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Phylogeography and systematics of the San Diego pocket mouse (*Chaetodipus fallax*)

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The systematics and phylogeography of the San Diego pocket mouse (*Chaetodipus fallax*), a species restricted to the Baja California Peninsula and adjacent southwestern California, were assessed using sequences of the mitochondrial cytochrome-*b* gene (*Cytb*). Genetic relationships were evaluated among the 6 recognized subspecies of *C. fallax* (including the island population, *C. f. anthonyi*) in 3 geographic regions from individuals representing 22 populations. Analysis of molecular variance and multiple phylogenetic analyses indicated 3 main clades: northern populations in the southwestern Mojave Desert and Los Angeles Basin north of the Salton Trough; central populations from south of the Salton Trough and throughout the state of Baja California; and southern populations from west of the Vizcaíno Desert in Baja California Sur and adjacent Isla Cedros. These clades do not correspond to the currently recognized subspecies, and each could be considered a distinct subspecies pending analysis of nuclear DNA or characters (e.g., morphology) encoded by nuclear DNA. DOI: 10.1644/09-MAMM-A-135.

Key words: Baja California, California, *Chaetodipus*, cytochrome *b*, genetic structure, Heteromyidae, phylogenetics, phylogeography

The San Diego pocket mouse (*Chaetodipus fallax*) is restricted to the central and northern Baja California Peninsula and southwestern California. Although its range is one of the smallest among *Chaetodipus* spp. (Patton and Álvarez-Castañeda 1999), it occurs in a wide variety of temperate and arid habitats. These range from chaparral in the Transverse Ranges of southern California through coastal sage and deserts of the Baja California Peninsula, including Isla Cedros (Cedros Island) in the Pacific Ocean, ~25 km from the peninsula (Lackey 1996; Patton and Álvarez-Castañeda 1999; Fig. 1). The species inhabits 3 distinct geographic regions: the southwestern margin of the Mojave Desert (at sufficient elevation to support Joshua trees [*Yucca brevifolia*]) and the northeastern margin of the Los Angeles Basin; coastal and inland desert areas south of the Salton Trough in California and Baja California; and the Vizcaíno Desert of Baja California Sur and adjacent Isla Cedros (Hall 1981; Lackey 1996).

The population on Isla Cedros originally was described as a full species, *Chaetodipus anthonyi*, based on its slightly smaller size, ruddier color, and cranial characters (versus *C. fallax*—Osgood 1900). Williams et al. (1993) considered it a subspecies of *C. fallax* (resembling *C. f. inopinus*), although no morphological, genetic, or cytogenetic comparisons were made.

Currently, *C. fallax* has 6 recognized subspecies (Lackey 1996): *C. f. anthonyi* from Isla Cedros; *C. f. fallax* from southern California through the coastal sage zone into the northern part of the Baja California Peninsula; *C. f. inopinus* on the narrow coastal strip from Santa Catarina southward to the Vizcaíno Desert in the very northern part of the state of Baja California Sur; *C. f. majusculus* in a coastal zone between the ranges of *C. f. fallax* and *C. f. inopinus*; *C. f. pallidus* in the eastern San Bernardino Mountains in California; and *C. f. xerotrophicus* in the Central Desert in the southern part of the state of Baja California (Fig. 1).

This study examined phylogeographic relationships among populations of *C. fallax* (including the Isla Cedros population) using mitochondrial cytochrome-*b* (*Cytb*) sequences considering the 3 geographic regions occupied by this species, populations in the peninsular areas and Isla Cedros, and current subspecies as distinct evolutionary units.

