SPECIATION IN THE DESERT POCKET MOUSE (*CHAETODIPUS PENICILLATUS* WOODHOUSE)

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Variation in mitochondrial DNA was studied across the range of *Chaetodipus penicillatus.* Sequence data from the COIII gene and restriction-enzyme analysis of a 2,150 base pair fragment indicated a significant genetic demarcation between samples assigned to *C. p. pricei* and those assigned to *C. p. eremicus.* Sequence and restriction data also show that populations assigned to *C. p. eremicus* share a common history not shared by populations assigned to *C. p. pricei.* These data are concordant with independent evidence from nuclear data of divergence among populations of *C. penicillatus* at protein and chromosomal levels. Furthermore, the overall pattern of phylogeographic population structure in *C. penicillatus* is consistent with an hypothesis of long-term isolation and divergence of Chihuahuan and Sonoran desertscrub biotas. We recommend that *C. p. eremicus* be recognized as a distinct species. The appropriate binomial for populations thus far examined from the Chihuahuan Desert is *Chaetodipus eremicus.*

Key words: *Chaetodipus penicillatus eremicus,* mtDNA variation, phylogenetic species, phylogeography

Pocket mice of the genera *Perognathus* and *Chaetodipus* present a number of previously intractable systematic problems (Patton and Rogers, 1992*a,* 1992*b*) due to at least two features of their evolutionary history: that extant nominate species characteristically are separated from one another by large amounts of genetic divergence (Patton et al., 1981); that external morphological evolution has been highly conservative in these genera. Both of these features also may contribute to errors in our understanding of the extent to which geographically widespread nominate species may comprise a set of distinct evolutionary lineages, i.e., distinct phylogenetic (Cracraft, 1989) or evolutionary (Wiley, 1981) species.

The desert pocket mouse, *Chaetodipus penicillatus,* is widespread in warm desertscrub habitats throughout the Chihuahuan, Sonoran, and Mojave deserts in western North America. In a study on systematics of chaetodipine pocket mice based on chromosomal and allozymic data, Patton et al. (1981) postulated that *C. penicillatus* comprised several cryptic species. Patton (1970) described three main cytotypes within *C. penicillatus,* all with 2n = 46, but FN = 48, 54, or 56. This study concentrates mainly on differences between cytotypes with FN = 48 and 56, which correspond to *C. p. pricei* (plus *C. p. penicillatus*) and *C. p. eremicus,* respectively, although the FN = 54 cytotype also is represented. Patton et al. (1981) demonstrated a large nuclear genetic divergence between chromosome race B representing Chihuahuan Desert populations (i.e., *C. p. eremicus*), and chromosome races A and C representing Sonoran and Mojave desert populations (i.e., *C. p. pricei, C. p. penicillatus,* and *C. p. angustirostris*). That study reported one fixed difference at the 6PGD allozymic locus that was geographically concordant with chromosome races A and B. However, these au-

thors did not formally recognize a new species within *C. penicillatus* because of small samples. The purposes of our study were to characterize the magnitude and geographic structure of variation in mitochondrial DNA (mtDNA) within *C. penicillatus,* to assess patterns of congruence among mtDNA data and previous studies of nuclear genomic, chromosomal, and morphological variation as a basis for understanding the pattern of phylogeographic population structure within *C. penicillatus,* and to use those data to understand major patterns of speciation within *C. penicillatus.*

Materials and Methods

Individuals examined for variation in mtDNA were drawn from populations representing four subspecies of *C. penicillatus* (Table 1) previously supported as distinct from one another based on morphological (Hoffmeister and Lee, 1967), chromosomal (Patton, 1970), and nuclear genomic (Patton et al., 1981) evidence. Our sampling design allows representation of the fundamental races of the desert pocket mouse that have been postulated based on chromosomal and nuclear-genomic data. Additionally, to assess the degree of congruence among all available datasets across a zone of contact between two previously postulated cryptic species (chromosome races A and B), we have obtained most of our samples from populations within the ranges of *C. p. pricei* and *C. p. eremicus,* which come into contact with one another in southwestern New Mexico.

