systematics, evolution, paleoecology, Cenozoic, Tertiary, Pleistocene

When and where did extant lineages of North American aridlands rodents arise? Rodents that characterize North American aridlands communities (Brown, 1987) represent a taxonomically diverse assemblage. Within the autochthonous aridlands family Heteromyidae, the subfamily Perognathinae is comprised of two genera of pocket mice (*Perognathus* and *Chaetodipus*) and is recorded in the fossil record back to the Late Arikarean North American Land Mammal Age (NALMA; Lindsay, 1972; Savage and Russell, 1983). Ancestors of two families with arid-adapted lineages, Cricetidae and Sciuridae, arrived in North America from Asia during or subsequent to the Barstovian NALMA (Savage and Russell, 1983).

Pleistocene glacial-interglacial cycles have attracted great attention from biogeographers and paleoecologists attempting to explain the development of current patterns of biotic diversity (e.g., Betancourt et al., 1990; Haffer, 1982; Mayr and O'Hara, 1986), but to what extent are these events causally associated with lineage divergence and biogeographic structure? For western North American aridlands, Hubbard (1973) developed a model of avian evolution that postulated speciation in late Pleistocene glacial refugia. Findley (1969) used glacial-interglacial cycles to explain divergence between sister-species of mammals in the Sonoran and Chihuahuan deserts. Pleistocene speciation hypotheses associated with gla-

cial-interglacial cycles more recently have been questioned due to their a priori exclusion of alternative pre-Pleistocene explanations (Bush, 1994; Cracraft, 1988; Lynch, 1988; Mayden, 1988).

Newer evidence from fossil and isotope records have refined the understanding of late Cenozoic paleoclimates (Webb and Bartlein, 1992). A general cooling trend culminated in late Pliocene-Pleistocene (late Blancan to Rancholabrean NALMAs) glacial-interglacial cycles. Importantly, a shift in the periodicity and magnitude of glacial-interglacial cycles occurred at 7.0×10^5 years ago, wherein a dominant 4.1×10^4 -year cycle prior to that time was replaced by a strong 1.0×10^5 -year signal. The seven glacial cycles subsequent to that transition have been not only considerably longer, but also more extreme than previous episodes. Thus, if one is to invoke glacial-interglacial cycles as fundamental mechanisms of lineage diversification in western North American aridlands, geographic isolation initiating divergence typically would date to within the latest 7.0×10^5 years (i.e., mid-late Pleistocene divergence). An even more restrictive hypothesis would predict lineage diversification dating to the latest glacial period, beginning 8.5×10^4 years ago (i.e., latest Pleistocene divergence).

Arid regions in western North America (Fig. 1) developed during the past 2.8×10^7 years in response to the general uplifting and expansion of the North American cordillera (Fig. 2). From late Oligocene to late Miocene time (Arikareean to Hemphillian NALMAs) localized hardwood forests and woodland savannas gradually were replaced with steppe and semidesert habitats. This trend culminated in a rapid latest-Miocene (late Hemphillian NALMA) expansion of regional deserts, grasslands, and shrubsteppes. The late Hemphillian generally is recognized as a significant time in the evolution of western North American mammals (Webb, 1977), as it coincides with a large extinction event marking the end of the

Clarendonian chronofauna. The late Hemphillian upheavals could have had a pronounced effect on the evolution of aridlands taxa by accelerating the extinction rate of older lineages or the origination rate of new lineages. In short, a long history of geologic and late Tertiary climatic trends in western North America provide an array of possible pre-Pleistocene divergence alternatives to a glacial-interglacial mechanism underlying lineage divergence.

Choosing between temporally different hypotheses for a causal relationship between earth and biogeographic histories requires an inference of divergence times among evolutionary lineages. Two potential sources are available for estimating times of divergence: fossils (Grande, 1985); molecular clocks (Page, 1990). Both methods suffer from inherent problems. Fossils could suffer from incomplete representation in the fossil record or absence of appropriate characters to diagnose a particular cladogenetic event. Assumptions underlying use of a molecular clock include: additive and approximately linear genetic divergence between taxa; genetic distance can be measured between taxa; rates of divergence can be calibrated based on independent dates. The concept of a universal molecular clock has been criticized due to heterogeneity in molecular evolutionary rates as well as errors involved with estimating those rates (Hillis and Moritz, 1990; Li et al., 1990). However, if generation times (Li et al., 1990) or metabolic rates (Martin and Palumbi, 1993; Rand, 1994) are primary sources of rate-heterogeneity, one should be able to substantially reduce the error in estimating rates of molecular divergence by calibrating the rate of divergence for a specified molecular sequence within a specified group of organisms. For example, the temporally well-resolved split between *Mus* and *Rattus* (Jaeger et al., 1986) at 1.0×10^7 years ago recently has been used to calibrate rates of molecular divergence in a wide variety of muroid rodents (Catzefflis et al., 1993).

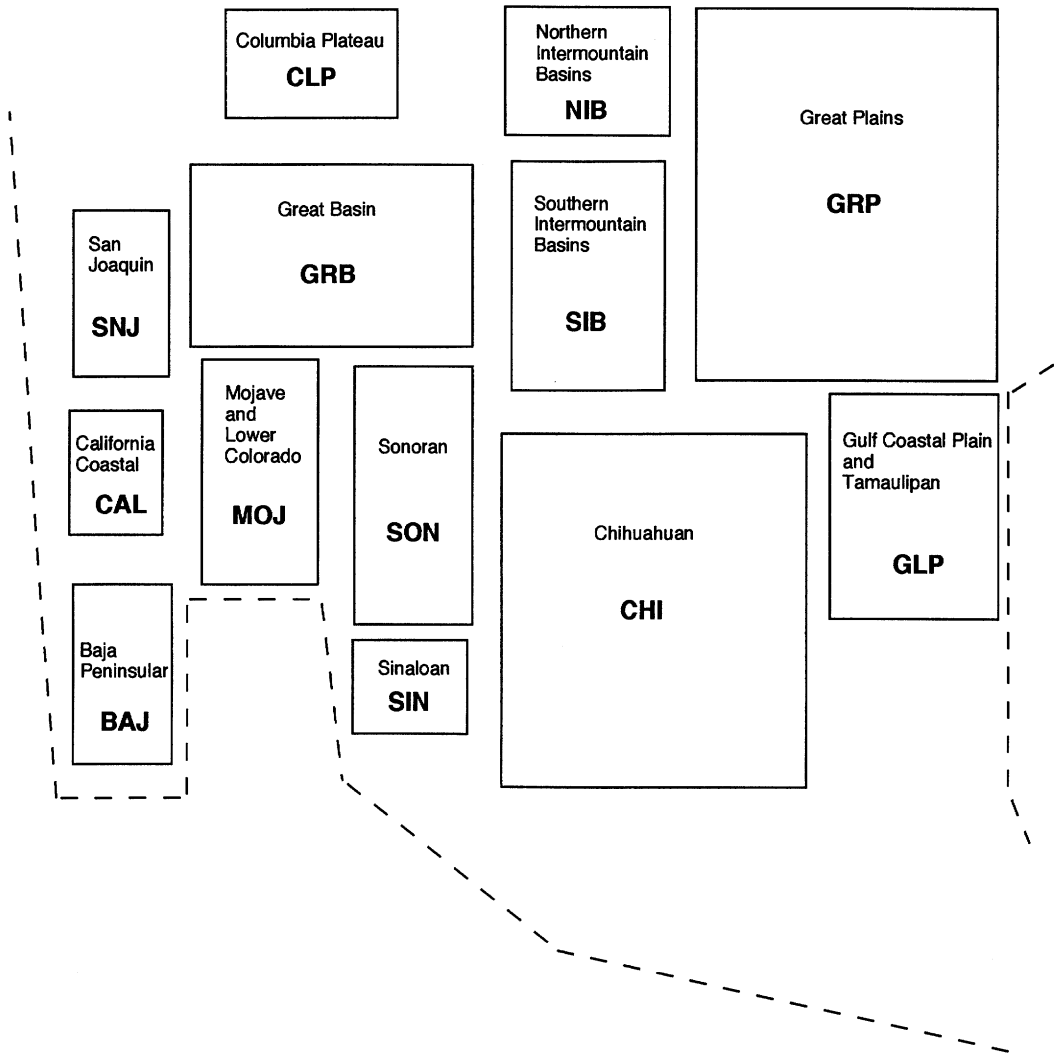


FIG. 1.—Arid regions of western North America as defined in this study. Biogeographic relationships for the California Coastal and Baja Peninsular regions were not evaluated in this study.

