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Comparative Phylogeography of Baileys' Pocket Mouse (*Chaetodipus baileyi*) and the *Peromyscus eremicus* Species Group: Historical Vicariance of the Baja California Peninsular Desert

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Phylogenetic analysis of 699 bp of the mitochondrial DNA (mtDNA) COIII and 450 bp of the cytochrome *b* genes among 14 species of coarse-haired pocket mice (Heteromyidae: *Chaetodipus*) corroborated previous indications that genetic divergence between species and species groups within the genus is generally very high, suggesting old times of divergence, and that the nominal species *C. baileyi* represents a highly divergent lineage within the genus, with no closely related extant sister species. Analysis of phylogeographic structure among 51 individuals from 12 localities throughout the geographic range of *C. baileyi* revealed three geographically separate mtDNA haplotype lineages. The oldest split separates populations east and west of the Colorado River, a pattern that is congruent with chromosomal and allozyme electrophoretic evidence. We consider the western populations to represent a distinct species, *C. rudinoris.* Within *C. rudinoris,* mtDNA haplotypes are further subdivided into northern and southern lineages along the Baja California Peninsula. Comparison of phylogeographic structure in the *baileyi* species group and the codistributed *Peromyscus eremicus* species group implies two points of codivergence and thus supports two historical vicariance hypotheses proposed for biotas distributed across the peninsular and continental warm deserts: a late Neogene (3 Ma) northern extension of the Sea of Cortéz and a mid-Pleistocene (1 Ma) mid-peninsular seaway across Baja California. © 2000 Academic Press

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INTRODUCTION

The biogeography and evolution of the mammalian fauna of the Baja California Peninsula, western Mexico, has been a topic of interest to biologists since E. W. Nelson and E. A. Goldman surveyed the Peninsula on horseback for the U. S. Bureau of Biological Survey in 1905 and 1906 (Nelson, 1921). Huey (1964) provided a description of the Peninsula's mammals as of 1960, and a general description of the mammalian biogeography of the region by Orr (1960) was followed by more detailed analyses of the ecological (Lawlor, 1983a,b) and historical biogeography of the mammals of the Peninsular mainland and surrounding islands (Hafner and Riddle, 1997). In concert with these studies have been descriptions of the other terrestrial biota of the Peninsula, notably of the plants (Axelrod, 1979, 1983; Shreve, 1942; Wiggins, 1960, 1980) and herpetofauna (Grismer, 1994; Murphy, 1983a,b; Savage, 1960; Seib, 1980). Overall, the view of the Baja California Peninsular biota has shifted dramatically from that of a peripheral, depauperate subset of the Sonoran Desert (as initially described by Shreve, 1942) populated with terrestrial vertebrates that invaded the Peninsula from the north during the later Pleistocene (Orr, 1960; Savage, 1960) to a highly unique regional desert (Peninsular Desert) with an evolutionary history long distinct from that of the neighboring Sonoran Desert (Grismer, 1994; Hafner and Riddle, 1997; Murphy, 1983a,b).

Of the 97 species of native Recent mammals known from the Baja California Peninsula and surrounding islands (Hafner and Riddle, 1997; Hall, 1981; Woloszyn and Woloszyn, 1982), 14 are insular endemics and 43 others have sufficient vagility to make them less useful for detailed biogeographic analysis (26 are bats; 17 are of larger body size). Of the remaining 40 species of small, nonvolant mammals of the peninsular mainland, 11 form the core species of the Peninsular Desert fauna (Hafner and Riddle, 1997). Of those 11 species, all but 3 have distributions extending to various distances beyond the peninsula into the Mojave, Sonoran, and Chihuahuan deserts of southwestern North America. Thus, at the nominal species level, desert mammals seem to reflect the pioneering floristic analyses of Shreve (1942), who considered deserts of Baja Califor-

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nia to represent a subset of the Sonoran Desert. However, recent analyses of North American desert rodents (Lee *et al.*, 1996; Riddle, 1996; Walpole *et al.*, 1997) call into question the utility of nominal species as units of analysis for investigating North American desert biogeography, for two reasons. First, allopatric evolutionary lineages appear often to be embedded within widespread species (i.e., cryptic lineages), and second, phylogenetic analyses indicate that currently recognized species often do not reflect natural (i.e., monophyletic) clades (Riddle and Hafner, 1999; Riddle *et al.*, 2000).

A subset of five widespread species or species groups of small, terrestrial rodents are codistributed throughout the Peninsular, Mojave, and Sonoran regional deserts (circum-Gulf distributional pattern; Hafner and Riddle, 1997): *Chaetodipus baileyi, Dipodomys merriami,* the *Peromyscus eremicus* and *Neotoma lepida* species groups, and the genus *Ammospermophilus.* Their distribution makes these taxa particularly useful for assessing historical biogeographic components of faunal assembly across these regional deserts and selecting between alternative biogeographic models proposed for the region.

Biogeographic Models

Orr (1960) and Savage (1960) relied almost exclusively on late Pleistocene climatic oscillations to explain the origin and evolution of peninsular mammals and herpetofauna, respectively. Both studies predated acceptance of plate tectonics and continental drift and so were handicapped by the prevailing static view of continental configurations. Consequently, both studies emphasized the recency of invasion of desert taxa from the north, with endemic forms arising only as a result of isolation on the peninsula in Pleistocene glacial-age refugia. Such a wholesale recent invasion would result in a pattern of homogeneity or smooth clinal variation from northern, "source" populations south along the peninsula, or at most limited divergence of peninsular populations from those of adjacent regions in southern California and northeastern Baja California. More specifically, transition between peninsular and adjacent forms that diverged in Pleistocene refugia should be roughly coincident with the northern margin of the Peninsular Desert, at about 30°N latitude (Hafner, 1981; Savage, 1960).