Restriction-enzyme analysis was conducted on DNA samples of 44 *C. penicillatus* from 12 localities (Table 1). Total genomic DNA was isolated according to the protocol of Hillis et al. (1990). Using the polymerase chain reaction (PCR), primers within the met-tRNA (transfer RNA) and cytochrome-oxidase subunit I (COI) gene were used to amplify a mtDNA fragment of ca. 2,150 bp (base pairs) that includes the NADH subunit 2 gene, five intervening tRNAs, and 705 bp of the COI gene ND2-CO1 (Mullis and Faloona, 1987). Primer sequences have been published elsewhere (Lee et al., 1994). The amplified fragment was digested with the following restriction enzymes according to manufacturers' protocols: *Aci* I; *Bsp* 1286; *Bst*U I; *Dde* I; *Hae* III; *Hha* I; *Hinc* II; *Hinf* I; *Mbo* I; *Msp* I; *Rsa* I; *Sau*96 I; *Taq* I.

Due to relatively low overall sequence divergence among individuals examined in this study, we could infer single restriction-site differences among pairs of haplotypes through direct examination of fragment patterns (Dowling et al., 1990). Data were treated as restriction sites and coded as present, absent, or missing. The composite matrix of restriction-site variation among haplotypes was used to calculate estimates of sequence divergence among each pair of different haplotypes using the method of Jukes and Cantor (1969) as implemented in RESTSITE 1.2 (Miller, 1991), with standard errors obtained through a jackknife approach. In a separate analysis, discrete character-state changes were used to construct a network of site gains and losses.

Nine individuals of *C. penicillatus,* representative of haplotypes identified in the restriction-site analysis, and two individuals of *C. intermedius* (the sister taxon of *C. penicillatus*—Riddle, 1995) were further analyzed for nucleotide-sequence variation in 387 bp of the mtDNA cytochrome oxidase subunit III (COIII) gene. Methods and primers have been reported elsewhere (Riddle, 1995). Sequence-divergence values were calculated using the DNADIST algorithm in the Phylogeny Inference Package (PHYLIP 3.5—Felsenstein, 1993). Sequence character-state data (A, C, G, T, or missing) were analyzed in a maximum-parsimony framework using the bootstrap branch-and-bound algorithm in PAUP 3.0 (Phylogenetic analysis using parsimony—Swofford, 1993).

Specimens examined.—Voucher specimens are deposited at the University of Nevada–Las Vegas and in the Natural History Collection, Angelo State University. Sample sizes followed by GenBank accession number if a sequence is available are in parentheses: *Chaetodipus penicillatus* sample 1 (1; U-21630)—30 miles E Barstow, San Bernardino Co., California; sample 2 (3; U-21626)—27 miles NW Puerto Penasco, Sonora, Mexico; sample 3 (3)—5 miles NW San Carlos, Sonora, Mexico; sample 4 (3)—Organ Pipe National Cactus Monument headquarters, Pima Co., Arizona; sample 5 (15; U-21625)—0.5 mile N Organ Pipe National Cactus Monument, Pima Co., Arizona; sample 6 (2)—Picacho Peak State Park, Pinal Co., Arizona; sample 7 (2)—1 mile E Granite Gap on New Mexico 80, Hidalgo Co., New Mexico; sample 8 (2)—Animas Mountains, Red Hill, Hidalgo Co., New Mexico; sample 9 (1)—14 miles S Road Forks,

TABLE 1.—*Restriction-site haplotype data for* Chaetodipus penicillatus. *Subspecies designations follow Hoffmeister and Lee (1967). Asterisks in last column denote postulated composite haplotypes for specimens with some missing data.*