Materials and Methods

Samples.—A data set of 650 base pairs (bp) of *Cytb* was analyzed for 60 individuals from 22 populations representing all recognized subspecies (Fig. 1; Table 1). The specimens

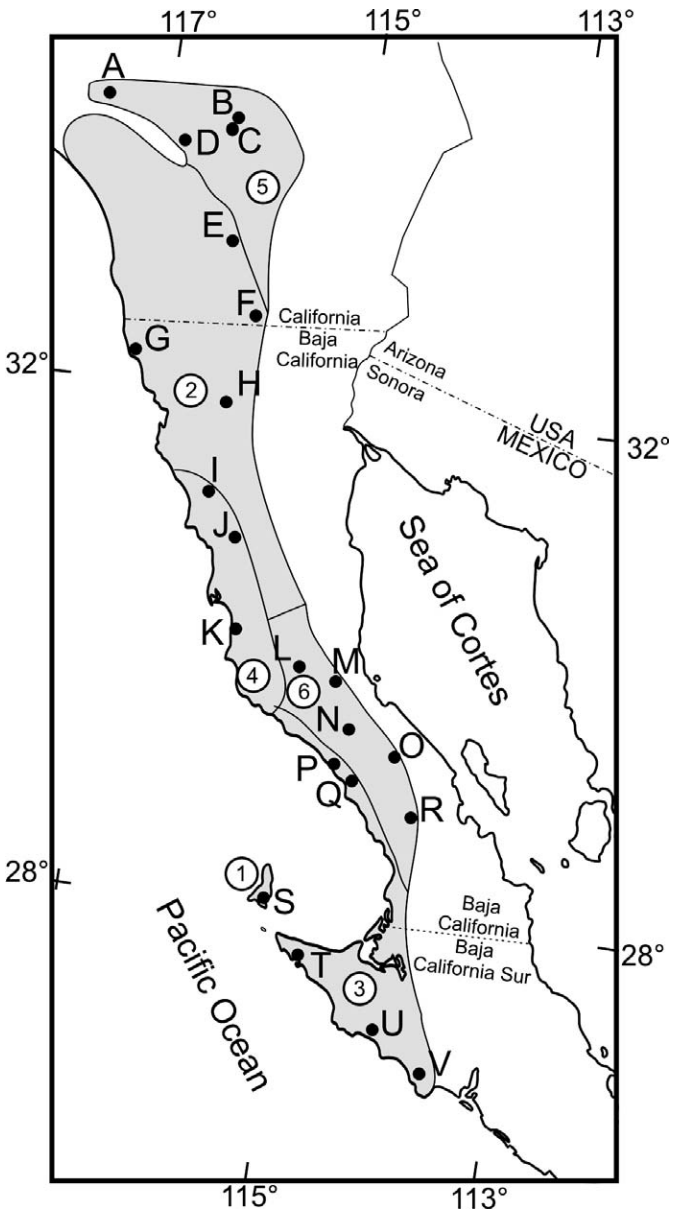

Fig. 1.—Location (A–V) of specimens of *Chaetodipus fallax* examined for sequencing (complete localities in Appendix I): 1) *C. f. anthonyi*, 2) *C. f. fallax*, 3) *C. f. inopinus*, 4) *C. f. majusculus*, 5) *C. f. pallidus*, and 6) *C. f. xerotrophicus*. Map is redrawn from Hall (1981).

used in this study are deposited at the Centro de Investigaciones Biológicas del Noroeste (CIB) and the Museum of Vertebrate Zoology, University of California (MVZ; Appendix I). A sequence of *Cytb* of *C. fallax* from Genbank (AY926402) was included in the analyses.

Laboratory procedures.—Genomic DNA was extracted from liver tissues preserved in 95% ethanol, using a DNeasy kit DNA (QIAGEN, Valencia, California). The fragment of the *Cytb* gene (~800 bp) was amplified with primer pairs MVZ05 (CGA AGC TTG ATA TGA AAA ACC ATC GTT)/MVZ16 (AAA TAG GAA RTA TCA YTC TGG TTT RAT). The following conditions for initial double-strand amplification were used: 12.5 µl (10 ng) template, 4.4 µl double-distilled H_2O, 2.5 µl of each primer (10 nM concentration), 0.474 µl (0.4 nM) deoxynucleoside triphosphates, 0.5 µl (3 mM) $MgCl_2$, 0.125 µl Taq polymerase (Invitrogen, Carlsbad, California), and 1× Taq buffer to a final volume of 25 µl. Amplification conditions consisted of initial denaturizing for 3 min at 94°C followed by 37 cycles of denaturizing at 94°C for 45 s, 1 min annealing at 50°C, and 1 min extension at 72°C. Amplified products were purified using a QIAquick PCR Purification Kit (QIAGEN).