Murphy (1983a,b), Grismer (1994), and Upton and Murphy (1997) have developed alternative, vicariance-based models underlying historical assembly of a Peninsular Desert herpetofauna. Three geomorphological events following the initial formation of the Gulf of California (=Sea of Cortéz) 5.5 Ma but predating the major climatic cycles of the Pleistocene may have been important as vicariant events in the earlier evolution of arid-adapted biota of the region. Northern extensions of the Sea of Cortéz as far north as the San Gorgonio Pass in southern California (forming the San Gorgonio Constriction) and Lake Mojave between California and Arizona (Boues Embayment) isolated the Peninsular from the Mojave and Sonoran deserts about 3 Ma. Two transpeninsular seaways divided the peninsula itself: the Isthmus of La Paz (ca. 24°N latitude) isolated the Cape Region >3 Ma (Grismer, 1994), and an hypothesized midpeninsular seaway may have flowed across the peninsula (ca. 27°30′N latitude) about 1 Ma (Upton and Murphy, 1997). A peninsular endemic lineage that resulted from these deeper-history vicariant events would have a sister taxon within continental warm desert regions, and the two lineages should approach one another near the head of the Gulf of California. If multiple peninsular lineages resulted from these deep-history events, they should be about as divergent as both are from the continental form (if separated by the Isthmus of La Paz), or significantly less divergent from each other than from the continental form (if separated by the more-recent midpeninsular seaway).

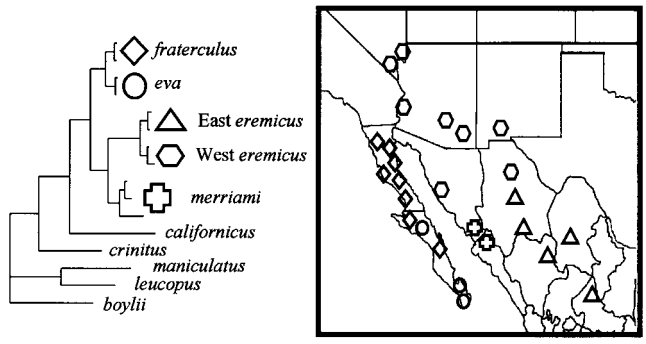

FIG. 1. Reproduced maximum-likelihood tree from Riddle *et al.* (2000) for the *Peromyscus eremicus* species group (left), and lineage distributions (right) across continental (*merriami,* West *eremicus,* and East *eremicus*) and peninsular (*fraterculus* and *eva*) deserts.

Peromyscus eremicus Species Group

Elsewhere (Riddle *et al.*, 2000), we have demonstrated that the *P. eremicus* species group is clearly divisible into a set of continental (*merriami* and *eremicus*) and peninsular (southern = *eva;* northern = *fraterculus;* Fig. 1) lineages. Moreover, we have argued that divergence of the continental and peninsular lineages is congruent with the northern extensions of the Sea of Cortéz during the Pliocene and that divergence among the peninsular forms was causally associated with the midpeninsular seaway (1 Ma) rather than the older Isthmus of La Paz. Congruent patterns among other circum-Gulf taxa would provide support for this explanation as a more general pattern of evolution among the regional biota.

Chaetodipus baileyi (Merriam, 1894)

C. baileyi is an inhabitant of desert-scrub habitats in the southwestern warm deserts (Sonoran and Penin-

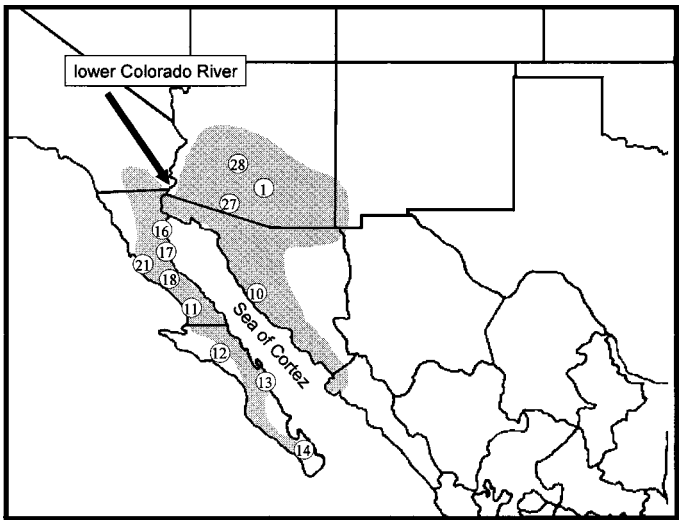

FIG. 2. Distribution of *Chaetodipus baileyi* (redrawn from Hall, 1981) and sampling localities, numbered as in Riddle *et al.* (2000).

sular), ranging into Sinaloan thorn-scrub to the south and Chihuahuan desert-scrub to the east, giving it a characteristic circum-Gulf distribution (Fig. 2). Cytogenetic and allozyme studies indicate a division into two geographic groups, divided by the Colorado River (Patton, 1972, 1977; Patton and Rogers, 1993; Patton *et al.,* 1981). No comprehensive systematic review of quantitative morphological variation within the species is available. Additionally, no robust statements of phylogenetic affinities of *baileyi* within the genus *Chaetodipus* are yet available, although it has long been considered one of three species in this genus (along with *formosus* and *hispidus*) that is somewhat intermediate morphologically between *Chaetodipus* and the silky pocket mice, genus *Perognathus* (Patton *et al.,* 1981).

The current study uses mtDNA sequence data to (1) assess phylogenetic relationships among species in *Chaetodipus,* with emphasis on the placement of *baileyi* within the genus; (2) analyze and map mtDNA phylogeographic structure within *baileyi;* (3) recommend taxonomic revisions within nominal *baileyi;* and (4) assess comparative biogeographic structure between *baileyi* and the *P. eremicus* species group, specifically addressing biogeographic history within and among peninsular and western continental regional deserts.