Specimen number	Locality	Sample number	Subspecies	Restriction endonuclease haplotypes[1]													Composite haplotype
9263	MX Sonora	2	pricei	A	A	A	A	A	A	C	A	A	A	A	A	A	1
9267	MX Sonora	2	pricei	A	A	A	A	A	A	C	A	A	A	A	A	A	1
9277	MX Sonora	2	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
11054	MX Sonora	3	pricei	A	A	A	A	A	A	C	A	A	A	A	A	A	1
11056	MX Sonora	3	pricei	A	A	A	A	A	A	C	A	A	A	A	A	A	1
11057	MX Sonora	3	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
392	AZ Pima	4	pricei	A	A	A	A	A	A	A	?	A	C	A	A	A	2*
393	AZ Pima	4	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
396	AZ Pima	4	pricei	B	A	A	A	A	A	A	A	A	C	A	A	A	3
411	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
412	AZ Pima	5	pricei	A	A	A	A	A	A	A	D	A	C	A	A	A	4
414	AZ Pima	5	pricei	B	A	A	A	A	A	A	A	A	C	A	A	A	3
415	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
416	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
413	AZ Pima	5	pricei	A	A	A	B	A	A	A	A	A	C	A	A	A	5
417	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
418	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
419	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
422	AZ Pima	5	pricei	A	A	A	A	A	A	A	B	A	C	A	A	A	6
421	AZ Pima	5	pricei	A	A	A	B	A	A	A	A	A	C	A	A	A	5
420	AZ Pima	5	pricei	A	A	A	A	A	A	A	B	A	C	A	A	A	2
424	AZ Pima	5	pricei	A	B	A	A	A	A	A	A	A	C	A	A	A	7
425	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
423	AZ Pima	5	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
328	AZ Pinal	6	penicillatus	A	B	A	A	A	A	A	A	A	C	A	A	A	7
329	AZ Pinal	6	penicillatus	B	A	A	A	A	A	A	A	A	C	A	A	A	3
922	CA San Bernardino	1	angustirostris	A	A	A	A	A	A	A	?	A	A	A	A	A	8*
387	NM Hidalgo	7	pricei	A	A	A	A	A	A	A	?	A	A	A	A	A	8*
388	NM Hidalgo	7	pricei	A	A	A	A	A	A	A	A	A	C	A	A	A	2
1033	NM Hidalgo	9	pricei	A	A	A	A	A	A	A	?	A	A	A	A	A	8*
3614	NM Hidalgo	8	pricei	?	A	A	?	A	A	?	A	A	A	A	?	A	8*

TABLE 1.—*Continued.*

Specimen number	Locality	Sample number	Subspecies	Restriction endonuclease haplotypes[1]													Composite haplotype
3615	NM Hidalgo	8	pricei	A	A	A	A	A	A	A	A	A	A	A	A	A	8
10363	TX Culberson	10	eremicus	C	C	A	C	B	B	B	C	C	B	A	C	A	9
10364	TX Culberson	10	eremicus	C	C	A	C	B	B	B	C	C	B	A	C	A	9
1065	TX Pecos	12	eremicus	C	C	A	D	B	B	B	C	C	B	A	C	A	10
1066	TX Pecos	12	eremicus	C	C	A	C	B	B	B	?	C	B	A	C	A	9*
1055	TX Presidio	11	eremicus	C	C	A	C	B	B	B	?	B	B	A	B	A	11*
1056	TX Presidio	11	eremicus	C	C	A	C	B	B	B	C	B	B	A	B	A	11
1057	TX Presidio	11	eremicus	C	C	A	C	B	B	B	?	B	B	A	B	A	11*
1058	TX Presidio	11	eremicus	C	C	A	C	B	B	B	?	B	B	A	B	A	11*
1060	TX Presidio	11	eremicus	?	C	A	?	B	B	B	C	B	B	A	B	A	11*
1061	TX Presidio	11	eremicus	C	C	A	C	B	B	B	C	B	B	A	B	A	11
1062	TX Presidio	11	eremicus	C	C	A	C	B	C	B	C	B	B	A	B	A	12
1064	TX Presidio	11	eremicus	?	C	A	C	B	B	B	C	B	B	A	?	?	11*

[1] Restriction endonucleases from left to right are: *Aci* I, *Bsp* 1286 I, *Bst*U I, *Dde* I, *Hae* III, *Hha* I, *Hinc* II, *Hinf* I, *Mbo* I, *Msp* 1, *Rsa* I, *Sau*96 I, *Taq* I.

Hidalgo Co., New Mexico; sample 10 (2)—2.3 miles N Van Horn, Culberson Co., Texas; sample 11 (8; U-21629)—5 miles N Presidio, Presidio Co., Texas; sample 12 (2; U-21627)—3 miles S Imperial, Pecos Co., Texas. *Chaetodipus intermedius* (1; U-21612)—5 miles NW San Carlos, Sonora, Mexico.