Templates were cycle-sequenced with MVZ05/MVZ16 for *Cytb* amplifications using a Taq FS kit (Applied Biosystems Inc., Foster City, California) and run on an ABI 377 automated sequencer (Applied Biosystems Inc.). Sequences were edited and visually aligned using Sequencher version 4.1.4 software (Gene Codes, Ann Arbor, Michigan) and translated into amino acids for confirmation of alignment. Haplotypes included in Appendix I have been deposited in GenBank (accession numbers GQ175230–GQ175276).

Genetic structure.—Intraspecific *Cytb* gene genealogies were inferred for 60 samples from 22 populations using the statistical parsimony method (Templeton 2001) implemented in the program TCS version 1.18 (Clement et al. 2000). This program allows estimation of phylogenetic relationships at low levels of divergence and provides a 95% plausible set for all haplotype connections. A minimum spanning network was obtained to depict the relationship among the 45 unique haplotypes identified.

Distribution of genetic variance of population structure was obtained using analysis of molecular variance (AMOVA—Excoffier et al. 1992; Weir and Cockerham 1984) conducted in the program Arlequin version 2.001 (Schneider et al. 2000). Three population clustering designs were used for testing the hypotheses of genetic structure reflecting the 3 geographic regions, the Isla Cedros population as a distinct species, and the 6 currently recognized subspecies (Table 2). Variation percentages were obtained directly from the matrix of squared-distances between all pairs of haplotypes in each case (Excoffier et al. 1992), and the genetic structure was estimated by means of F_{ST} (Weir and Cockerham 1984).

Spatial AMOVA was performed using SAMOVA version 1.0 (Dupanloup et al. 2002). This analysis defines groups of populations that are geographically homogeneous and maximally differentiated from each other when a particular number of groups is specified. The method is based on a simulated annealing procedure that maximizes the proportion of total genetic variance from differences between groups of populations (largest F_{CT} value). We tested 3, 2, and 6 groups (corresponding to the 3 hypotheses above) using the entire data set.

Phylogenetic analyses.—From 45 haplotypes identified, we selected samples with 20 unique haplotypes that corresponded to representative specimens of the 3 geographic regions and 6 recognized subspecies to be included in phylogenetic analyses. We applied maximum-parsimony, maximum-likelihood, and distance methods in PAUP* 4.0b10 (Swofford 2002). For the maximum-parsimony analysis, all characters were equally weighted, and a heuristic search was performed with 1,000

Table 1.—Localities ($n = 22$) of the specimens of *Chaetodipus fallax* examined. Letter of the locality (L) as in Fig. 1; sample size (n) per locality; haplotype number (H) as in Fig. 3; the subscript is the number of specimens with that haplotype for that sample. All latitudes are north and longitudes are west, and are in decimal degrees. CA = California; BC = Baja California, México; BCS = Baja California Sur, México.