METHODS

Sampling Design

A total of 51 individuals of *C. baileyi* from 12 localities (Fig. 2), 1 each from 13 other nominal species in the genus *Chaetodipus,* and 1 *Dipodomys nelsoni* were included in the analysis (Appendix). Of the 15 recognized species of *Chaetodipus* (Williams *et al.,* 1993; Lee *et al.,* 1996), all were represented except *C. lineatus,* the status of which has been questioned and likely represents spineless individuals of *C. nelsoni.* 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) for analysis, and are maintained in the NMMNH permanent collections. Genomic DNA preparation, PCR amplification, and sequencing of a 699-bp portion of the mtDNA COIII gene follow methods in Riddle *et al.* (2000). The same methods were used to produce a data set from the mtDNA cytochrome *b* gene using primers MVZ05 and MVZ14 (Smith, 1998) for PCR amplification and then using 450 bp of sequence produced using primer MVZ05. GenBank accession numbers for new sequences are AY009253–AY009316 for COIII and AY009238–AY009252 for cytochrome *b.*

Analyses

Phylogeny and sequence divergence. We generated maximum-likelihood (ML), maximum-parsimony (MP), and neighbor-joining (NJ) phylogenetic hypotheses using PAUP* v. 4.0b2 (Swofford, 1999) and MEGA v. 1.01 (Kumar *et al.,* 1993). The phylogenetic position and degree of evolutionary divergence of *baileyi* within an array of 13 other species in *Chaetodipus* (*D. nelsoni* was used to root the tree) was evaluated by constructing ML and MP trees using combined COIII (699 bp) and cytochrome *b* (450 bp) sequences (1149 bp total). The most appropriate model of sequence evolution for ML analysis was chosen using the hierarchical likelihood ratio test implemented in Modeltest 3.0 (Posada and Crandall, 1998). Two character-weighting strategies were employed in MP analyses. First, all characters were weighted equally (no a priori assumptions about mutational rate heterogeneity across classes of characters), and second, because 3rd position transitions were highly saturated among species (data available upon request), these characters were eliminated in the second MP analysis. Bootstrap resampling was used to evaluate MP support for each of the nodes on the ML tree under each character-weighting strategy.

We used two criteria (MP and NJ) to provide an assessment of haplotype phylogeny among all *baileyi* COIII haplotypes (using several species of *Chaetodipus* to root the tree): the former was performed with a heuristic search (random addition sequence, 60 replications, tbr branch swapping) and the latter using the Tamura–Nei (1993) model of DNA substitution. These trees were used to map the geographic distributions of haplotypes and lineages and to select exemplar haplotypes for subsequent analyses of any alternative, phylogenetically and biogeographically plausible hypotheses.

Taxonomy and biogeography. An assessment of geographic congruence between estimates of phylogeographic population structure within *baileyi* based on karyology (Patton and Rogers, 1993), allozymes (Patton *et al.*, 1981), and mtDNA (this study) provides the basis for evaluating current species-level taxonomy under a congruence criterion (Avise and Ball, 1990). Area relationships inferred from the distribution of *baileyi* haplotypes were examined qualitatively for congruence with the *P. eremicus* species group (Fig. 1) to assess the likelihood of geographic codivergence of evolutionary lineages (i.e., common vicariance) across these taxa associated with postulated historical vicariance events.

RESULTS

Nucleotide composition of the combined COIII and cytochrome *b* genes among species of *Chaetodipus* is similar to mammalian cytochrome *b* (Irwin *et al.*, 1991) in percentages: A = 26.8, T = 33.2, C = 25.4, G = 14.6. Of 1149 characters, 472 are variable and 372 are parsimony informative. Of the latter, 298 are 3rd codon position nucleotides. At the 3rd codon position, the transition to transversion ratio ranges from 0.9 to 11.0, with a mean of 2.1, indicating a high level of saturation of transition substitutions. Haplotype diversity is high within *baileyi*—43 haplotypes were recorded among 51 individuals (Appendix), ranging in variability from 1 to 75 nucleotide differences.

Phylogenetic analysis among species. The hierarchical analysis of models of DNA substitution implemented in Modeltest 3.0 selected the general time reversible model (Yang, 1994), with a gamma distribution of rate heterogeneity among sites and assuming some sites to be invariant, as most appropriate for the combined COIII and cytochrome *b* data set among 14 species of *Chaetodipus.* Under this model, the ML tree (Fig. 3) was found through a heuristic search (random addition, one replication, tbr branch swapping: 1207 rearrangements evaluated, −lnL = 7739.54839, proportion of sites invariant = 0.52, alpha shape parameter = 1.335693). This tree depicts *baileyi, formosus,* and *hispidus* as basal lineages, with long branches between each other and relative to remaining species of *Chaetodipus.* Among-lineage rate heterogeneity is significant at the 5% level in these data when this tree is evaluated against a null hypothesis that includes a molecular clock constraint, using a likelihood ratio statistic ($\chi^2 = 52.14$, $P < 0.05$).

Several previous analyses (Patton *et al.*, 1981; Riddle, 1995) have indicated a substantial divergence between various extant species of North American pocket mice. As such, our expectation is that the more rapidly evolving portions of mtDNA protein-coding genes (e.g., 3rd position transitions) will be generally saturated among species of *Chaetodipus.* Under the MP criterion

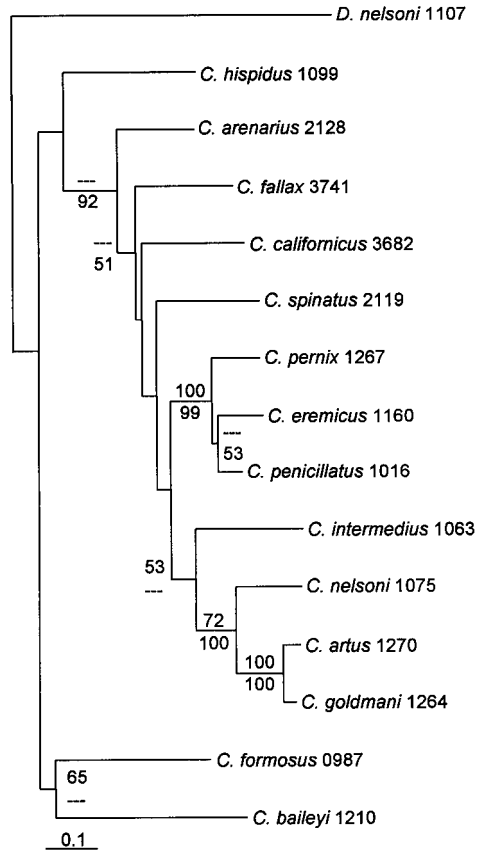

FIG. 3. Maximum-likelihood tree (see text for model parameters) among 14 species of *Chaetodipus,* with *Dipodomys nelsoni* used as an outgroup. Numbers at nodes summarize support for a particular clade from 1000 maximum-parsimony bootstrap replications (top, all characters weighted equally; bottom, 3rd position transitions removed).