Results

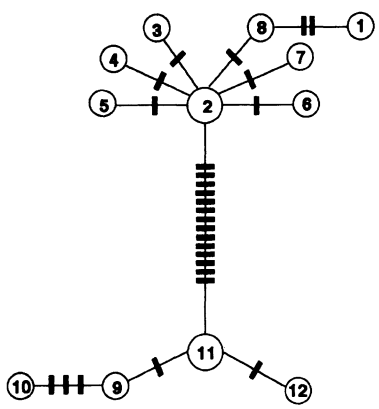
Twelve composite ND2-COI haplotypes were identified among the 44 specimens of *C. penicillatus* examined (Table 1). Multiple haplotypes were found at nearly all localities from which more than a single individual was available (Table 1). A total of 46 restriction-sites were inferred using 12 tetranucleotide and one heptanucleotide restriction endonucleases (Appendix I). The frequency distribution of haplotypes was highly variable, with haplotype 02 being present in 14 (32%), haplotype 11 in 7 (16%), and haplotype 08 in 5 (11%) of the individuals. If one uses restriction-site changes to construct a connection network, with the two most common haplotypes forming the hubs (Fig. 1a), a strong pattern of geographic structuring emerges. Haplotypes 01 through 08 form a closely related cluster that collectively were found in Sonoran, Mojavean, and Sonoran-Chihuahuan ecotonal desert localities. Likewise, haplotypes 09–12 were found only in Chihuahuan Desert localities. No haplotype within either group differs by more than four restriction-site changes, but haplotypes in the first group differ from those in the latter group by a minimum of 14 restriction-site changes. Estimates of sequence divergence between operational taxonomic units (OTUs) grouped according to locality are summarized in Table 2. As depicted in an unweighted pair-group method with arithmetic averages (UPGMA) tree (Fig. 1b), localities in the Chihuahuan Desert differ by ca. 7% divergence from localities in the Sonoran and Mojavean deserts, and Sonoran-Chihuahuan transition zone. All haplotypes from Culberson, Pecos, and Presidio counties represent the subspecies *C. p. eremicus*. The single Mojave Desert individual from San Bernardino Co., California (haplotype 08), representing the subspecies *C. p. angustirostris,* was similar to haplotypes occurring throughout the range of the Sonoran Desert subspecies *C. p. pricei* and *C. p. penicillatus.*

Sequence-divergence estimates from the COIII gene (Table 3), demonstrate ca. 1.1–3.7% divergence among individuals within either the Chihuahuan or Mojavean-Sonoran haplotype groups, with ca. 9.0–12.5% divergence between each of these haplotype groups. These values are consistent with the magnitude of divergence estimated from ND2-COI restriction-site data. In the COIII gene, divergence between *C. intermedius* and *C. penicillatus* increases to ca. 23%. A parsimony analysis of COIII character-state data (Fig. 1c) clearly corroborates the patterns of regional haplotype structure described previously for restriction-site data.

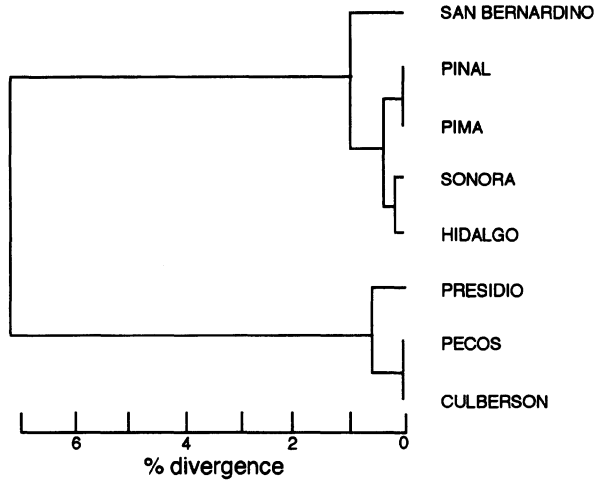
Discussion

The results of this study suggest strong differentiation of mtDNA between Chihuahuan (*C. p. eremicus*) and Sonoran-Mojavean (*C. p. pricei, C. p. penicillatus,* and *C. p. angustirostris*) populations of *C. penicillatus.* Two different approaches to assaying variation in mtDNA from two different gene regions (a total of ca. 2,540 bp surveyed) have produced essentially congruent estimates of sequence divergence between three groups of haplotypes, ranging from ca. 7% (ND2-COI restriction-site data) to ca. 11% (COIII sequence data) between Chihuahuan and Sonoran-Mojavean haplotypes, and 3–4% COIII sequence divergence between one Mojavean (*C. p. angustirostris*) and Sonoran haplotypes.