L	Locality	State	Latitude	Longitude	n	$H_{\text{no. specimens}}$
A	Etiwanda Wash	CA	34.1638	−117.5034	1	1_1
B	Pioneertown	CA	34.1513	−116.4790	3	2_1, 3_1, 4_1
C	Morongo Valley	CA	34.0981	−116.4914	3	5_1, 6_1, 7_1
D	Banning, Riverside Co.	CA	33.9053	−116.8837	4	1_1, 8_2, 9_1
E	Borrego Spring	CA	33.2087	−116.3749	1	10_1
F	Jacumba	CA	32.6422	−116.1030	1	11_1
G	Rosarito	BC	32.2588	−116.9736	5	12_1, 13_3, 14_1
H	Ojos Negros	BC	31.9243	−116.1252	5	15_1, 16_1, 17_1, 18_1, 19_1
I	San Vicente	BC	31.2479	−116.1187	3	20_1, 21_1, 22_1
J	Colonet	BC	30.9044	−115.8811	2	23_1, 24_1
K	El Rosario	BC	30.1833	−115.7641	5	25_3, 26_1, 27_1
L	Misión San Fernando	BC	29.9666	−115.2500	1	28_1
M	Cataviña	BC	29.9000	−114.9500	3	29_1, 30_1, 31_1
N	Pico Fernando	BC	29.5413	−114.7752	1	32_1
O	Laguna Chapala	BC	29.3544	−114.3429	4	33_1, 34_1, 35_1, 36_1
P	San José	BC	29.2411	−114.8272	1	37_1
Q	Punta Blanca	BC	29.1200	−114.6816	2	38_1, 39_1
R	Punta Prieta	BC	28.9341	−114.1651	3	18_3
S	Isla Cedros	BC	28.0368	−115.1833	4	40_3, 41_1
T	Bahía Tortugas	BCS	27.7266	−114.8247	1	42_1,
U	Bahía Asunción	BCS	27.2642	−114.1804	2	43_1, 44_1
V	Punta Abreojos	BCS	26.9594	−113.7591	5	43_1, 45_4

replicates, random addition of sequences, and implementing the tree-bisection-reconnection branch-swapping method. Species designated as outgroups following Alexander and Riddle (2005) were *Chaetodipus californicus* (AY926401), *C. arenarius* (AY926399), *C. dalquesti* (AY926400), and *C. spinatus* (AY926398). For all analyses that resulted in multiple most-parsimonious trees, consensus trees were constructed using the 50% majority rule.

Genetic distances were calculated using the Jukes–Cantor and the Kimura 2-parameter models. The latter is the most commonly used model for comparing levels of divergence among studies (Baker and Bradley 2006). Genetic distance matrices among individuals were used to generate a neighbor-joining tree, and the support for nodes was assessed with bootstrap analyses, including a fast heuristic procedure with 1,000 pseudoreplicates.

The general time reversible (GTR+G+I) model with gamma-distribution among-site rate variation and a fraction of invariable sites was shown to be the most appropriate for the data using the model comparison in MrModeltest version 2 (Nylander 2004) under the Akaike information criterion (AIC). The GTR+G+I model then was used for maximum-likelihood searches consisting of 1,000 random replicates with tree-bisection-reconnection branch swapping. Bootstrap values $\geq$50% are reported for branch support.

A Bayesian inference analysis was performed with MrBayes version 3.0b4 software (Ronquist and Huelsenbeck 2003) using the GTR + G + I model and 4 separate runs

Table 2.—Results of the AMOVA using different population arrangements in relation to the 3 hypotheses of genetic structure: 1) 3 groups by geographical regions; 2) Isla Cedros in relation to the peninsula; and 3) 6 subspecies. AG = among groups; AP = among populations; WP = within populations. See Table 1 for list of localities.

Model	Localities	Variance component	% variance
Geographical regions	1) A–D	$\Phi_{ct} = 8.61$	AG = 76.28
	2) E–R	$\Phi_{sc} = 0.99$	AP = 8.76
	3) S–V	$\Phi_{st} = 1.69$	WP = 14.96
C. anthonyi versus *C. fallax*	1) S	$\Phi_{ct} = 2.63$	AG = 26.42
	2) A–R, T–V	$\Phi_{sc} = 5.34$	AP = 53.64
		$\Phi_{st} = 1.98$	WP = 19.94
6 subspecies	1) B, C, E (*pallidus*)	$\Phi_{ct} = 0.01$	AG = 1.92
	2) A, D, F–H (*fallax*)	$\Phi_{sc} = 0.10$	AP = 20.79
	3) I–K (*majusculus*)	$\Phi_{st} = 0.39$	WP = 77.29
	4) L–O, R (*xerotrophicus*)		
	5) P, Q, T–V (*inopinus*)		
	6) S (*anthonyi*)		

implementing the Metropolis coupled Markov chain Monte Carlo simulation starting from a random tree. Each run was conducted with 5×10^6 generations and sampled at intervals of 1,000 generations. The first 3,000 samples of each run were discarded as burn-in, and all remaining sampled trees were analyzed to find the posterior probability of clades. A consensus tree was generated with the 50% majority-rule algorithm, and the percentage of samples recovered in a particular clade was assumed to be that clade's posterior probability.