(heuristic search, random addition sequence, 40 replications, tbr branch swapping), three trees were generated with all characters weighted equally (parsimony informative characters = 387, length = 1701, CI = 0.39, RI = 0.36); one tree resulted when 3rd position transitions were removed (parsimony informative characters = 358, length = 755, CI = 0.39, RI = 0.45). Bootstrap values from these trees provided high support for several nodes on the ML tree (Fig. 4). Under equal weighting, these include one clade comprising the species *eremicus, pernix,* and *penicillatus* and another clade comprising *nelsoni, artus,* and *goldmani* (with high support for *artus* and *goldmani* as a clade). When 3rd position transitions are removed, support is high for those clades, as well as for one including all species except *baileyi, hispidus,* and *formosus.* In all three MP trees, *baileyi, hispidus,* and *formosus* are basal clades within *Chaetodipus.*

Phylogenetic analysis within baileyi. Both MP (all characters weighted equally, search options as described above) and NJ (Tamura–Nei model of DNA

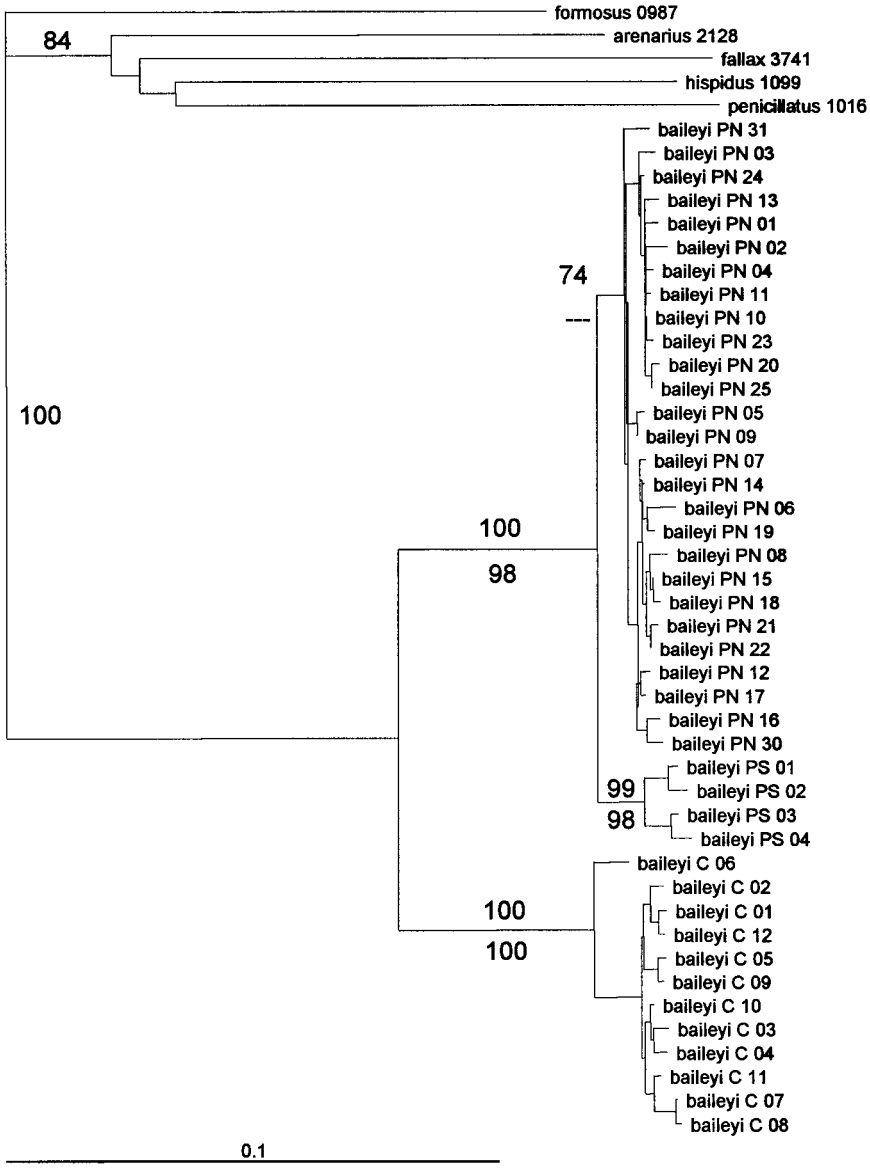

FIG. 4. Neighbor-joining tree of corrected (Tamura and Nei, 1993) estimates of sequence divergence among 43 variable haplotypes from *C. baileyi*, with five species of *Chaetodipus* used as outgroups. Numbers along branches summarize results of 1000 bootstrap replications. Haplotypes of *C. baileyi* are identified as members of a Continental (C), Peninsular North (PN), or Peninsular South (PS) lineage (mapped in Fig. 5).

substitution) analyses produced similar depictions of COIII haplotype phylogeny within *baileyi* (Fig. 4): three distinct lineages are apparent, two of which form a sister group relative to the third. Mapping all variable haplotypes within *baileyi* (Fig. 5) demonstrates an unambiguous geographic separation of individuals into separate northern peninsular, southern peninsular, and continental lineages. We refer to these lineages as Peninsular North, Peninsular South, and Continental and designate haplotypes as PN, PS, and C.