In the present study, patterns of divergence are investigated within the heteromyid genera *Perognathus* and *Chaetodipus* and the cricetid genus *Onychomys* (Fig. 3) using sequence data from the mitochondrial (mt) DNA genes COIII and cytochrome *b*. The utility of mtDNA for investigating biogeographic (or “phylogeographic”) patterns has been reviewed elsewhere (Avice, 1994). Species and species-group (sensu Williams, 1978) relationships in *Perognathus* have not been evaluated previously within a rigorous phylogenetic framework

(Patton and Rogers, 1994a), and the only previous molecular study of *Chaetodipus* involved phenetic analysis of allozymic data (Patton et al., 1981). The first objective of this study is to examine phylogenetic and biogeographic relationships within and among species-groups in *Perognathus*, within and among selected taxa in *Chaetodipus*, and among exemplar individuals representing previously postulated evolutionary lineages of *Onychomys* (Riddle and Honeycutt, 1990). Subsequently, phylogenetic, genetic divergence, paleoecologic,

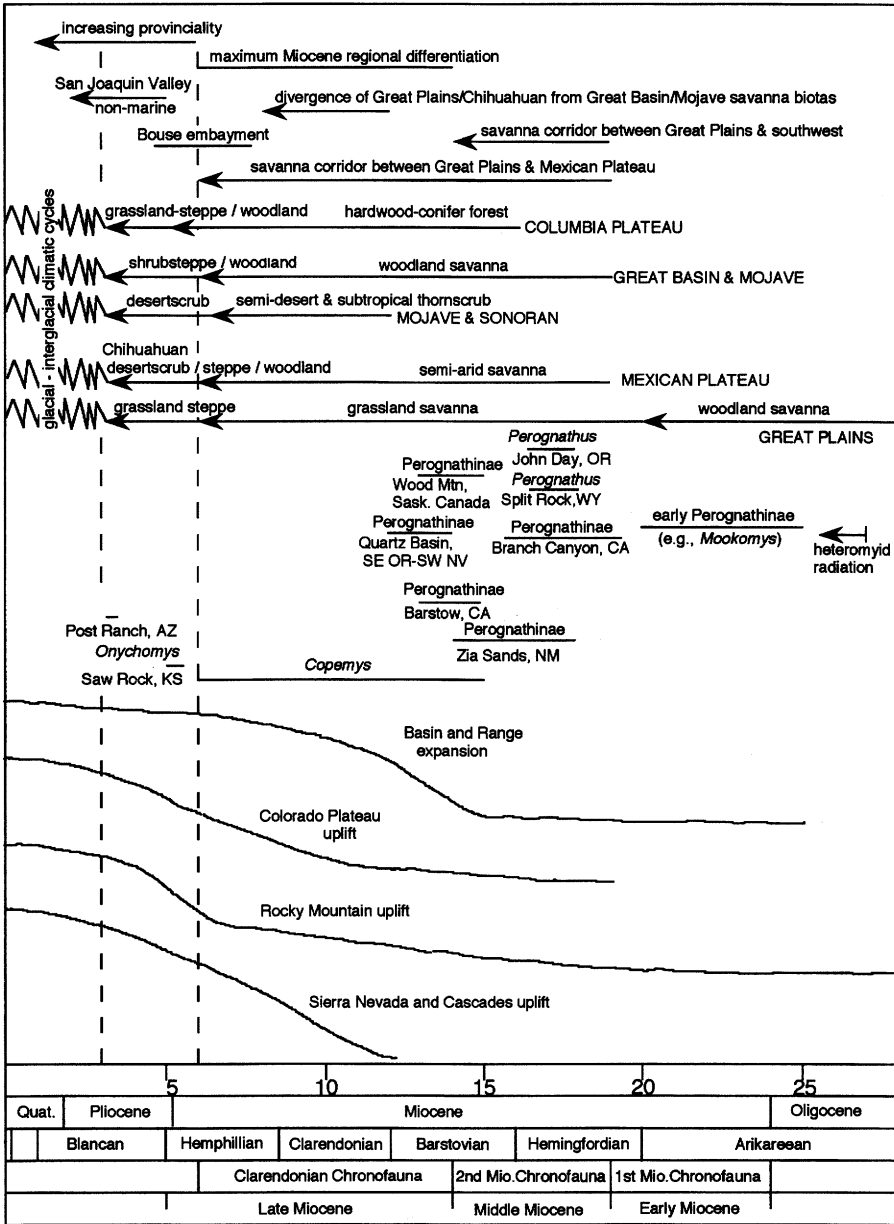


FIG. 2.—A summary of geological, fossil, and paleoecological evidence for the development of aridlands in western North America. Vertical dotted lines delineate three temporal domains (discussed in text). Selected fossil records for pocket mice are shown to illustrate late Oligocene to mid-Miocene geographic distributions. *Copemys* is probably the common ancestor of modern North American cricetine rodents (including *Onychomys*). Bottom set of lines represent relative rates of uplift or expansion of physiographic regions, not absolute scales of transition (Betancourt et al., 1990; Carlton and Eshelman, 1979; Gawne, 1975; Leopold and Denton, 1987; Lindsay, 1972; Munthe, 1988; Riddiman et al., 1989; Savage and Russell, 1983; Storer, 1970; Webb, 1977; Webb and Bartlein, 1992; Whistler, 1984).

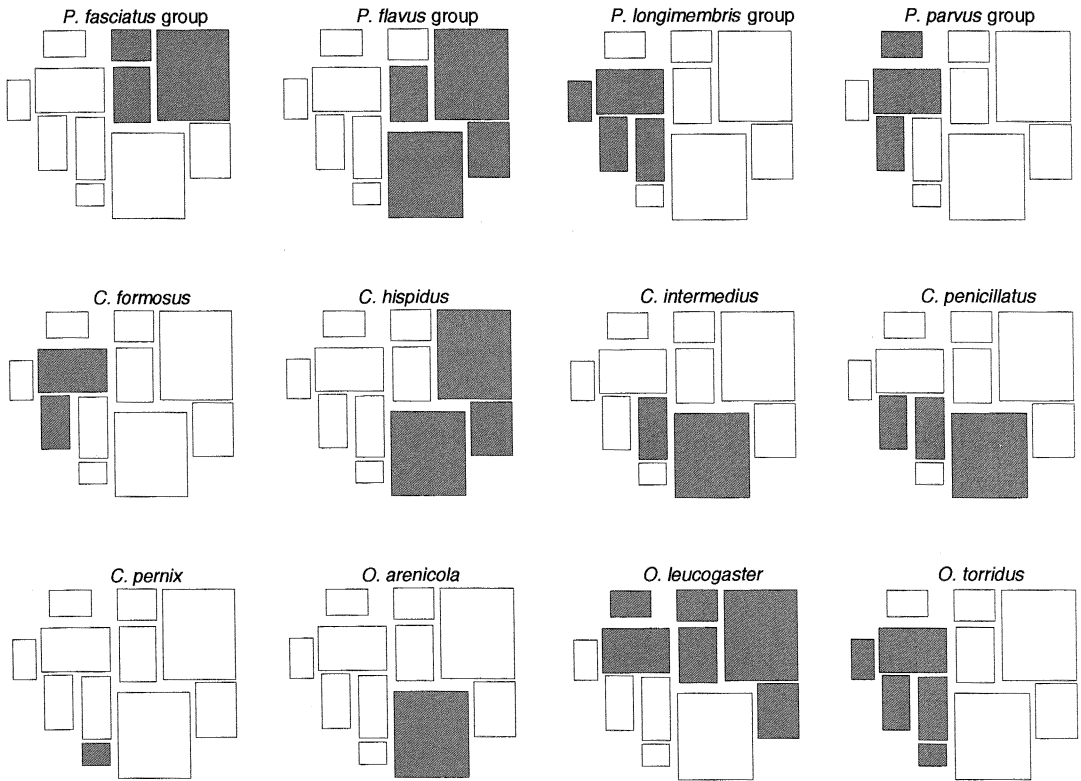


FIG. 3.—Geographic distribution of *Perognathus*, *Chaetodipus*, and *Onychomys* taxa examined in this study among regions depicted in Fig. 1 (minus California Coastal and Baja Peninsular regions).

and geologic evidence are used to evaluate hypotheses of lineage divergence. Finally, an attempt is made to develop a generalized model of late Cenozoic biogeography in western North American aridlands (with the exception of Baja Peninsular and California Coastal regions).

MATERIALS AND METHODS

MtDNA sequences from 15 specimens of *Perognathus*, 12 of *Chaetodipus*, and 9 of *Onychomys* were used in this study (Appendix I). Individuals were selected as representative of specified regions (Fig. 1). Additional sequences from individuals not reported here were used to confirm the taxonomic identity as well as the geographic representation of reported sequences. Genomic DNA was isolated from frozen tissues following methods of Hillis et al. (1990). Two separate gene regions were targeted for analysis. Primers described by Smith and Patton (1991)

were used to amplify by polymerase chain reaction >400 base pairs of the cytochrome-*b* gene. The cytochrome subunit 3 (COIII) gene (784 base pairs) was amplified using the following primers (identified by reference to the 3' base number in the published sequence of *Mus*—Bibb et al., 1981): L8586, 5'-TAC GTA TTC ACC CTT CTA GTA AGC CT-3'; L8618, 5'-CAT GAT AAC ACA TAA TGA CCC ACC AA-3'; H9323, 5'-ACT ACG TCT ACG AAA TGT CAG TAT CA-3'; H9375, 5'-ACT AAG AGA GTA GGA TCC TCA TCA ATA-3'. Single-stranded dideoxy DNA sequencing was performed according to the protocol of Allard et al. (1991) with Sequenase 2.0 polymerase enzyme and reagents (United States Biochemical, Cleveland, OH) and Sequetide nucleotide triphosphates (DuPont New England Nuclear, Boston, MA).

MacVector version 3.5 sequence-analysis software (International Biotechnologies, Inc., New Haven, CT) was used to edit aligned se-

TABLE 1.—Nucleotide sequence datasets derived from segments of COIII and cytochrome-b genes, with beginning and ending bases identified according to published sequence of *Mus* (Bibb et al., 1981). Sequence divergence between *Mus* and *Rattus* (Gadaleta et al., 1989) calculated to calibrate rates of divergence of specified sequence datasets, assuming divergence time of 1.0×10^7 years ago (Jaeger et al., 1986).