Results

Genetic variation.—We obtained sequence data for 650 bp of the *Cytb* gene from 60 individuals among 22 localities within the range of *C. fallax*. Average base composition was A = 26.5%, C = 25.9%, G = 13.9%, and T = 33.6; 95 (14.7%) polymorphic sites, 83 (12.8%) transitions, 21 (3.3%) transversions, and 45 unique haplotypes were identified (Table 1). Gene diversity (h; mean ± SD) was 0.9869 ± 0.0061, nucleotide diversity was 0.0226 ± 0.0114, and the mean number of pairwise differences was 14.7306 ± 6.6838.

Genetic structure.—Analysis of molecular variance with the cluster design of populations based on the 3 geographic regions showed a clear and significant structural pattern ($P < 0.01$, $F_{ST} = 0.2353$), with more than half of the total pool of variation (76.2%) contained among the groups. We found no significant difference between the island and peninsular populations (26.4%; $P > 0.05$, $F_{ST} = 0.8006$) or among the 6 subspecies (1.9%; $P > 0.05$; $F_{ST} = 0.2271$; Table 2).

The SAMOVA based on 2 groups (maximum $F_{CT} = 0.625$ between groups) included Isla Cedros, Vizcaíno Desert, and disjunct northern (southwestern Mojave Desert and Los Angeles Basin) populations in one group and populations from south of the Salton Trough in California and the northern Baja California Peninsula in a 2nd group (Fig. 2a). SAMOVA of 3 groups (maximum $F_{CT} = 0.478$) separated the single population from the Los Angeles Basin (Etiwanda, locality A), the 3 populations in the southwestern Mojave Desert (Pioneertown, Morongo Valley, and Banning; B–D), and all remaining populations, including that on Isla Cedros (E–V; Fig. 2b). Partitioning delineated by SAMOVA for 6 groups provided a maximum F_{CT} of 0.738. Populations from California (A–F) were separated into 4 groups, with the remaining 2 groups consisting of those from the state of Baja California (G–R) and those from the Vizcaíno Desert and Isla Cedros (S–V; Fig. 2c).

A minimum spanning network obtained from *Cytb* sequences and depicting relationships among 45 unique haplotypes (Table 1) indicated that the maximum number of mutational steps between haplotypes allowing parsimonious connections was 11 steps ($P \geq 0.95$). Using maximum parsimony within these limits, 3 geographically disjointed networks were obtained (Fig. 3). The 1st network includes populations from north of the Salton Trough (Los Angeles Basin and southwestern margin of the Mojave Desert; Fig. 3A). The 2nd network includes populations south of the Salton Trough and throughout the state of Baja California (Fig. 3C). The last network includes samples from the Vizcaíno Desert and Isla Cedros (Fig. 3B).