The continental lineage is appreciably more divergent from peninsular lineages (Table 1; mean Tamura–Nei sequence divergence (s.d.) = 10.5%) than the latter are from each other (mean s.d. = 2.7%). Sequence divergence between the two peninsular lineages is greater than divergence within either lineage (Peninsular North: mean = 0.9%, maximum = 1.8%; Peninsular South: mean = 1.3%, maximum = 1.8%). Of interest is whether Peninsular North and Peninsular South form significantly reciprocally monophyletic clades, given the lack of bootstrap support in the MP analysis for a monophyletic Peninsular North lineage (Fig. 5). In fact, it is possible to construct a number of alternative trees in which the Peninsular South clade is placed inside the Peninsular North clade that do not differ significantly from the MP trees (assessed using

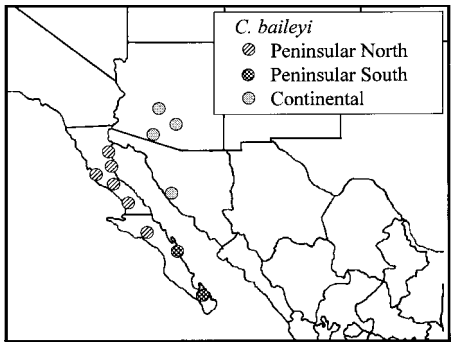

FIG. 5. Summarized distributions among sampling localities (Fig. 2) of 43 haplotypes within three haplotype lineages (from Fig. 4) of *C. baileyi.*

the Templeton test). However, if monophyly of the Peninsular South clade is eroded by putting any of the PS haplotypes as sister clades to Peninsular North, these trees do differ significantly ($P < 0.05$). Therefore, we find robust support for a monophyletic Peninsular South clade, but suggest that Peninsular North is either monophyletic or paraphyletic relative to Peninsular South.

DISCUSSION

How Many Species within Nominal baileyi?

Patton and Rogers (1993) recognized two groups of populations within *C. baileyi* based on karyotypic variability. Populations that occur east of the Colorado River generally possess supernumerary (or "B") chromosomes, whereas those from west of the river, including those sampled from the northern Baja California Peninsula, lack B chromosomes. Allozyme biochemical polymorphism (Patton *et al.,* 1981) likewise indicates appreciable divergence of populations into eastern and western groups, again separated by the Colorado River and Sea of Cortéz. This major distinction is reflected in current intraspecific taxonomy (Hall, 1981) only as the border between three eastern subspecies (*baileyi, domensis,* and *insularis* of Isla Tiburón) and five western subspecies (*extimus, hueyi, mesidios, rudinoris,* and *fornicatus* of Isla Monserrate).

Our analysis of mtDNA phylogeography within *baileyi* provides clear evidence for highly differentiated, reciprocally monophyletic gene lineages. Whereas evidence of multiple mtDNA gene lineages does not necessarily provide a sufficient basis for recognition of multiple species, the concordance of patterns of divergence across multiple, independently evolving characters can be interpreted as providing such evidence (Avise and Ball, 1990) because of the likelihood that such concordance has arisen from long-term absence of gene flow between divergent populations. A character concordance criterion provides even stronger evidence for separate species when available evidence suggests the absence of substantial introgression across a secondary contact zone, as is likely present in the vicinity of the present day lower Colorado River. Although no individuals used in this study were assayed for karyotype, allozyme, or morphological variation, we argue that known phylogeographic variation for those three sets of characters is congruent with separation of populations into western (Peninsular North and Peninsular South) vs eastern (Continental) lineages. Neither karyotypic (Patton and Rogers, 1993) nor allozymic (Patton *et al.,* 1981) variation has been sampled from populations within the range of the Peninsular South lineage.

Available evidence strongly indicates a long history of isolation and divergence of populations east and west of the current Colorado River, worthy of formal taxonomic recognition. We propose that populations of *C. baileyi* that occur west of the Colorado River and south throughout the Peninsular Desert of Baja California be recognized as a distinct species.

Chaetodipus rudinoris *(Elliot 1903)*

Perognathus baileyi rudinoris Elliot, 1903, *Field Columb. Mus. Publ. 74 Zool. Ser.* **3(10):** 167. Type locality "San Quintín, Baja California."

Perognathus knekus Elliot, 1903, *Field Columb. Mus. Publ. 74 Zool. Ser.* **3(10):** 169. Type locality "Rosarito, Sierra San Pedro Mártir, Baja California."

TABLE 1

Estimates of Divergence (above Diagonal) and Standard Errors (below Diagonal) among Haplotypes from the *Chaetodipus baileyi* Species Group, Using the Tamura–Nei (1993) Model of Sequence Evolution

	PN 14	PS 01	PS 03	PN 25	C 06	C 12
rudinoris PN 14	0	0.024	0.024	0.007	0.096	0.107
rudinoris PS 01	0.006	0	0.015	0.031	0.105	0.112
rudinoris PS 03	0.006	0.005	0	0.028	0.106	0.113
rudinoris PN 25	0.003	0.007	0.007	0	0.095	0.105
baileyi C 06	0.013	0.013	0.013	0.012	0	0.021
baileyi C 12	0.013	0.014	0.014	0.013	0.006	0

Perognathus baileyi hueyi Nelson and Goldman, 1929, *Proc. Biol. Soc. Washington* **42:** 106. Type locality "San Felipe, northeastern Baja California."

Perognathus baileyi extimus Nelson and Goldman, 1930, *J. Washington Acad. Sci.* **20:** 223. Type locality "Tres Pachitas, 700 ft., 36 mi. S La Paz, Baja California [Sur]."

Perognathus baileyi fornicatus Burt, 1932, *Trans. San Diego Soc. Nat. Hist.* **7(16):** 164. Type locality "Monserrate Island (lat. 25°38′N, long. 111°02′W), Gulf of California, Baja California [Sur]."

Perognathus baileyi mesidios Huey, 1964, *Trans. San Diego Soc. Nat. Hist.* **13(7):** 112. Type locality "San Borja Mission (ca. lat. 28°45′N), Baja California."