How congruent are the mtDNA results with independent estimates of variation in this taxon? Hoffmeister and Lee (1967) revised subspecific taxonomy according to morphological variation (Fig. 2), noting that specimens assigned to *C. p. pricei* are darker in color than those assigned to *C. p. eremicus.* This color difference was noted in this study as well. Hoffmeister and Lee



a



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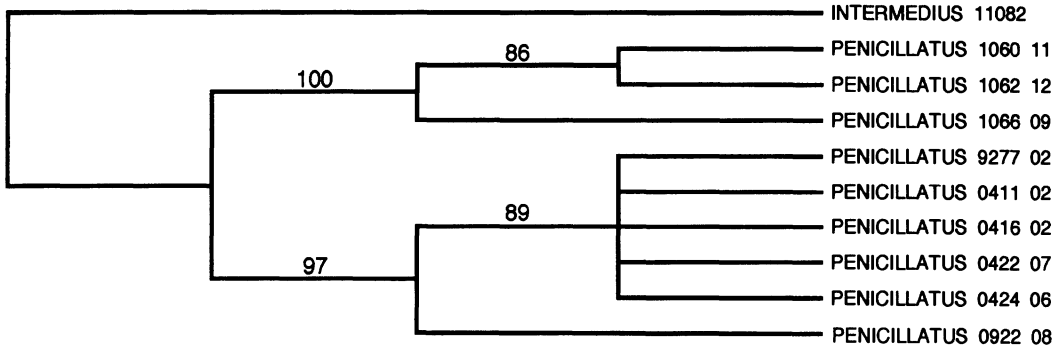

c

FIG. 1.—Trees postulating relationships among mtDNA haplotypes and populations grouped by county of occurrence: a, haplotype network depicting restriction-site changes (Appendix I) among composite haplotypes numbered as in Table 1; b, UPGMA tree constructed from matrix in Table 2; c, majority-rule maximum-parsimony tree summarizing phylogenetic information resulting from 1,000 branch-and-bound bootstrap replicates for *COIII* nucleotide sequence data with *Chaetodipus intermedius* as designated outgroup and individuals identified by specimen and composite haplotype numbers (Table 1); all 39 phylogenetically informative characters were weighted equally; consistency index = 0.774, retention index = 0.844.

TABLE 2.—*Sequence divergence values (below diagonal) and jackknife standard errors (above diagonal) from restriction-site data for* Chaetodipus penicillatus, *with OTUs grouped by locality (see Table 1).*

	Locality							
Locality	1	2	3	4	5	6	7	8
1 Culberson		0.017	0.000	0.015	0.015	0.004	0.022	0.016
2 Hidalgo	0.0708		0.018	0.002	0.002	0.018	0.002	0.001
3 Pecos	0.0000	0.0672		0.017	0.017	0.004	0.018	0.017
4 Pima	0.0683	0.0016	0.0686		0.000	0.017	0.009	0.004
5 Pinal	0.0688	0.0015	0.0699	0.0000		0.017	0.010	0.004
6 Presidio	0.0074	0.0632	0.0038	0.0648	0.0648		0.020	0.017
7 San Bernardino	0.0852	0.0013	0.0756	0.0122	0.0132	0.0749		0.009
8 Sonora	0.0687	0.0012	0.0698	0.0054	0.0053	0.0661	0.0127	

(1967) identified a zone of intergradation between Sonoran and Chihuahuan subspecies near the continental divide in southwestern New Mexico. This zone corresponds to the mtDNA shift between Sonoran haplotypes (present in Hidalgo Co., New Mexico) and Chihuahuan haplotypes. Data currently are not available to characterize the width of this contact zone relative to intergradation of mtDNA. Patton (1970) identified three chromosomal races within *C. penicillatus* (Fig. 2) that are largely congruent with morphological conclusions of Hoffmeister and Lee (1967). Neither morphological nor standard karyotypic data are likely to provide satisfying hypotheses relative to phylogenetic relationships among evolutionary lineages in small mammals (Baker et al., 1985). Phylogenetically informative character states may be obtainable from banded chromosomal analysis, but G-banded chromosomes currently are available only for *C. p. eremicus* (Lee et al., 1991). However, as can be seen in Fig. 2, population affinities demonstrated by allozymic distance data are completely congruent with our mtDNA assessment of phylogeographic population structure among four nominate subspecies of *C. penicillatus.*