Dataset	Size	mtDNA segment		Mus-Rattus					
		COIII	Cytochrome <i>b</i>	Sequence divergence			Divergence rate		
				10:1	20:1	TV	10:1	20:1	TV
COIII LONG	412	8664-9075		28.0	29.2	10.7	2.8	2.9	1.1
COIII SHORT	360	8664-9023		29.9	31.4	11.4	3.0	3.1	1.1
CYTB	300		14151-14450	22.3	23.0	8.4	2.2	2.3	0.8
COIII LONG + CYTB	712	8664-9075	14151-14450	25.5	26.4	9.7	2.6	2.6	1.0

quences and translate them to amino-acid sequences for verification of reading-frame integrity. Sequences were entered into MacClade (Maddison and Maddison, 1992) for manipulation and construction of stepmatrices. Characters were coded as five possible states: A; C; G; T; missing. Phylogenetic analyses were performed under a maximum-parsimony approach using PAUP (Swofford, 1991). Subsets of the total dataset (Table 1) were used in separate analyses. Relative levels of character support for internal nodes of a given phylogenetic hypothesis were evaluated using the bootstrap technique (Felsenstein, 1985). The rate of transformation of nucleotide bases is influenced by a variety of factors (e.g., codon position, degeneracy, functional constraints in a translated protein). Because this rate-heterogeneity influences the ability of parsimony analysis to produce the correct phylogeny, differential character-weighting approaches should be employed in phylogenetic tree construction (Huelsenbeck and Hillis, 1993). Three weighting strategies were employed in this study: GENPAR, generalized parsimony (all character transformations unordered and weighted equally); TVERS, transversion parsimony; MIXED, generalized parsimony of first and second codon-position characters, but transversion parsimony of third position characters.

Estimates of nucleotide-sequence divergence were calculated pairwise among lineages using the maximum-likelihood approach implemented in the DNADIST program in PHYLIP (Felsenstein, 1993). A well-known property of mammalian mtDNA involves the differential rate of accumulation of transition to transversion substitutions over time, with transversion substitutions accumulating at an approximately linear

rate well beyond the point at which the measurable transition substitution rate decreases due to a saturation effect (Brown, 1985; Irwin et al., 1991). Estimates of time of divergence from molecular data assume that the rate of divergence proceeds linearly with time. Therefore, transversion-only sequence-divergence values were used for most estimates of divergence time (Jukes-Cantor formula in DNADIST), although overall divergence values also were calculated among less divergent pairs of taxa (maximum-likelihood formula in DNADIST, with the 'T' option set to either 10 or 20 to correct for higher transition substitution rates).

RESULTS

Phylogenetic analyses.—Phylogenetic analyses of 412 base pairs from COIII plus 300 base pairs from cytochrome *b* (COIII LONG + CYTB—Table 1) provided high levels of bootstrap support for the four species groups of *Perognathus* proposed by Williams (1978): *P. fasciatus*; *P. flavus*; *P. longimembris*; *P. parvus* (Fig. 4). It has been assumed here that *Perognathus inornatus* represents the only perognathine species in the San Joaquin region. Hall (1981) considered this area within the range of *P. longimembris* as well, but, according to Williams (1978:609), "... the recorded sympatry ... between *P. inornatus* and *P. longimembris* appears to be the result of species misidentification." A phylogenetic distinction between *P. longimembris* and *P. inornatus* is indicated, although *P. longimembris* and *P. inornatus* form a clade rel-

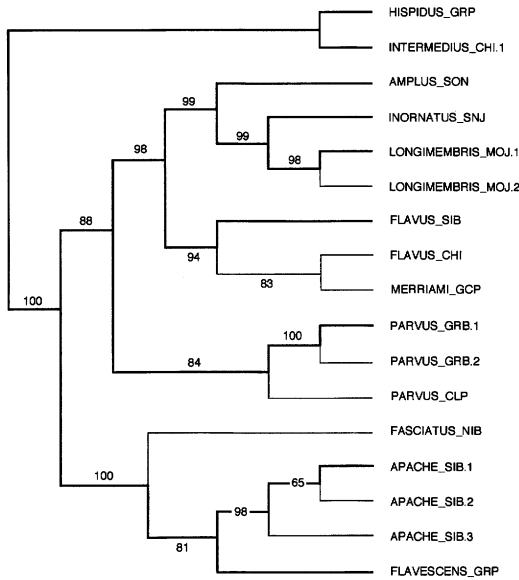


FIG. 4.—Maximum-parsimony phylogenetic tree generated using PAUP for *Perognathus* (see Appendix I for specimen and Fig. 1 for region codes). *Chaetodipus hispidus* and *C. intermedius* were designated as outgroups. The highest bootstrap value (of 1,000 iterations) among the three different character-weightings is shown: TVERS—number above line; MIXED, number on line; or GENPAR, number below line. Thick lines: tree generated using largest dataset (COIILONG + CYTB) and BRANCH AND BOUND. Thin lines: additions based on separate analyses of smaller datasets that were consistent with the COIILONG + CYTB tree. APACHE_SIB.2, APACHE_SIB.3, FLAVUS_CHI, LONGIMEMBRIS.MOJ.2, and MERRIAMLGCP added based on analysis of CYTB (HEURISTIC, TBR, RANDOM ADDITION = 10). FASCIATUS_NIB, PARVUS_CLP, and PARVUS_GRB.2 added based on analysis of COIILONG (HEURISTIC, TBR, RANDOM ADDITION = 10).

ative to *Perognathus amplus*. A monophyletic *P. flavus* group is supported by the CYTB dataset, and Chihuahuan *P. flavus* groups with *Perognathus merriami* relative to *P. flavus* of the Southern Intermountain Basins. A monophyletic *P. fasciatus* group is strongly supported, with *P. apache* and *P. flavescens* forming a clade relative to *P. fasciatus*. COIILONG provides evidence

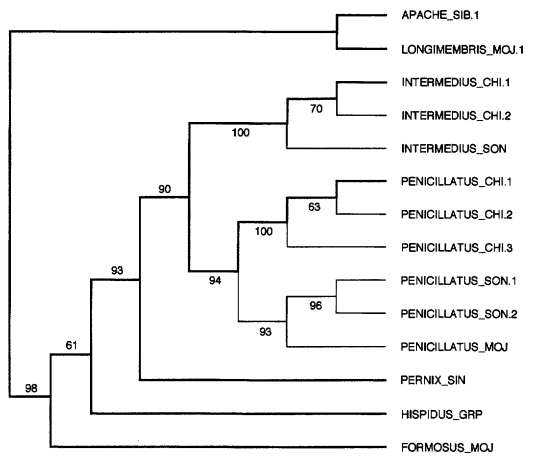


FIG. 5.—Maximum-parsimony phylogenetic tree generated using PAUP for *Chaetodipus*. *Perognathus apache* and *P. longimembris* are designated outgroups. Numbers along branches designate bootstrap values for different character-weightings as described in the legend for Fig. 4. Thick lines: BRANCH AND BOUND using COIILONG + CYTB. Thin lines: *Chaetodipus intermedius* and *C. penicillatus* sequences added to primary tree following separate BRANCH AND BOUND analysis of COIISHORT with *Chaetodipus hispidus* designated as outgroup.

for a *P. parvus* clade including individuals from the Great Basin and Columbia Plateau, although data are currently unavailable from the species of the proposed *P. parvus* group (*Perognathus alticola* and *Perognathus xanthonotus*) from the Mojave region. All three datasets support a clade joining the *P. longimembris* and *P. flavus* groups. Subsequent grouping of the *P. parvus* group with the *P. longimembris*-*P. flavus* clade is indicated with relatively strong bootstrap support using TVERS character weighting.

With the exception of *Chaetodipus formosus*, monophyly of chaetodipine pocket mice relative to other heteromyids has not been contentious (e.g., Hafner and Hafner, 1983; Patton et al., 1981). Phylogenetic analyses (Fig. 5) support the monophyly of *Chaetodipus*, including *C. formosus*, relative to *Perognathus*, with a basally unresolved divergence of *Chaetodipus hispidus*,

C. formosus, and the common ancestor of remaining taxa. The basal divergence of *C. formosus* and *C. hispidus* is in accord with a high degree of morphological and karyotypic divergence of these species from other chaetodipines (reviewed by Hafner and Hafner, 1983; Patton and Rogers, 1994a). *C. hispidus* is the only widespread chaetodipine in the Great Plains region (Fig. 3). Similarly, *C. formosus* is the only western chaetodipine with a substantial distribution throughout the Mojave plus Great Basin regions. *Chaetodipus penicillatus* and *Chaetodipus intermedius* represent two warm-desert taxa that form a clade relative to the Sinaloan thornscrub taxon *Chaetodipus pernix*. Although *C. penicillatus* is widespread throughout the Sonoran, Mojave, and Chihuahuan regions, COIISHORT provides support for at least two phylogeographically distinct lineages embedded within this nominate species (Fig. 5). Within the geographically widespread *C. intermedius*, one individual from the western edge of the Chihuahuan region is grouped with a northern Chihuahuan specimen relative to a Sonoran animal.

Five geographically distinct *Onychomys* lineages were postulated by Riddle and Honeycutt (1990) using mtDNA restriction-site data. Subsequently, Riddle et al. (1993) supported the restriction-site topology of the *Onychomys leucogaster* radiation using cytochrome-*b* sequence data. Those studies were used to identify taxon and region exemplars for analysis of COIII variation (Fig. 6). Phylogenetic analysis of COIISHORT provided high levels of bootstrap support for an *Onychomys arenicola-Onychomys leucogaster* clade relative to *Onychomys torridus*, in agreement with allozymic (Sullivan et al., 1986) and mtDNA restriction-site (Riddle and Honeycutt, 1990) analyses.