Distribution. West of the Colorado River in southern California to Banner, San Diego Co., south throughout Baja California and Baja California Sur to 30 km N Todos Santos. Island populations occur on Isla Smith (Lawlor, 1971; included by Hall, 1981, in the Peninsular mainland subspecies, *C. r. mesidios*) and Isla Monserrate (*C. r. fornicatus*). Pending detailed assessment of geographical variation within *C. rudinoris,* we provisionally retain recognition of five subspecies (as indicated by Hall, 1981, except restricting *C. r. hueyi* to west of the Colorado River): *extimus, fornicatus, hueyi, mesidios,* and *rudinoris.*

Remarks. It is likely that additional collecting will reveal a somewhat broader distribution of *C. rudinoris* across the Baja California Peninsula. In this report, we include two localities (10 km SW Loreto, 420 ft.; and 30 km N Todos Santos, 650 ft.) that increase the reported distribution of the species in Baja California Sur. The Peninsular North lineage includes the subspecies *hueyi, rudinoris,* and *mesidios;* the Peninsular South lineage includes the subspecies *extimus* and probably the insular subspecies, *fornicatus.* No samples from either *C. r. rudinoris* or *C. r. fornicatus* were included in the mtDNA analysis.

Evolution of the baileyi Species Group

The *baileyi* species group (including *C. baileyi* and *C. rudinoris*) represents an ancient and relatively poorly diversified lineage within the endemic western North American radiation of extant species of chaetodipine pocket mice. Along with *formosus* and *hispidus,* the *baileyi* species group appears to have diverged well before the subsequent proliferation of remaining species in this diverse genus. Fossils are currently uninformative regarding estimated time of origination of this genus (Wahlert, 1993) because paleontologists have not diagnosed pocket mice into two separate genera (*Perognathus* and *Chaetodipus*), which are now known to represent highly divergent lineages in the family Heteromyidae. However, fossils identified as *Perognathus,* some of which may represent *Chaetodipus,* are known as early as the Hemingfordian North American Land Mammal Age (NALMA), about 20 Ma (Korth and Reynolds, 1991). In further support for an early Miocene origination of the genus, *Cupidinimus,* a basal member of the subfamily Dipodomyinae (including *Dipodomys*) also has a fossil record extending to about 20 Ma (Wahlert, 1993). Whereas we would hesitate to attempt a precise estimate of divergence time for *baileyi* due to significant rate heterogeneity among species of *Chaetodipus* and absence of better fossil-based calibration points, we submit that the *baileyi* species group most likely split from other lineages (assuming a dipodomyine vs perognathine divergence about 20 Ma) during the middle Neogene (16–5.5 Ma).

A middle Neogene time frame for the origin of the *baileyi* species group is supported by biogeographically based explanations for the near-simultaneous divergence of *hispidus, formosus,* and the ancestor of the *baileyi* species group (Fig. 3). *Chaetodipus hispidus* (proposed as a distinct subgenus, *Burtognathus,* by Hoffmeister, 1986) is an inhabitant of arid grassland and semidesert habitats east of the Rocky Mountains and Sierra Madre Occidental, and *formosus* inhabits desert-scrub habitats in the Mojave Desert, northward into the Great Basin, and southward into Baja California. During the middle Neogene, diversity and provinciality of arid land mammalian faunas in western North America increased in association with uplifting interior mountain ranges and expansion of the Basin and Range geomorphological province (Barnosky, 1986; Riddle, 1995; Webb, 1983). Heteromyid rodents reached their greatest diversity of the Tertiary, and perognathines became the dominant subfamily (Korth, 1994). Initial diversification in *Chaetodipus* could have coincided with a middle Miocene separation of ancestral arid land biotas into at least three provinces: eastern grasslands and savannas (*hispidus*), semideserts and woodlands in the Basin and Range (*formosus*), and semideserts and subtropical thorn-scrub in western Mexico (ancestor of the *baileyi* species group; ancestor of remaining extant species of *Chaetodipus*). As additional support for the general timing of events proposed here, we note that the suggestion of an explosive initial diversification of a cluster of eight lineages in *Chaetodipus* (Fig. 3) is consistent with a middle to late Neogene transformation of landscapes from relatively humid woodland savannas and subtropical thorn forests to more arid desert-scrub and desert grassland habitats. This transformation is evidenced in the paleomammalogical record, which indicates the demise of the savanna-adapted Clarendonian chronofauna and the proliferation of arid and semiarid rodents in western North America (Webb, 1983), and in the paleobotanical record, which indicates the development of regional deserts (Axelrod, 1979).

TABLE 2

Estimates of Divergence (above Diagonal) and Standard Errors (below Diagonal) among Haplotypes from the *Peromyscus eremicus* Species Group, Using the Tamura–Nei (1993) Model of Sequence Evolution

	M 07	M 04	M 02	W 17	W 13	E 07	E 01	F 08	F 04	V 06	V 02
merriami M 07	0	0.015	0.055	0.095	0.087	0.085	0.083	0.078	0.083	0.087	0.087
merriami M 04	0.005	0	0.048	0.087	0.079	0.081	0.077	0.076	0.076	0.079	0.079
merriami M 02	0.010	0.009	0	0.118	0.110	0.104	0.096	0.094	0.094	0.096	0.092
eremicus W 17	0.013	0.013	0.016	0	0.015	0.039	0.042	0.113	0.113	0.117	0.125
eremicus W 13	0.013	0.012	0.015	0.005	0	0.030	0.033	0.103	0.102	0.110	0.114
eremicus E 07	0.012	0.012	0.014	0.008	0.007	0	0.009	0.106	0.106	0.110	0.113
eremicus E 01	0.012	0.012	0.014	0.008	0.007	0.004	0	0.105	0.105	0.110	0.114
fraterculus F 08	0.012	0.012	0.013	0.015	0.014	0.014	0.014	0	0.006	0.034	0.034
fraterculus F 04	0.012	0.012	0.013	0.015	0.014	0.014	0.014	0.003	0	0.037	0.037
eva V 06	0.013	0.012	0.014	0.015	0.015	0.015	0.015	0.007	0.008	0	0.009
eva V 02	0.013	0.012	0.013	0.016	0.016	0.015	0.016	0.007	0.008	0.004	0

Note. See Riddle *et al.* (2000) for haplotype data.