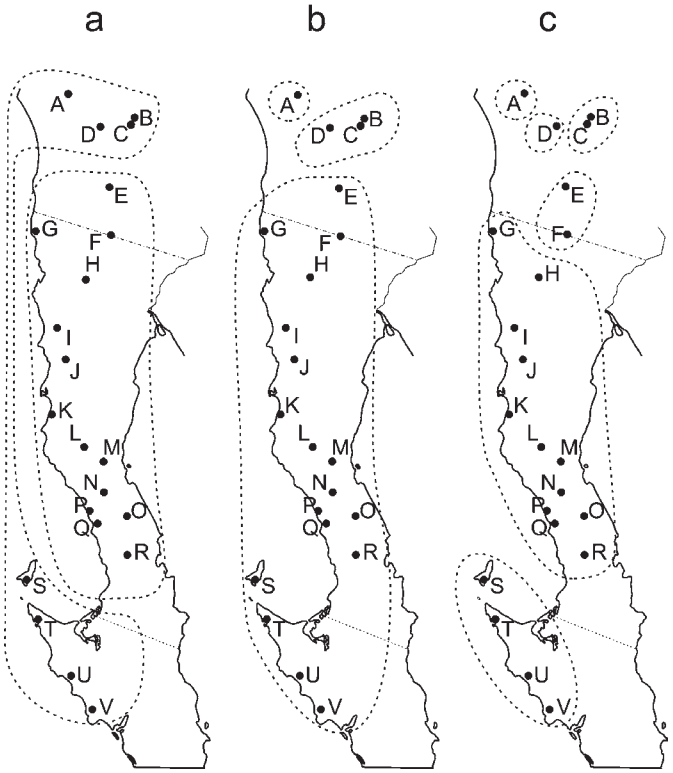

Fig. 2.—The SAMOVA grouping of populations defined under the criteria of geographical homogeneity and maximal differentiation from each other: a) 2, b) 3, and c) 6 unsupervised clusters using the entire data set.

Phylogenetic analyses.—All analyses clearly indicate that *C. anthonyi* is well within the clade of *C. fallax* (Fig. 4). The maximum-parsimony analysis of the molecular data of 650 bp of the *Cytb* gene yielded 1 tree (length = 372, consistency index = 0.723, retention index = 0.734, rescaled consistency index = 0.531). The analysis shows 3 main clades (tree not shown): the Northern clade includes populations north of the Salton Sea; the Central clade includes all samples south of the Salton Sea and throughout the state of Baja California; and the Southern clade includes the populations from the Vizcaíno Desert and Isla Cedros.

Average genetic distances (minimum and maximum values) within subspecies, obtained by using the Jukes–Cantor and the Kimura 2-parameter models, respectively, are (Table 3): *C. f. pallidus* 0.9% (0.5–1.2%), 1% (0.5–1.3%); *C. f. fallax* 0.7% (0.2–1.1%), 0.6% (0.2–1.1%); *C. f. xerothrophicus* 0.7% (0.2–1.1); and *C. f. inopinus* 2.9% (0.0–5.6%). For *C. f. anthonyi* and *C. f. majusculus* no average genetic distances are presented because only 1 and 2 populations were analyzed, respectively. Average distances among the 3 clades—Northern, Central, and Southern—are shown in Table 4. The distance analysis with the neighbor-joining method, using both models, showed similar results to those obtained with the maximum-parsimony criteria. The Central clade is supported