Levels of genetic divergence.—Sequence divergence was estimated between sister-taxa supported by phylogenies in Figs. 4, 5, and 6. Values differed only slightly when transition bias was corrected by setting the

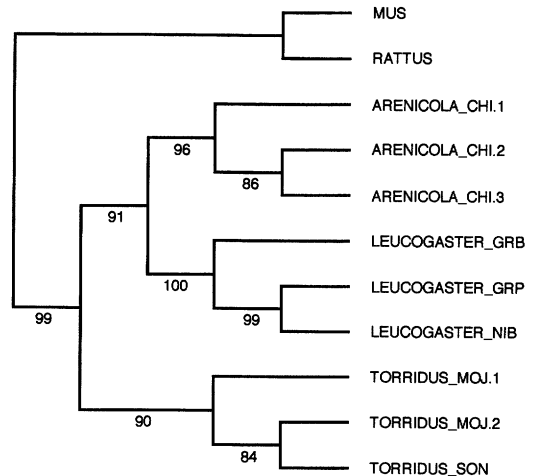


FIG. 6.—Maximum-parsimony phylogenetic tree generated using PAUP for *Onychomys* (BRANCH AND BOUND analysis of COIISHORT; *Mus* and *Rattus* designated as outgroups). Numbers along branches refer to bootstrap values for GENPAR character-weighting.

'T' option to either 10 or 20 in DNADIST. Divergence time estimated using rates of divergence in Table 1 were consistently larger for divergence at TS = 10 than for transversion divergence. This pattern could result if transition substitutions were exhibiting a saturation effect between *Mus* and *Rattus* (Table 1), thereby resulting in a systematic underestimate of divergence rates based on values at TS = 10. In support of this explanation, if one assumes that the actual rate of divergence could be higher than values given in Table 1, an hypothetical rate of 4.5%/million years produces a close fit to values derived from transversion divergence when the estimate at TS = 10 is between ca. 20 and 10%. In short, transversion divergence probably gives more reliable estimates of divergence time for pairwise comparisons exceeding ca. 10%, whereas divergence at TS = 10 probably is more reliable (using an estimated divergence rate of 4.5%/million years) for values below ca. 10% because few transversion substitutions occur between closely-related sequences. Branch lengths in Fig. 7 reflect

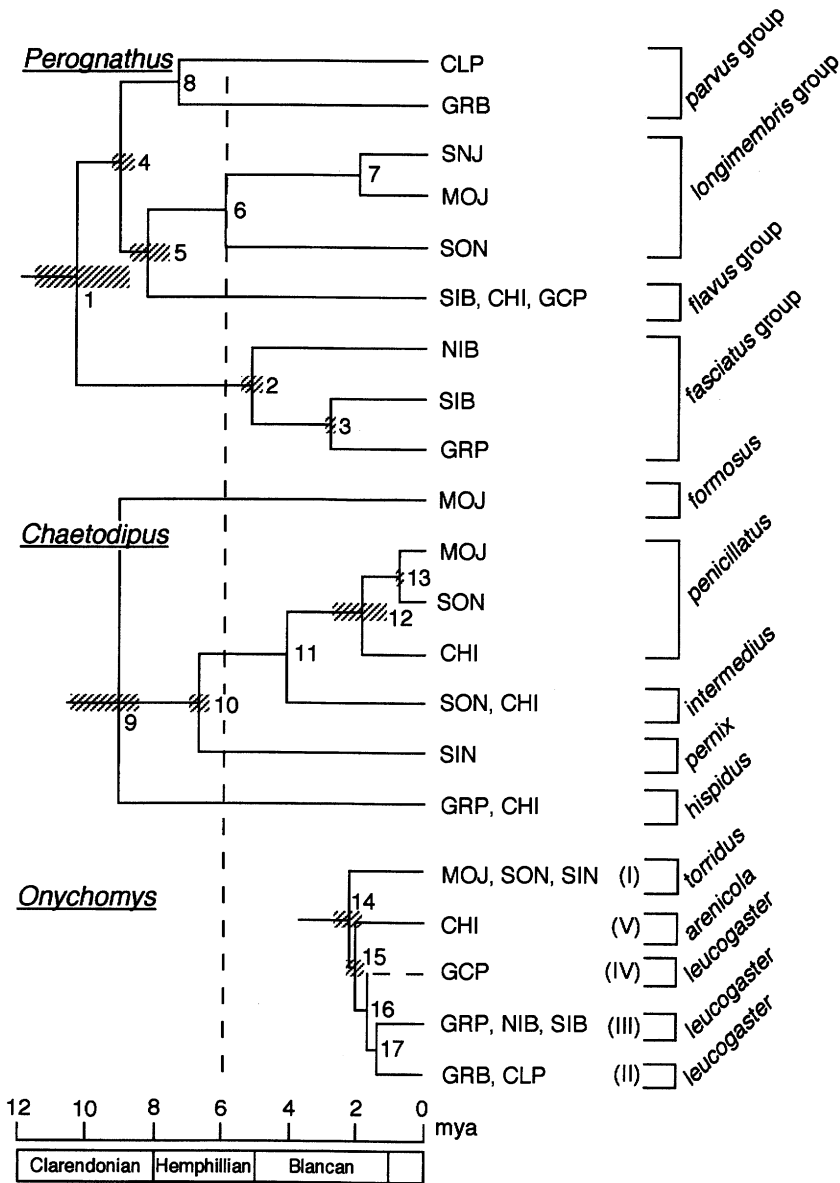


FIG. 7.—Area cladograms generated by replacing regions for taxa (Figs. 4, 5, and 6) for *Perognathus*, *Chaetodipus*, and *Onychomys*. Branch lengths are scaled based on estimated levels of genetic divergence between sister-groups (transversions-only values for all components except 7 and 12–17, which are based on overall sequence divergence values). Boxes at some nodes depict range of divergence values where multiple comparisons were available. Roman numerals I–V refer to postulated areas of endemism for *Onychomys* (the position of area IV is inferred from data in Riddle and Honeycutt, 1990; Riddle et al., 1993). Additional phylogeographic evidence supports components 2 and 3 (Nickle, 1994); component 8 (C. S. Ferrell, in litt); component 6 (McKnight, 1989); components 12 and 13 (T. E. Lee et al., in litt.); components 14–17 (Riddle and Honeycutt, 1990; Riddle et al., 1993). MYA = million years ago.

means and ranges of divergence values among phylogenetic lineages given in Figs. 4, 5, and 6.

DISCUSSION

When did extant aridlands rodents originate?—The validity of incorporating molecular estimates of divergence time into biogeography would be compromised if the time of lineage splitting between mtDNA haplotypes could occur with high probability well before a postulated geographic isolation event, in which case genetic distances between mtDNA haplotypes would not necessarily be associated with times of isolation. Suppose that the present census population size of females for a given species of pocket mice is 10^6 . Neutrality theory predicts that the expected mean time to common ancestry of two mtDNA alleles would be ca. 10^6 generations, or at one generation per year, ca. 1×10^6 years (Avise, 1994). This would be the approximate amount of error expected in estimating the time of a geographic isolation event from genetic divergence among mtDNA haplotypes if long-term effective population size of females consistently reflected current census population size. However, empirical studies commonly have demonstrated much lower levels of diversity in mtDNA within populations than would be expected from neutrality theory (Avise, 1994), indicating that evolutionarily effective population sizes are typically at least an order of magnitude lower than census population sizes. In short, at the time scales considered in this study, intrapopulational diversity in mtDNA preceding geographic isolation should not be a significant source of error.

Maximum levels of genetic divergence among extant lineages are exceedingly different in pocket mice and grasshopper mice (Fig. 7). Furthermore, the overall range of variation in *Perognathus* and *Chaetodipus* exceeds that in *Onychomys* by an order of magnitude. Although rates of molecular evolution are known to vary across taxa, factors believed to underlie rate-heteroge-

neity (i.e., generation time, body size, and metabolic rate) are unlikely to explain an appreciable amount of this variation. Further control on rate-heterogeneity accrues from examining the same gene regions across all three genera. Differences in divergence times provide a more likely explanation for the observed levels of variation across taxa. Unfortunately, fossil pocket mice are not adequately rich in diagnostic morphological traits to discriminate between species-groups or genera (Wahlert, 1993) and, therefore, do not provide a basis for calibrating rates of molecular divergence internally. However, *Onychomys bensoni* represents the first fossil *Onychomys* west of the Rocky Mountain axis (Post Ranch, Arizona, $2.5\text{--}3.5 \times 10^6$ years ago—Carleton and Eshelman, 1979; Savage and Russell, 1983). Carleton and Eshelman (1979) considered *O. bensoni* a basal member of the *O. torridus* lineage. Molecular estimates of divergence (Fig. 7) between *O. torridus* and *O. arenicola*-*O. leucogaster* are, thus, in agreement with fossil evidence of lineage divergence. Within this context, one can view the close correspondence in levels of divergence between geographically overlapping Chihuahuan and Sonoran populations of *Onychomys* and *C. penicillatus* as additional support for rate-equivalence among pocket mice and grasshopper mice.