Collectively, all these studies suggest the hypothesis that populations of *C. p. angustirostris* from eastern California and northern Baja California shared a recent, but diagnosable, common ancestry relative to populations in central and southern Arizona, although details of intergradation between populations in California and western Arizona currently are unavailable. Evidence presented in the present study supports recognition of distinct subspecies within an evolutionary lineage concept of subspecies (Avise and Ball, 1990; O'Brien and Mayr, 1991). Therefore, *C. p. angustirostris* is supportable as a distinct subspecies based on congruent information from several independent character systems. There is little genetic distinction between populations in central and eastern Arizona and Sonora. However, *C. p. penicillatus* has not been investigated sufficiently to assess any evolutionary distinction between *C. p. pricei* and *C. p. penicillatus.*

All Sonoran and Mojavean populations of *C. penicillatus* have shared a divergent common ancestry relative to populations in the Chihuahuan Desert of New Mexico, Texas, and Chihuahua. Previous investigators (e.g., Findley, 1969; Hubbard, 1973) have postulated east-west separation of desertscrub across the Rocky Mountain axis during Pleistocene glacial maxima. The most recent glacial-stage began about 8.5×10^4 years ago (Webb and Bartlein, 1992), which would be the approximate amount of time available for lineage sorting and divergence of mtDNA haplotypes in eastern versus western populations of desert pocket mice under the model proposed by Findley

TABLE 3.—*Nucleotide-sequence divergence values among 387 base pairs of the mtDNA* CO III *gene (below diagonal) and number of transition and transversion differences (above diagonal) for nine* Chaetodipus penicillatus *(designated according to specimen and composite haplotype numbers shown in Table 1) and one* C. intermedius. *Values were calculated using the Kimura two-parameter model with transition/transversion ratio = 10.*

Specimen	Specimen number	Composite haplotype number	Specimen									
			1	2	3	4	5	6	7	8	9	10
1 *C. intermedius*	11082			43/21	44/23	48/18	49/20	49/18	49/18	47/19	46/17	44/27
2 *C. penicillatus*	1060	11	0.24		3/0	26/6	31/5	27/5	30/5	27/5	25/5	3/2
3 *C. penicillatus*	1062	12	0.23	0.01		29/6	30/5	29/6	28/5	25/6	26/5	5/2
4 *C. penicillatus*	9277	02	0.24	0.10	0.10		5/1	2/0	5/1	4/1	8/2	29/9
5 *C. penicillatus*	0411	02	0.24	0.11	0.10	0.02		6/1	6/0	5/3	12/1	31/8
6 *C. penicillatus*	0416	02	0.23	0.10	0.11	0.01	0.02		3/1	4/1	10/2	29/9
7 *C. penicillatus*	0422	06	0.23	0.10	0.10	0.02	0.02	0.01		4/2	11/1	28/9
8 *C. penicillatus*	0424	07	0.24	0.10	0.10	0.01	0.02	0.01	0.02		9/3	27/9
9 *C. penicillatus*	0922	08	0.24	0.09	0.10	0.03	0.04	0.03	0.03	0.03		24/9
10 *C. penicillatus*	1066	09	0.24	0.01	0.02	0.12	0.12	0.12	0.11	0.12	0.11	

(1969) and Hubbard (1973). Alternatively, Riddle and Honeycutt (1990) and Riddle (1995) favored an hypothesis of late Pliocene or early Pleistocene time of vicariance between Chihuahuan and Sonoran populations of desertscrub-adapted small vertebrates. The latter hypothesis is consistent with several attributes related to the development of arid landscapes in western North America. First, paleoecological evidence indicates a rapid, latest Miocene expansion of regional deserts in western North America (Webb, 1977), prior to maximum uplifting of the southern Rockies and Sierra Madre Occidental mountain chains during the early Pleistocene (Ruddiman et al., 1989). Second, times of divergence estimated from levels of mtDNA sequence-divergence between eastern and western populations of *C. penicillatus,* as well as between populations of grasshopper mice (*Onychomys torridus* versus the *O. arenicola* plus *O. leucogaster* clade), are consistent with a late Pliocene or early Pleistocene time of vicariance (Riddle et al., 1993). Third, as with *C. penicillatus,* phylogeographic distinction between Sonoran and Chihuahuan populations is indicated in a range of desertscrub small vertebrates; e.g., other small mammals including *Ammospermophilus* (Hafner, 1981), and reptiles including *Sceloporus magister* (D.I. Orange et al., in litt.), and *Crotaphytus collaris* (D.I. Orange, pers. comm.). In short, several examples of taxonomic, biogeographic, and gene tree congruence support an hypothesis of long-term isolation and divergence of a substantial assemblage of Chihuahuan and Sonoran desertscrub small vertebrates. Interestingly, in a large fraction of the examples of east-west sister taxa thus far established, earlier morphologically based assessment subsumed populations within a single widespread species. That such morphological crypsis appears to be a common factor underlying evolutionary divergence between Sonoran and Chihuahuan small vertebrates suggests that additional examples of east-west historical divergence