Comparative Phylogeography

Peninsula vs continent. Although the *baileyi* species group appears to have had ancient origins in the evolutionary history of *Chaetodipus*, the development of three geographically discrete lineages within *C. baileyi* is a much more recent event (Fig. 5). The *baileyi* species group appears to provide a second mammalian example (along with the *P. eremicus* species group; Riddle *et al.*, 2000) of the "northern Pliocene vicariant complex" that Grismer (1994) proposed as a generalized pattern for at least 10 reptilian taxa. Both of these rodent species groups have circum-Gulf distributions, although the *eremicus* species group also has a distribution (and additional lineage divergence) extending throughout the Chihuahuan Desert. Average sequence divergence between *C. baileyi* and *C. rudinoris* is 10.5% (Table 1), and that of *P. eremicus* + *merriami* and *P. fraterculus* is 10.0% (Table 2). Although we think it likely that rates of evolution in mtDNA genes differ between muroid (including *Peromyscus*) and geomyoid (including *Chaetodipus*) rodents (Spradling *et al.*, 2000), the magnitude of such rate heterogeneity is currently unknown. Levels of sequence divergence between peninsular and continental lineages are very similar for both species groups and are consistent with a late Neogene or early Pleistocene codivergence of ancestrally widespread lineages into two geographically separated populations (Fig. 6). Additional support for a peninsular vs continental codivergence hypothesis can be inferred from the observation that these species groups demonstrate parallel patterns of divergence between northern and southern peninsular lineages at similar levels of sequence divergence (see below). Therefore, to reject a codivergence hypothesis,

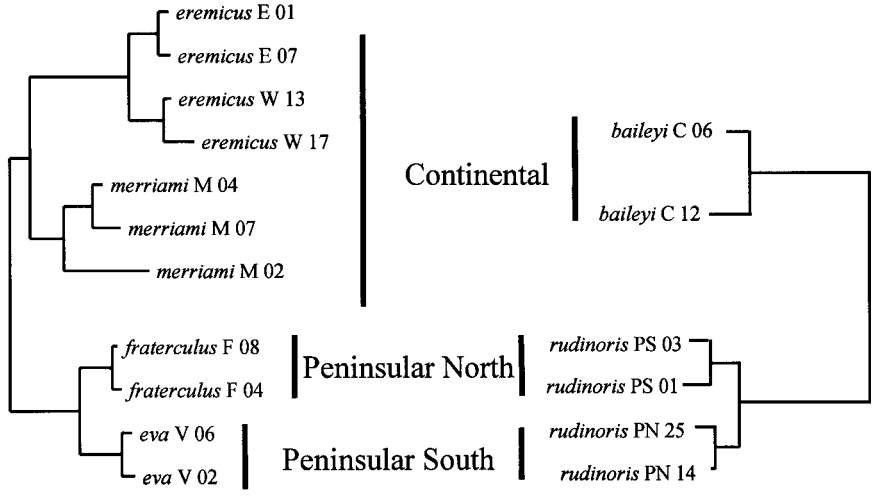

FIG. 6. Neighbor-joining trees of corrected (Tamura–Nei, 1993) estimates of sequence divergence for the *Peromyscus eremicus* species group (left tree) and *Chaetodipus baileyi* species group (right tree), depicting points of postulated historical codivergence across three codistributed lineages within each species group.

one would need to account for two independent points of spatial congruence in lineage distribution and divergence among species groups.

Colorado River vs Sea of Cortéz. Grinnell (1914), describing the effectiveness of the Colorado River as a barrier to the dispersal of desert mammals, felt that the Colorado presented an absolute barrier to eight species: *Peromyscus crinitus, Thomomys chrysonotus, T. riparius, Ammospermophilus harrisii, A. leucurus, Perognathus* (=*Chaetodipus*) *intermedius, P.* (=*C.*) *formosus,* and *P.* (=*C.*) *spinatus.* Subsequently, *P. crinitus* was found on both sides of the river (Hall and Kelson, 1959), and the *Thomomys* (synonymized under *T. bottae*) have been shown to share high genetic similarity (Smith and Patton, 1980). Hafner (1981) demonstrated greater morphological overlap between *A. harrisii* and *A. leucurus* immediately adjacent to the Colorado River than between subspecies of *A. leucurus* in northern Baja California, indicating the possibility of introgressive hybridization between these two nominal species across the river. Thus, of the eight original species listed by Grinnell (1914), coincidences of the distributional limits of only the three species of *Chaetodipus* and the river have not been questioned. Contact between *P. eremicus* (continental form) and the newly named peninsular species, *P. fraterculus* (Riddle *et al.,* 2000) occurs west of the Colorado River, based on morphological comparisons (Legg, 1978). Based on the distributional pattern of B chromosomes and allozyme complements, *C. baileyi* and its peninsular sister taxon, *C. rudinoris,* occupy opposite banks of the Colorado River. Additionally, Lee *et al.* (1996) provided preliminary evidence for divergent mtDNA haplotype lineages east and west of the Colorado River in *C. penicillatus.* Thus, the Colorado River as it currently exists may be an important barrier to dispersal in *Chaetodipus,* whereas northern extensions of the Sea of Cortéz during the Pliocene were more general vicariant mechanisms responsible for isolation of peninsular from continental lineages. Alternatively, different locations for contact between peninsular and continental lineages may accurately reflect differential reaction to the two northern extensions of the Gulf: the San Gorgonio extension along present-day Salton Sea and the Boues Embayment of the Colorado River. It is interesting to note that both the Colorado River and the earlier northern extensions of the Gulf appear to have played a role in divergence and current distributions of the three species of woodrats formerly included within *Neotoma lepida.* Mascarello (1978) indicated the existence of the three forms based on a wide variety of characters, noting that populations west of the Salton Sea and south throughout the Baja California Peninsula appeared distinct, and recommended recognition of *N. devia* to represent populations east of the Colorado River. Planz (1992) has proposed recognition of the Peninsular form as *N. intermedia;* populations between the Salton Sea and the Colorado River remain as *N. lepida.*