Sequence-divergence values suggest that lineage divergence among most *Perognathus*, *Chaetodipus*, and *Onychomys* clades was not causally associated with late Pliocene-Pleistocene glacial-interglacial cycles (Fig. 7). If glacial-interglacial cycles were fundamental forcing events causing lineage divergence, climatically-mediated divergence of aridlands sister-taxa most likely would have occurred during one of the large-magnitude glacial cycles within the past 7.0×10^5 years (mid-late-Pleistocene-divergence model). The increase in divergence rates that would be required to make empirical estimates of divergence (Fig. 7) consistent with that model range from 16-

to two-fold. Similarly, rate increases required to be consistent with the latest-Pleistocene-divergence model (within the past 1.0×10^5 years) would range from ca. 114- to 14-fold. Thus, even those values that indicate divergence during the Blancan NALMA would require a two- to five-fold rate increase to be consistent with a 7.0×10^5 -year time of isolation and 14- to 38-fold increase to support a 1.0×10^5 -year time of isolation. Furthermore, if geographic and molecular congruence between Chihuahuan and Sonoran populations of *Onychomys* and *C. penicillatus* indicate a concordant time of geographic isolation, parallel rate increases of the same magnitudes would have been required in two phylogenetically unrelated groups of rodents to support either of the glacial-interglacial models.

As time since population isolation increases, the level of geographic concordance across independent characters should increase as well (Avice, 1994). For example, mtDNA and allozymic data provide similar estimates of divergence times among species of *Chaetodipus* (Patton et al., 1981); mtDNA, allozymic, and karyologic data diagnose separate Mojave, Sonoran, and Chihuahuan populations of *C. penicillatus* (Patton et al., 1981; T. E. Lee et al., in litt.); mtDNA, allozymic, karyologic, and morphologic data diagnose *O. torridus* relative to *O. arenicola* (Riddle and Honeycutt, 1990; Sullivan et al., 1986); and mtDNA and karyologic (Williams, 1978) data define congruent species-groups in *Perognathus*.

Based on all available evidence, one must consider causal events associated with the basic historical biogeographic structure of North American aridlands rodents other than those that invoke Pleistocene glacial-interglacial cycles (e.g., Findley, 1969; Hubbard, 1973). These results suggest that the prevailing paradigm under which late Pleistocene scenarios of lineage divergence in aridlands rodents have been proposed (e.g., Findley, 1969; Hinesley, 1979; Williams, 1978) and generally accepted

(Schmidly et al., 1994) are in need of fundamental reevaluation.

Where did extant aridlands rodents originate?—The Perognathinae were widely distributed during the Blancan and Clarendonian NALMAs (Fig. 2). Basal splits between extant lineages of *Perognathus* and *Chaetodipus* appear to have occurred prior to the concomitant extinction of the Clarendonian chronofauna and expansion of regional deserts, grasslands, and shrubsteppes during the latest Hemphillian (Fig. 7). However, given that confidence intervals around these estimates are unknown, discrimination between late Clarendonian versus Hemphillian divergence times may not be possible from molecular divergence estimates alone. Several other lines of evidence are consistent with Webbs' (1983) suggestion, based on the observation that extinction was most pronounced in lower-crowned, browsing ungulates and less so in hypsodont forms, that late Hemphillian changes led to loss of diverse savanna habitats in favor of expanding grasslands, steppes, and deserts. At the generic level, *Perognathus* and *Chaetodipus* tend to differ markedly from one another in their ecological preferences (e.g., Hoffmeister, 1986: table 4.1). The perognathine pocket mice are more likely to occupy grassland and shrubsteppe habitats in cooler and more seasonal environments, although *P. amplus* is a Sonoran desertscrub-adapted perognathine pocket mouse. The chaetodipine pocket mice generally are inhabitants of warm deserts and subtropical thornscrub, the main exceptions being *C. hispidus*, an inhabitant of grassland steppes and dry woodlands, and *C. formosus*, an inhabitant of cold desert grassland and shrubsteppes in addition to Mojave desertscrub. Therefore, both genera demonstrate basal splits between lineages that currently are represented by grassland steppe, shrubsteppe, and woodland species. The evolution of desertscrub species apparently occurred subsequent to the basal splits in each genus, which is in accord with the late Tertiary sequence of

progressive aridlands development as evidenced by paleoecological and geological data (Fig. 2). Additionally, the *C. pernix* versus *C. penicillatus*-*C. intermedius* split could signal the expansion of Sonoran desertscrub in the Sierra Nevada rainshadow at the expense of northernmost subtropical-thornscrub habitats (Axelrod, 1979). Divergence of *P. amplus* from *P. longimembris* at this time indicates the widespread occurrence of a desertscrub-adapted perognathine lineage. The putative mid-Blancan divergence of Chihuahuan from Sonoran lineages of *C. penicillatus* and *Onychomys* points to an early Blancan development of desertscrub in the Chihuahuan region, and a similar argument applies to the divergence of *P. inornatus* in San Joaquin from *P. longimembris* in Mojave regions.

The late Tertiary record provides a relatively robust body of evidence for causal relationships between geotectonic events, paleoecological patterns, and the development of western North American aridlands (Fig. 2). The Perognathinae appear to have originated in concert with the earliest development of savanna landscapes in western North America. Molecular estimates suggest divergence between *Chaetodipus* and *Perognathus* during the Barstovian or early Clarendonian NALMA. Co-occurring species with chaetodipine (e.g., *P. furlongi*) and perognathine (e.g., *P. minutus*) features are known from Barstovian fossil assemblages in southern California (Lindsay, 1972). Provinciality probably was not substantial given paleoecological evidence for faunal continuity between the Great Plains and Southwest and geological evidence for relatively low topographic relief between these regions. Available data, therefore, do not suggest a geographic isolation event associated with the divergence of *Chaetodipus* and *Perognathus*.

Within *Chaetodipus*, *Perognathus*, and *Onychomys*, taxa that occur in neighboring regions (Fig. 3) tend to be grouped into related clades (Fig. 7). Given the putatively deep branching points within and among

species-groups in *Perognathus*, this strong signal of geographic adjacency of sister-taxa suggests that geographic ranges of extant lineages have not shifted appreciably through time. If they had, one would expect to find regional disjunction among taxa within a species group. Yet, the much more recent divergence of *Onychomys* in relation to most pocket mouse lineages (Fig. 7) suggests that some degree of latest-Hemphillian to early Blancan ecological connectivity must have existed among arid regions, raising an interesting question: what would have prevented species of *Perognathus* and *Chaetodipus* from dispersing throughout the aridlands system in concert with the range expansion of *Onychomys* during late Hemphillian or early Blancan time? One explanation is that a high degree of habitat fidelity evolved early in the radiation of perognathine and chaetodipine lineages. In this sense, perognathines and chaetodipines would be relatively "stenobiotic" species relative to grasshopper mice (Vrba, 1992).

A generalized model of aridlands biogeographic history.—One of the fundamental goals of historical biogeography is to identify common underlying causes for patterns of diversification among independent taxa with overlapping geographic distributions. An attempt is made here to derive a spatio-temporal sequence of events that incorporate molecular biogeographic, paleoecologic, and geologic evidence (Fig. 8; Appendix II). The validity of this model relies on several assumptions, e.g., that phylogenies are correct, that estimates of divergence times are approximately correct, and that cryptic interregional dispersal of lineages does not overwhelm the biogeographic pattern associated with isolation and divergence. Many regions appear at more than one spatial and temporal branching point in this model. For example, an Hemphillian (SON + MOJ + SNJ versus CHI + GRP + GCP + SIB) relationship is postulated at component E, whereas the same relationship occurs again during the Blancan at component H. One would need to invoke an interven-