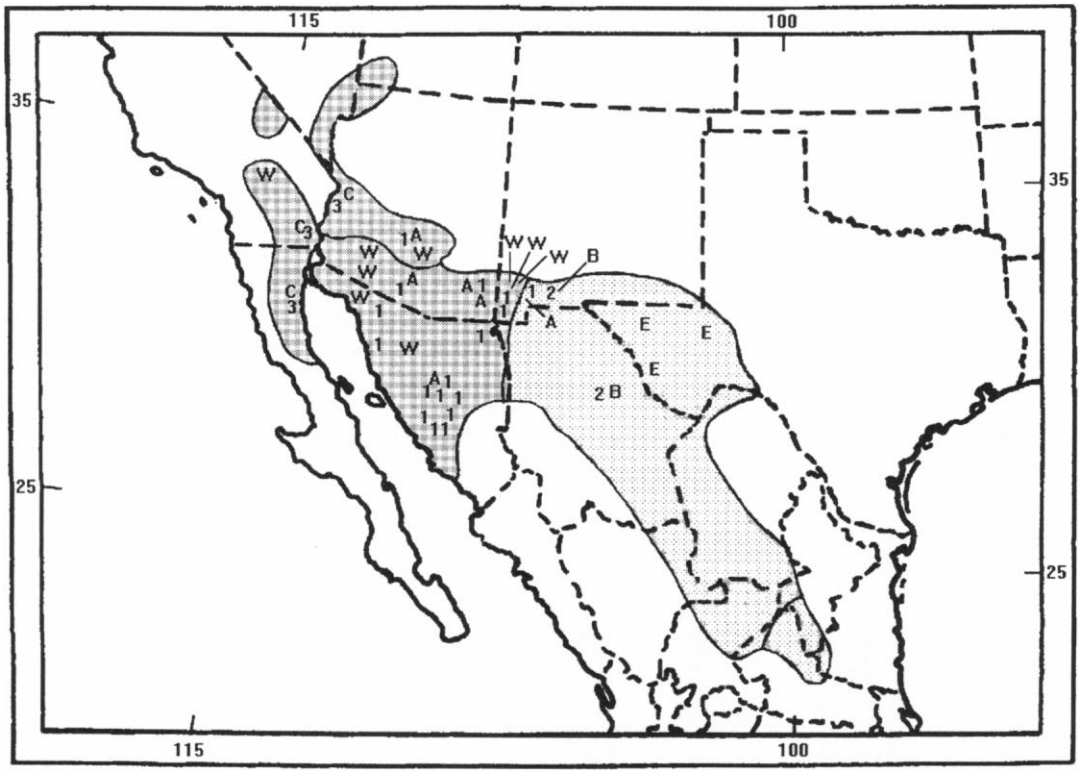

FIG. 2.—The geographic distribution of *Chaetodipus penicillatus* (dark shading) and the proposed new species *Chaetodipus eremicus* (pale shading). Subspecies boundaries are drawn according to Hoffmeister and Lee (1967). Symbols designate the following character distributions. E and W designate the mtDNA haplotype assemblages 9–12 and 1–8, respectively (Fig. 1). 1, 2, and 3 designate allozymic groups from Patton et al. (1981) as follows: group 1—2–4, 7, 8, 12–22; group 2—6, 10; group 3—1, 5, 9; a, b, and c designate chromosome races 48, 56, and 54, respectively, from Patton et al. (1981).

are possible (e.g., for small mammals, *C. intermedius, Dipodomys merriami,* and *Peromyscus eremicus*).