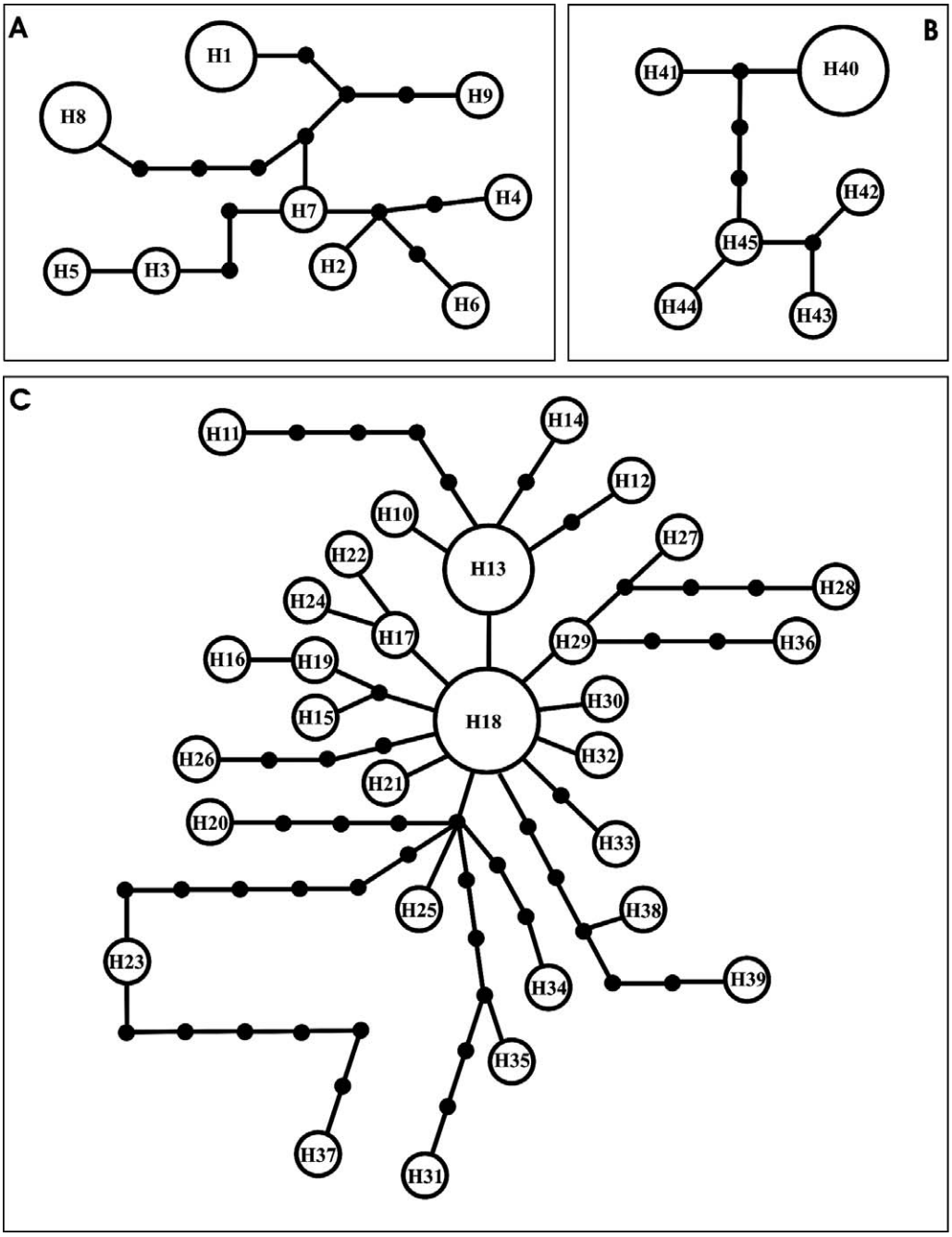

FIG. 3.—Haplotype networks for the 650-base pairs cytochrome-*b* data include 22 populations from the Baja California Peninsula and southern California. Each small closed circle on the line between adjacent haplotypes in the network represents a single base substitution. The key to the haplotypes is given in Table 1 and Appendix I; some of the haplotypes are present in more than 1 population. A) Network of the clade of the Northern group (southwestern Mojave Desert and Los Angeles Basin); B) network of Southern group (Vizcaíno Desert and Isla Cedros); and C) network of Central group (south of Salton Trough in California and Baja California).

with a 100% bootstrap and the other 2 clades with 99% bootstrap for each one (tree not shown). Bayesian inference converged on essentially the same tree topology (Fig. 4).

The maximum-likelihood analysis with the GTR+G+I evolutionary model produced only 1 tree (score = 2,862.27, AIC = 5,744.54, I = 0.568, G = 4.303; Fig. 4). The tree presents the same 3 main clades, with the exception of the Etiwanda population from the Los Angeles Basin, which is not included within the Northern clade. Whereas maximum-parsimony and Bayesian inference analyses indicate that the Southern and Northern clades are weakly supported sister groups, the maximum-likelihood analysis instead places the Southern and Central clades as sister groups.