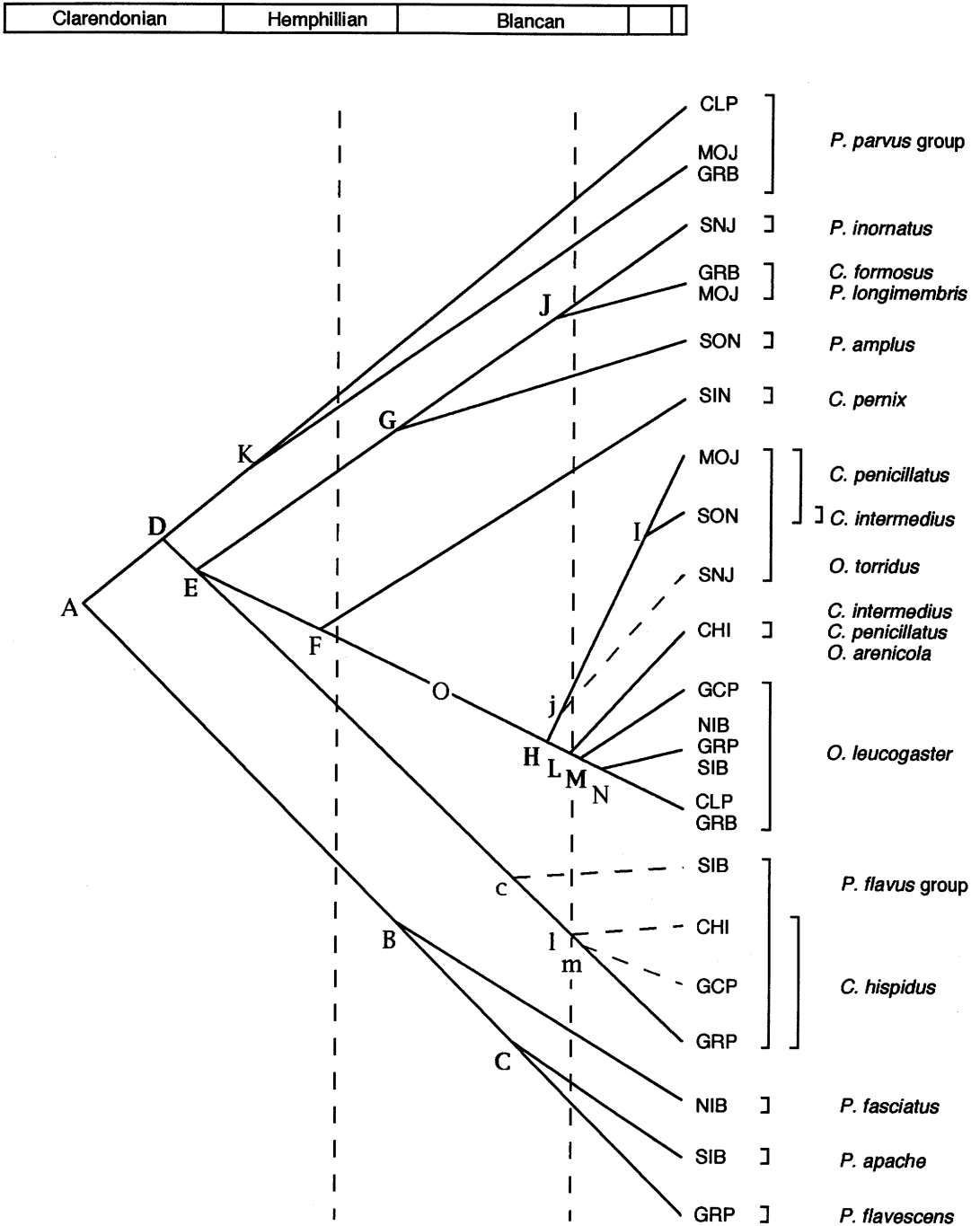


FIG. 8.—Generalized hypothesis of area relationships consistent with molecular biogeographic, paleoecologic, and geologic evidence (Fig. 2 and Appendix II). Cladogram was constructed by manually combining taxonomic area cladograms (Fig. 7) for *Chaetodipus*, *Perognathus*, and *Onychomys* under the assumptions described in the text. Letters at nodes: Postulated isolating events as described in Appendix II. Bold letters: components listed in Table 2. Lower-case letters and dashed lines: refer to events in Appendix II shown here to illustrate several testable hypotheses of area relationships.

TABLE 2.—A sampling of mammalian sister taxa whose distributions and putative phylogenetic relationships suggest tests for the generality of specific isolating events postulated in this study. Events are described in Appendix II and depicted in Fig. 8. *Dipodomys* groups from Patton and Rogers (1994b). *Ammospermophilus* data from Hafner (1981).

Event	Putative sister-taxa
C	<i>Perognathus flavus</i> [SIB]– <i>P. flavus</i> [GRP] <i>Dipodomys spectabilis</i> group [SIB]– <i>D. ordii</i>
D	<i>Dipodomys</i> [widespread]– <i>Microdipodops</i> [GRB]
E	<i>D. ordii</i> + <i>D. spectabilis</i> – <i>D. heermanni</i> group [GRB, MOJ, SNJ]– <i>D. merriami</i> group + <i>D. deserti</i> [SON, MOJ, SNJ, CHI]
G	<i>D. merriami</i> [MOJ]– <i>D. merriami</i> [SON]
H	<i>C. intermedius</i> [CHI]– <i>C. intermedius</i> [SON] <i>D. merriami</i> [CHI]– <i>D. merriami</i> [MOJ] <i>Ammospermophilus interpres</i> [CHI]– <i>A. harrisi</i> + <i>A. leucurus</i> + <i>A. nelsoni</i> <i>Peromyscus eremicus</i> [CHI]– <i>P. eremicus</i> [SON, MOJ]
J	<i>D. nitratoides</i> [SNJ]– <i>D. merriami</i> [MOJ] <i>D. heermanni</i> + <i>D. californicus</i> + <i>D. ingens</i> [SNJ]– <i>D. panamintinus</i> [MOJ] <i>O. torridus</i> [SNJ]– <i>O. torridus</i> [MOJ, SON] <i>A. nelsoni</i> [SNJ]– <i>A. leucurus</i> [MOJ]
L	<i>P. flavus</i> [CHI]– <i>P. flavus</i> [GRP] <i>C. hispidus</i> [CHI]– <i>C. hispidus</i> [GRP]
M	<i>P. merriami</i> [GCP]– <i>P. flavus</i> [GRP] <i>C. hispidus</i> [GCP]– <i>C. hispidus</i> [GRP] <i>D. compactus</i> [GCP]– <i>D. ordii</i>

ing round of interregional dispersal events to account for this pattern (as, for example, would be predicted with a late Hemphillian expansion of aridlands).

To the extent that Fig. 8 depicts a robust hypothesis of aridlands area relationships, postulated isolating events should pertain to lineage divergence in other members of the diverse North American aridlands biota. Table 2 provides a sampling of mammalian rodent taxa that would be suitable for testing the generality of hypotheses of isolating events and subsequent area relationships specified in Fig. 8.

Biotic responses to late Pliocene-Pleistocene climatic cycles.—Fundamental questions in community ecology and paleoecology concern the magnitude of responses of individual species to Pleistocene climatic cycles and the stability of species associations through time (Delcourt and Delcourt, 1991). Graham (1986) has shown that mammalian species in central and eastern North America experienced large extralimital range shifts in response to Pleistocene climatic cycles. Results of the current study suggest a profoundly different view of biotic responses to Pleistocene events in aridlands rodents, in which late Cenozoic geotectonic evolution of the North American cordillera formed a spatial template setting discrete upper boundaries on the scale of range shifts during late Pliocene-Pleistocene climatic cycles. Thus, the spatial scale of Pleistocene range shifts may have differed substantially for animals inhabiting the topographically complex western versus the more uniform central-eastern North American landscapes, which is in accord with Vrba's (1992) predictions.

CONCLUDING COMMENTS

This study has presented a model for North American aridlands rodents that deemphasizes the causal role of Pleistocene glacial-interglacial cycles in the generation of fundamental patterns of lineage diversification and historical biogeographic structure. The strength of the model lies in the high levels of agreement between several sources of evidence, i.e., geologic, paleoecologic, phylogenetic, and molecular divergence. Rejection of the temporal framework advanced here in favor of either of the Pleistocene glacial-interglacial models discussed would require one to provide evidence for the following alternative interpretations. First, rates of molecular divergence would need to be highly accelerated several to many-fold over those estimated from *Mus* and *Rattus* in three phylogenetically independent lineages with similar body sizes, metabolic rates, and generation times

(*Chaetodipus*, *Perognathus*, and *Onychomys*), which is inconsistent with a developing body of theory and empirical data. Second, one could invoke large-scale extinction events prior to mid-Pleistocene time reducing each genus to essentially a single lineage, with subsequent middle to late Pleistocene radiation of all extant perognathine, chaetodipine, and grasshopper mouse lineages, which is inconsistent with the fossil and geotectonic record.

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LITERATURE CITED

- ALLARD, M. W., D. L. ELLSWORTH, AND R. L. HONEYCUTT. 1991. The production of single-stranded DNA suitable for sequencing using the polymerase chain reaction. *BioTechniques*, 10:24–26.
- AVISE, J. C. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, London, United Kingdom, 511 pp.
- AXELROD, D. I. 1979. 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, 228 pp.
- BETANCOURT, J. L., T. R. VAN DEVENDER, AND P. S. MARTIN. 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, 467 pp.
- BIBB, M. J., ET AL. 1981. Sequence and gene organization of mouse mitochondrial DNA. *Cell*, 26:167–180.
- BROWN, J. H. 1987. Variation in desert rodent guilds: Patterns, processes, and scales. Pp. 185–203, in *Organization of communities: past and present* (J. H. R. Gee and P. S. Giller, eds.). Blackwell Scientific, Oxford, United Kingdom, 576 pp.
- BROWN, W. M. 1985. The mitochondrial genome of animals. Pp. 95–130, in *Molecular evolutionary genetics* (R. J. MacIntyre, ed.). Plenum Press, New York, 610 pp.
- BUSH, M. B. 1994. Amazonian speciation: a necessarily complex model. *Journal of Biogeography*, 21: 5–17.
- CARLETON, M. D., AND R. E. ESHELMAN. 1979. A synopsis of fossil grasshopper mice, genus *Onychomys*, and their relationships to Recent species. *University of Michigan Papers on Paleontology*, 21:1–63.
- CATZEFLIS, F. M., A. W. DICKERMAN, J. MICHAUS, AND J. A. W. KIRSCH. 1993. DNA hybridization and rodent phylogeny. Pp. 159–172, in *Mammal phylogeny: placentals* (F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds.). Springer-Verlag, Inc., Secaucus, New Jersey, 321 pp.
- CRACRAFT, J. 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. *Systematic Zoology*, 37:221–236.
- DELCOURT, H. R., AND P. A. DELCOURT. 1991. Quaternary ecology: a paleoecological perspective. Chapman and Hall, London, United Kingdom, 242 pp.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39: 783–791.
- . 1993. PHYLIP (phylogeny inference package). Version 3.5. University of Washington [Seattle] (on disk).
- FINDLEY, J. S. 1969. Biogeography of southwestern boreal and desert animals. Pp. 113–128, in *Contributions in mammalogy* (J. K. Jones, Jr., ed.). Miscellaneous Publications, Museum of Natural History, University of Kansas, 51:1–428.
- GADALETA, G., G. PEPE, G. DE CANDIA, C. QUAGLIARIELLO, E. SBISA, AND C. SACCONI. 1989. The complete nucleotide sequence of the *Rattus norvegicus* mitochondrial genome: cryptic signals revealed by comparative analysis between vertebrates. *Journal of Molecular Evolution*, 28:497–516.
- GAWNE, C. E. 1975. Rodents from the Zia Sand Miocene of New Mexico. *American Museum Novitates*, 2586:1–25.
- GRAHAM, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. Pp. 300–313, in *Community ecology* (J. Diamond and T. J. Case, eds.). Harper and Row, New York, 665 pp.
- GRANDE, L. 1985. The use of paleontology in systematics and biogeography, and a time control refinement for historical biogeography. *Paleobiology*, 11: 234–243.
- HAFFER, J. 1982. General aspects of the refuge theory. Pp. 6–24, in *Biological differentiation in the tropics* (G. T. Prance, ed.). Columbia University Press, New York, 714 pp.
- HAFNER, D. J. 1981. Evolution and historical zoogeography of antelope ground squirrels, genus *Ammospermophilus* (Rodentia: Sciuridae). Ph.D. dissert., The University of New Mexico, Albuquerque, 224 pp.
- HAFNER, J. C., AND M. S. HAFNER. 1983. Evolutionary relationships of heteromyid rodents. *Great Basin Naturalist Memoirs*, 7:3–29.
- HALL, E. R. 1981. *The mammals of North America*. Second ed. John Wiley & Sons, New York, 1:1–600 + 90, 2:601–1181 + 90.
- HILLIS, D. M., AND C. MORITZ. 1990. An overview of applications of molecular systematics. Pp. 502–515, in *Molecular systematics* (D. M. Hillis and C. Mo-