Congruence among several independent character systems demonstrating a demarcation between populations of the desert pocket mouse in Hildalgo Co., New Mexico, is unequivocal in supporting recognition of a distinct species under phylogenetic (Cracraft, 1989) or evolutionary (Wiley, 1981) species concepts. We agree with advocates of the utility of a phylogenetically based system for recognition of species-level taxa (e.g., Avise and Ball, 1990; Frost and Hillis, 1990; McKitrick and Zink, 1988), and propose recognition of a new species of desert pocket mouse accordingly. Additionally, evidence from chromosomes and nuclear genomic data (Patton et al., 1981) suggests absence of introgression in this zone and therefore supports recognition of a distinct species under a biological species concept (Mayr, 1963) as well.

Woodhouse (1852) described *Perognathus penicillatus* from the San Francisco Mountains, Arizona. Following Hafner and Hafner (1983), we recognize the genus-level status of *Chaetodipus.* Hoffmeister and Lee (1967) contested Woodhouse's claim and designated 1 mile SW of Parker, Yuma Co., Arizona, as the type locality. The type locality of *C. p. pricei* (Allen, 1894) was from Oposura, Sonora, Mexico. The type localities of *C. p. penicillatus* and *C. p. pri-*

cei are all Sonoran Desert localities. Mearns (1898) described *P. eremicus*. Osgood (1900) recognized *P. eremicus* as a subspecies of *P. penicillatus*. The type locality for *C. p. eremicus* is Fort Hancock, Hudspeth Co., Texas, a Chihuahuan Desert locality. Moreover, the geographic range of *C. p. eremicus* Hall (1981) conforms to generally recognized boundaries of the Chihuahuan Desert (Morafka, 1974; Shreve, 1942).

The appropriate available name for the Chihuahuan Desert pocket mouse is *Chaetodipus eremicus* Mearns, and we provide a synonymy below. This proposed new species conforms, as far as we know, with all distributional and morphological attributes offered under the formal description of the subspecies *Perognathus penicillatus eremicus* Mearns in Hoffmeister and Lee (1967). Therefore, we propose that *Perognathus penicillatus eremicus* Mearns (Hoffmeister and Lee, 1967) be elevated to the species *Chaetodipus eremicus*. *Chaetodipus penicillatus atrodorsalis* Dalquest probably is included within this new species based on geographical, morphological (Hoffmeister and Lee, 1967), and chromosomal (Patton, 1970) data.

Chaetodipus eremicus (Mearns)

Perognathus (*Chaetodipus*) *eremicus* Mearns, 1898:300. Type locality "Fort Hancock, Hudspeth County, Texas."

[*Chaetodipus*]. *penicillatus:* Hafner and Hafner, 1983:24. Elevation of subgenus to generic status.

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Appendix I.—*Restriction-site character-state data for composite haplotypes reported in Table 1.*

Haplotype	*Aci* I	*Bsp* 1286 I	*Bst*U I	*Dde* I	*Hae* III	*Hha* I	*Hinc* II	*Hinf* I	*Mbo* I	*Msp* I	*Rsa* I	*Sau* 96 I	*Taq* I
1	00111	0011	0	001111	0101	01	11100	00101	0011	0111	1	0110	11
2	00111	0011	0	001111	0101	01	11111	00101	0011	0101	1	0110	11
3	00011	0011	0	001111	0101	01	11111	00101	0011	0101	1	0110	11
4	00111	0011	0	001111	0101	01	11111	01101	0011	0101	1	0110	11
5	00111	0011	0	011111	0101	01	11111	00101	0011	0101	1	0110	11
6	00111	0011	0	001111	0101	01	11111	00111	0011	0101	1	0110	11
7	00111	1011	0	001111	0101	01	11111	00101	0011	0101	1	0110	11
8	00111	0011	0	001111	0101	01	11111	00101	0011	0111	1	0110	11
9	11111	0111	0	101110	1111	00	11101	10101	1111	1101	1	0101	11
10	11111	0111	0	100110	1111	00	11101	10101	1111	1101	1	0101	11
11	11111	0111	0	101110	1111	00	11101	10101	0111	1101	1	1101	11
12	11111	0111	0	101110	1111	10	11101	10101	0111	1101	1	1101	11

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