Northern vs Southern Peninsula. Both the *C. baileyi* species group and the *P. eremicus* species group exhibit separate northern and southern lineages on the Baja California Peninsula (Fig. 6). Levels of divergence between the lineages within each species group are of a similar magnitude (2.7% s.d. between the two lineages of *C. rudinoris,* Table 1; 3.6% s.d. between *P. fraterculus* and *P. eva,* Table 2). These levels of divergence are about one third those between peninsular and continental lineages in each species group. If isolation of the latter sets of populations occurred during a late Neogene to early Pleistocene time frame, then separation of southern and northern peninsular lineages is consistent with models of peninsular vicariance within a mid- or late-Pleistocene time frame. We suggest therefore that these data are not consistent with a Pliocene isolation of the Cape Region through inundation of the Isthmus of La Paz (Grismer, 1994). Alternatively, the geographically coincident separation of at least three (the two mammals discussed here and the lizard genus *Uta*) and perhaps many more terrestrial vertebrates including the reptilian genera *Sauromalus* (Petren and Case, 1997), *Urosaurus* (Aquirre *et al.,* 1999), and *Pituophis* (Rodríguez-Robles and De Jesús-Escobar, 2000) and the bird genus *Toxostoma* (Zink *et al.,* 1997), supports the mid-Pleistocene midpeninsular seaway model of vicariance (Upton and Murphy, 1997).

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APPENDIX

Scientific names	Country	State	County	Locality	LVT number	Haplotype number	Locality number
Chaetodipus baileyi	USA	Arizona	Pinal	Picacho State Park	LVT-0336	C 01	1
Chaetodipus baileyi	USA	Arizona	Pima	0.5 mi N Organ Pipe Cactus N.M. off Hwy 85	LVT-0402	C 02	27
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1207	C 03	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1208	C 04	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1209	C 05	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1210	C 06	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1211	C 07	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1212	C 08	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1213	C 09	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1214	C 10	10
Chaetodipus baileyi	MX	Sonora		2 km N Puerto de la Libertad	LVT-1215	C 11	10
Chaetodipus baileyi	USA	Arizona	Maricopa	2.5 mi E Morristown	LVT-1915	C 12	28
Chaetodipus baileyi	MX	Baja California Sur		10 km SW Loreto	LVT-3594	PS 01	13
Chaetodipus baileyi	MX	Baja California Sur		10 km SW Loreto	LVT-3598	PS 02	13
Chaetodipus baileyi	MX	Baja California Sur		30 km N Todos Santos	LVT-3606	PS 03	14
Chaetodipus baileyi	MX	Baja California Sur		30 km N Todos Santos	LVT-3623	PS 03	14
Chaetodipus baileyi	MX	Baja California Sur		30 km N Todos Santos	LVT-3624	PS 04	14
Chaetodipus baileyi	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2109	PN 01	16
Chaetodipus baileyi	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2114	PN 02	16
Chaetodipus baileyi	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2122	PN 03	16
Chaetodipus baileyi	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2123	PN 04	16
Chaetodipus baileyi	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2124	PN 05	16
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2138	PN 06	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2139	PN 07	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2140	PN 07	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2141	PN 08	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2142	PN 09	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2152	PN 10	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2155	PN 11	17
Chaetodipus baileyi	MX	Baja California		18 mi S Puertecitos, Agua Dulce	LVT-2156	PN 12	17
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-2209	PN 13	11
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3577	PN 14	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3578	PN 15	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3579	PN 16	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3580	PN 17	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3581	PN 15	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3587	PN 18	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3588	PN 15	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3589	PN 19	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3590	PN 20	12
Chaetodipus baileyi	MX	Baja California Sur		20 mi W San Ignacio	LVT-3591	PN 07	12
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-3652	PN 14	11
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-3653	PN 21	11
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-3654	PN 22	11
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-3671	PN 23	11
Chaetodipus baileyi	MX	Baja California		27 km S Punta Prieta	LVT-3672	PN 24	11
Chaetodipus baileyi	MX	Baja California		1 km W Cataviña	LVT-3723	PN 25	18
Chaetodipus baileyi	MX	Baja California		Misión San Fernando	LVT-3729	PN 25	21
Chaetodipus baileyi	MX	Baja California		Misión San Fernando	LVT-3730	PN 30	21
Chaetodipus baileyi	MX	Baja California		Misión San Fernando	LVT-3731	PN 31	21
Chaetodipus baileyi	MX	Baja California		Misión San Fernando	LVT-3743	PN 07	21
Chaetodipus arenarius	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2128		
Chaetodipus artus	MX	Sinaloa		Presa Hidalgo, 10 km NE El Fuerte	LVT-1270		
Chaetodipus californicus	MX	Baja California		2 mi SW Laguna Hanson	LVT-3682		
Chaetodipus eremicus	MX	Coahuila		1 mi SE Hundido	LVT-1160		
Chaetodipus fallax	MX	Baja California		Misión San Fernando	LVT-3741		
Chaetodipus formosus	USA	California	Riverside	9 mi W, 1 mi S Quien Sabe Point	LVT-0987		
Chaetodipus goldmani	MX	Sonora		4 km N Navojoa	LVT-1264		
Chaetodipus hispidus	MX	Durango		7 mi NNW La Zarca	LVT-1099		
Chaetodipus intermedius	MX	Chihuahua		5 km NNW Chihuahua	LVT-1063		
Chaetodipus nelsoni	MX	Chihuahua		3 mi NE Parral	LVT-1075		
Chaetodipus penicillatus	USA	California	Imperial	1.5 mi S, 6.5 mi W Glamis	LVT-1016		

APPENDIX—*Continued*

Scientific names	Country	State	County	Locality	LVT number	Haplotype number	Locality number
Chaetodipus pernix	MX	Sonora		4 km N Navojoa	LVT-1267		
Chaetodipus spinatus	MX	Baja California		7 mi S, 7 mi E San Felipe	LVT-2119		
Dipodomys nelsoni	MX	Durango		7 mi NNW La Zarca	LVT-1105		

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