- ritz, eds.). Sinauer Associates, Inc., Sunderland, Massachusetts, 588 pp.
- HILLIS, D. M., A. LARSON, S. K. DAVIS, AND E. A. ZIMMER. 1990. Nucleic acids III: sequencing. Pp. 318–370, in *Molecular systematics* (D. M. Hillis and C. Moritz, eds.). Sinauer Associates, Inc., Sunderland, Massachusetts, 588 pp.
- HINESLEY, L. L. 1979. Systematics and distribution of two chromosomal forms in the southern grasshopper mouse, genus *Onychomys*. *Journal of Mammalogy*, 60:117–128.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press and Arizona Game and Fish Department [Tucson], 602 pp.
- HUBBARD, J. P. 1973. Avian evolution in the aridlands of North America. *Living Bird*, 12:155–196.
- HUELSENBECK, J. P., AND D. M. HILLIS. 1993. Success of phylogenetic methods in the four-taxon case. *Systematic Biology*, 42:247–264.
- IRWIN, D. M., T. D. KOCHER, AND A. C. WILSON. 1991. Evolution of the cytochrome *b* gene of mammals. *Journal of Molecular Evolution*, 32:128–144.
- JAEGER, J.-J., H. TONG, AND C. DENYS. 1986. The age of *Mus-Rattus* divergence: paleontological data compared with the molecular clock. *Comptes Rendus Academie des Sciences Paris (serie 2)*, 302:917–922.
- LEOPOLD, E. B., AND M. F. DENTON. 1987. Comparative age of grassland and steppe east and west of the northern Rocky Mountains. *Annals of the Missouri Botanical Garden*, 74:841–867.
- LI, W.-H., M. GOUY, P. M. SHARP, C. O'HUIGIN, AND Y.-W. YANG. 1990. Molecular phylogeny of Rodentia, Lagomorpha, Primates, Artiodactyla, and Carnivora and molecular clocks. *Proceedings of the National Academy of Sciences*, 87:6703–6707.
- LINDSAY, E. H. 1972. Small mammal fossils from the Barstow Formation, California. University of California Publications in Geological Sciences, 93:1–104.
- LYNCH, J. D. 1988. Refugia. Pp. 311–342, in *Analytical biogeography: an integrated approach to the study of animal and plant distributions* (A. A. Myers and P. S. Giller, eds.). Chapman and Hall, London, United Kingdom, 578 pp.
- MADDISON, W. P., AND D. R. MADDISON. 1992. *MacClade: analysis of phylogeny and character evolution*. Version 3.0. Sinauer Associates, Inc., Sunderland, Massachusetts (on disk).
- MARTIN, A. P., AND S. R. PALUMBI. 1993. Body size, metabolic rate, generation time, and the molecular clock. *Proceedings of the National Academy of Sciences*, 90:4087–4091.
- MAYDEN, R. L. 1988. Vicariance biogeography, parsimony, and evolution in North American freshwater fishes. *Systematic Zoology*, 37:329–355.
- MAYR, E., AND R. J. O'HARA. 1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evolution*, 40:55–67.
- MCKNIGHT, M. L. 1989. Biochemical investigations of the evolution and systematics of certain pocket mice (Rodentia: Heteromyidae). Ph.D. dissert., University of Illinois, Urbana, 117 pp.
- MUNTHE, J. 1988. Miocene mammals of the Split Rock Area, Granite Mountains Basin, Central Wyoming. University of California Publications in Geological Sciences, 126:1–136.
- NICKLE, D. C. 1994. Molecular phylogeography in the *Perognathus fasciatus* species group. M.S. thesis, University of Nevada Las Vegas, Las Vegas, 54 pp.
- PAGE, R. D. M. 1990. Temporal congruence and cladistic analysis of biogeography and cospeciation. *Systematic Zoology*, 39:205–226.
- PATTON, J., AND D. ROGERS. 1994a. Biochemical genetics. Pp. 259–269, in *Biology of the Heteromyidae*. Special Publication, The American Society of Mammalogists, 10:1–719.
- . 1994b. Cytogenetics. Pp. 236–258, in *Biology of the Heteromyidae*. Special Publication, The 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.
- RAND, D. M. 1994. Thermal habit, metabolic rate and the evolution of mitochondrial DNA. *Trends in Ecology and Evolution*, 9:125–131.
- RIDDLE, B. R., AND R. L. HONEYCUTT. 1990. Historical biogeography in North American arid regions: an approach using mitochondrial-DNA phylogeny in grasshopper mice (genus *Onychomys*). *Evolution*, 44:1–15.
- RIDDLE, B. R., R. L. HONEYCUTT, AND P. L. LEE. 1993. Mitochondrial DNA phylogeography in northern grasshopper mice (*Onychomys leucogaster*)—the influence of Quaternary climatic oscillations on population dispersion and divergence. *Molecular Ecology*, 2:183–193.
- RUDDIMAN, W. F., W. L. PRELL, AND M. E. RAYMO. 1989. Late Cenozoic uplift in southern Asia and the American West: rationale for general circulation model experiments. *Journal of Geophysical Research*, 95 D 15, 379–18, 391.
- SAVAGE, D. E., AND D. E. RUSSELL. 1983. *Mammalian paleofaunas of the world*. Addison-Wesley, London, United Kingdom, 432 pp.
- SCHMIDLY, D. J., K. T. WILKINS, AND J. N. DERR. 1994. Biogeography. Pp. 319–356, in *Biology of the Heteromyidae*. Special Publication, The American Society of Mammalogists, 10:1–719.
- SMITH, M. F., AND J. L. PATTON. 1991. Variation in mitochondrial cytochrome *b* sequence in natural populations of South American akodontine rodents (Muridae: Sigmodontinae). *Molecular Biology and Evolution*, 8:85–103.
- STORER, J. E. 1970. New rodents and lagomorphs from the upper Miocene Wood Mountain Formation of southern Saskatchewan. *Canadian Journal of Earth Sciences*, 7:1125–1129.
- SULLIVAN, R. M., D. J. HAFNER, AND T. L. YATES. 1986. Genetics of a contact zone between two chromosomal forms of the grasshopper mouse (genus *Onychomys*): a reassessment. *Journal of Mammalogy*, 67:640–659.
- SWOFFORD, D. 1991. *PAUP: phylogenetic analysis using parsimony*. Version 3.0. Illinois Natural History Survey, Champaign, Illinois (on disk).
- VRBA, E. S. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy*, 73:1–28.
- 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, The American Society of Mammalogists, 10:1–719.
- WEBB, S. D. 1977. A history of savanna vertebrates in the New World. Part I: North America. *Annual Review of Ecology and Systematics*, 8:355–380.
- . 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, 392 pp.
- WEBB, T., III, AND P. J. BARTLEIN. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annual Review of Ecology and Systematics*, 23:141–173.
- WHISTLER, D. P. 1984. An early Hemingfordian (early Miocene) fossil vertebrate fauna from Boron, western Mojave Desert, California. Natural History Museum of Los Angeles County, *Contributions in Science*, 355:1–36.
- WILLIAMS, D. F. 1978. Karyological affinities of the species groups of silky pocket mice (Rodentia, Heteromyidae). *Journal of Mammalogy*, 59:599–612.

APPENDIX I

Specimens examined.—Each specimen is identified by species name, region (coded as in Fig. 1), and locality of occurrence, followed by LVT (Las Vegas Tissue) number. GenBank accession numbers are available. *Perognathus amplus*: AMPLUS_SON, Arizona, Pima Co., LVT403. *Perognathus apache*: APACHE_SIB.1, New Mexico, Socorro Co., LVT599; APACHE_SIB.2, Arizona, Coconino Co., LVT598; APACHE_SIB.3, Utah, Grand Co., LVT701. *Perognathus fasciatus*: FASCIATUS_NIB, Wyoming, Sweetwater Co., LVT2525. *Perognathus flavescens*: FLAVESCENS_GRP, Nebraska, Sheridan Co., LVT2527. *Perognathus flavus*: FLAVUS_SIB, Arizona, Navajo Co., LVT702; FLAVUS_CHI, Texas, Culbertson Co., LVT600. *Perognathus inornatus*: INORNATUS_SNJ, California, Madera Co., LVT601. *Perognathus longimembris*: LONGIMEMBRIS_MOJ.1, California, San Bernardino Co., LVT746; LONGIMEMBRIS_MOJ.2, Nevada, Nye Co., LVT602. *Perognathus merriami*: MERRIAMI_GCP, Texas, Val Verde Co., LVT603. *Perognathus parvus*: PARVUS_GRB.1, Idaho, Cassia Co., LVT794; PARVUS_GRB.2; Nevada, Nye Co., LVT604; PARVUS_CPL, Oregon, Crook Co., LVT1921. *Chaetodipus formosus*: FORMOSUS_MOJ, Nevada, Clark Co., LVT458. *Chaetodipus hispidus*: HISPIDUS_GRP, Texas, Wood Co., LVT605. *Chaetodipus intermedius*: INTERMEDIUS_CHI.2, New Mexico, Hidalgo Co., LVT606; INTERMEDIUS_CHI.1, New Mexico, Socorro Co., LVT607; INTERMEDIUS_SON, Mexico, Sonora, LVT608. *Chaetodipus penicillatus*: PENICILLATUS_SON.1, Arizona, Pima Co., LVT416; PENICILLATUS_MOJ, California, San Bernardino Co., LVT623; PENICILLATUS_SON.2, Mexico, Sonora, LVT609; PENICILLATUS_CHI.3, Texas, Pecos Co., LVT610; PENICILLATUS_CHI.1, Texas, Presidio Co., LVT611; PENICILLATUS_CHI.2, Texas, Presidio Co., LVT612. *Chaetodipus pernix*: PERNIX_SIN, Mexico, Sinaloa, LVT613. *Onychomys arenicola*: ARENICOLA_CHI.1, New Mexico, Eddy Co., LVT614; ARENICOLA_CHI.2, New Mexico, Sierra Co., LVT615; ARENICOLA_CHI.3, New Mexico, Socorro Co., LVT616. *Onychomys leucogaster*: LEUCOGASTER_GRP, Kansas, Morton Co., LVT617; LEUCOGASTER_GRP, Utah, Beaver Co., LVT618; LEUCOGASTER_NIB, Wyoming, Carbon Co., LVT619. *Onychomys torridus*: TORRIDUS_SON, Arizona, Yavapai Co., LVT620; TORRIDUS_MOJ.1, California, San Bernardino Co., LVT621; TORRIDUS_MOJ.2, Utah, Washington Co., LVT622.

APPENDIX II.—*Isolating events postulated in this study to be associated with the biogeographic histories of Perognathus, Chaetodipus, and Onychomys, as derived from examination of paleoecologic, geologic (references in Fig. 2), and molecular biogeographic evidence. Phylogenetic components as in Fig. 7 and isolating events as in Fig. 8.*

Event	Phylogenetic components	Age (NALMA)	Features of postulated isolation event
A	1	Clarendonian $0.8-1.2 \times 10^7$ years ago	Trans-Rocky Mountain: Basin and Range expansion; northern Great Plains and Great Basin woodland savanna floras separated by intervening deciduous hardwood and montane conifer forest in Columbia Plateaus and Rocky Mountains floristic provinces
B	2	Hemphillian-Blancan	Northern Rocky Mountain basins-Great Plains: uplifting Rockies; floristic distinction between Rocky Mountains and Great Plains provinces; central Wyoming floras include xeric and desertscrub genera, e.g., <i>Sarcobates</i> , <i>Artemisia</i> , and <i>Ephedra</i> , absent from contemporaneous and subsequent Miocene central Great Plains floras; late Miocene erosion producing the modern intermountain basins landscape in Wyoming
C	3	Blancan $2.0-5.0 \times 10^6$ years ago	Southern Rocky Mountain basins-Great Plains: uplifting Rio Grande trough and Colorado Plateau
D	4	Clarendonian	Great Basin-Madreal: uplifting Sierras; floristic distinction between the Great Basin and Madreal provinces associated with elevationally-mediated temperature regimes defining northernmost extension of semidesert scrub and subtropical thornscrub
E	5, 9	Clarendonian-Hemphillian	Mojave-Sonoran/Sinaloan-Great Plains/Mexican Plateau: uplifting Sierras and Rockies; mammalian evidence for separation of savanna and steppe biotas east and west of the Rocky Mountains by intervening desertscrub and subtropical thornscrub
F	10	Hemphillian $5.0-8.0 \times 10^6$ years ago	Sonoran desertscrub-Sinaloan thornscrub ecological divergence: uplifting Sierras; possibly ecological microvicariance prior to current north-south geographic separation of these habitats
G	6	Hemphillian-Blancan	Sonoran-Mojave: bouse embayment (marine incursion) between Sonoran and Mojave
H	12, 14	Blancan	Chihuahuan-Sonoran: uplifting southern Rockies; desertscrub development in Chihuahuan with eventual Pliocene or early Pleistocene separation of Sonoran and Chihuahuan desertscrub
I	13	Blancan-Irvingtonian	Sonoran-Mojave: late Pliocene-Pleistocene climatic cycles; lower Colorado River with riparian ecosystems
J	7	Blancan	San Joaquin-Mojave: uplifting Sierras; San Joaquin transformed from a shallow-marine embayment to a non-marine basin during the Pliocene
K	8	Hemphillian	Columbia Plateau-Great Basin: uplifting Cascades and Blue Mountains; paleoecological reconstructions suggest Pliocene date for development of appropriate habitat on Columbia Plateau, but extensive late Miocene volcanic activity may have created patches of grass-forb habitat prior to regional rainshadow effects
L	15	Blancan	Great Plains-Chihuahuan: uplifting southern Rockies; ecological separation of Great Plains grasslands from developing Chihuahuan desertscrub

APPENDIX II.—*Continued.*

Event	Phylogenetic components	Age (NALMA)	Features of postulated isolation event
M	16	Blancan-Irvingtonian	Great Plains-Gulf Coastal Plain: late Pliocene-Pleistocene climatic cycles producing intervening Gulf Coastal marine incursions southeast of the Balcones Escarpment
N	17	Blancan-Irvingtonian	Trans-Rocky Mountain: uplifting Rockies and late Pliocene-Pleistocene climatic cycles separating arid ecoregions across Rocky Mountains
O	11	Hemphillian-Blancan	Sonoran ecological divergence: possibly ecological (substrate) microvicariance within Sonoran ecoregion; <i>Chaetodipus penicillatus</i> and <i>Chaetodipus intermedius</i> broadly overlap in geographic distribution, but exhibit substrate-specific habitat partitioning; alternatively, consistent with macrogeographic Mojave-Sonoran isolation (Bouse embayment) or Chihuahuan-Sonoran isolation

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LINKED CITATIONS

- Page 2 of 4 -



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Paleobiology, Vol. 11, No. 2. (Spring, 1985), pp. 234-243.

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Journal of Mammalogy, Vol. 60, No. 1. (Feb., 1979), pp. 117-128.

Stable URL:

<http://links.jstor.org/sici?sici=0022-2372%28197902%2960%3A1%3C117%3ASADOTC%3E2.0.CO%3B2-G>

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Annals of the Missouri Botanical Garden, Vol. 74, No. 4. (1987), pp. 841-867.

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Wen-Hsiung Li; Manolo Gouy; Paul M. Sharp; Colm O'HUigin; Yau-Wen Yang

Proceedings of the National Academy of Sciences of the United States of America, Vol. 87, No. 17. (Sep., 1990), pp. 6703-6707.

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LINKED CITATIONS

- Page 3 of 4 -



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Proceedings of the National Academy of Sciences of the United States of America, Vol. 90, No. 9. (May 1, 1993), pp. 4087-4091.

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Systematic Zoology, Vol. 37, No. 4. (Dec., 1988), pp. 329-355.

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Evolution, Vol. 40, No. 1. (Jan., 1986), pp. 55-67.

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Systematic Zoology, Vol. 39, No. 3. (Sep., 1990), pp. 205-226.

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Journal of Mammalogy, Vol. 62, No. 3. (Aug., 1981), pp. 477-492.

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Brett R. Riddle; Rodney L. Honeycutt

Evolution, Vol. 44, No. 1. (Feb., 1990), pp. 1-15.

Stable URL:

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LINKED CITATIONS

- Page 4 of 4 -



Genetics of a Contact Zone between Three Chromosomal Forms of the Grasshopper Mouse (Genus *Onychomys*): A Reassessment

Robert Miles Sullivan; David J. Hafner; Terry L. Yates

Journal of Mammalogy, Vol. 67, No. 4. (Nov., 1986), pp. 640-659.

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Journal of Mammalogy, Vol. 73, No. 1. (Feb., 1992), pp. 1-28.

Stable URL:

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Annual Review of Ecology and Systematics, Vol. 8. (1977), pp. 355-380.

Stable URL:

<http://links.jstor.org/sici?sici=0066-4162%281977%298%3C355%3AAHOSVI%3E2.0.CO%3B2-U>

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Annual Review of Ecology and Systematics, Vol. 23. (1992), pp. 141-173.

Stable URL:

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Journal of Mammalogy, Vol. 59, No. 3. (Aug., 1978), pp. 599-612.

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