DISCUSSION

All analyses are consistent in placing the Isla Cedros population (S) within *C. fallax*, in agreement with Williams et

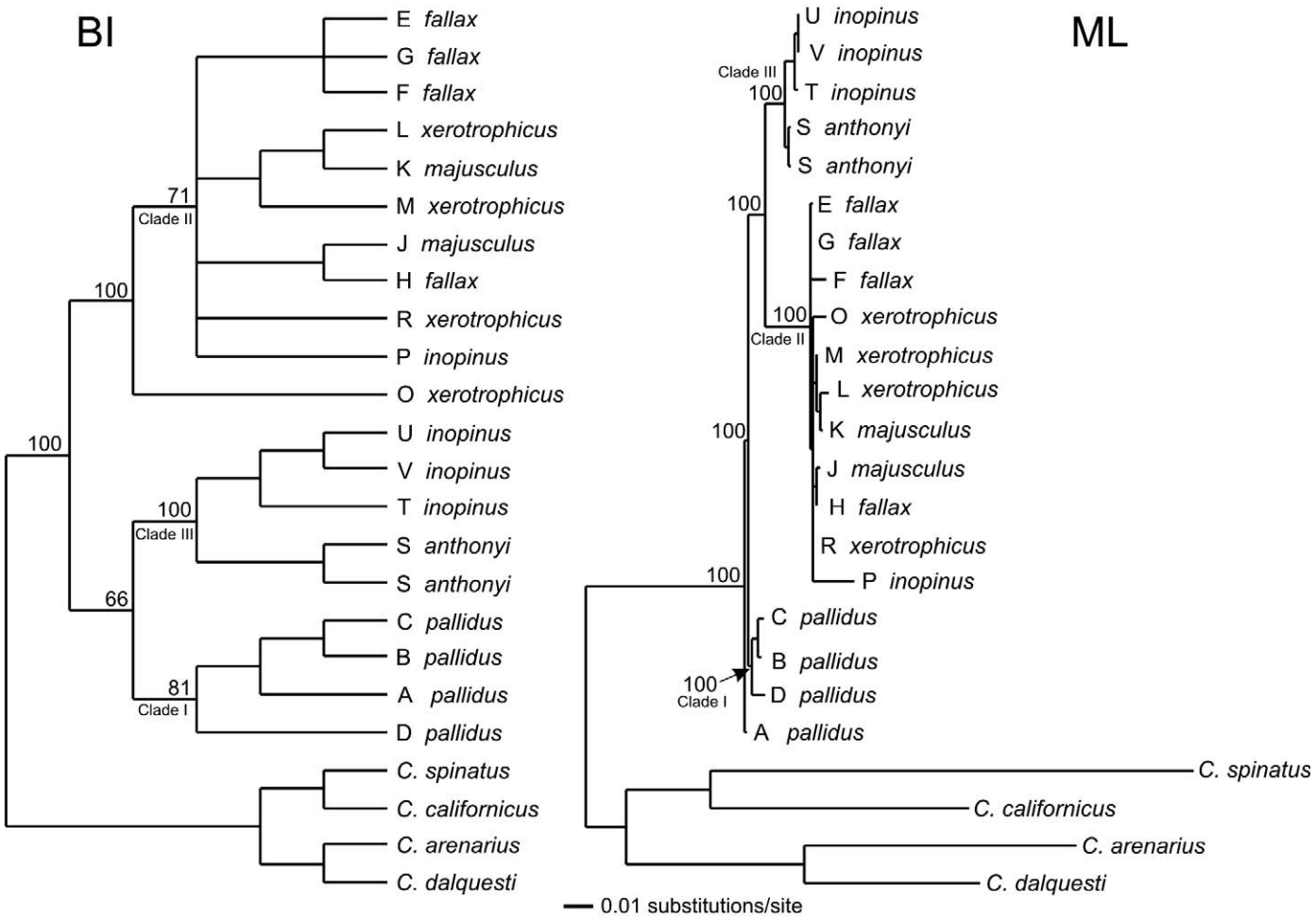

Fig. 4.—Bayesian inference (BI) and maximum-likelihood (ML) trees for *Chaetodipus fallax* constructed from the cytochrome-*b* data set of 20 representative haplotypes (650 base pairs), using *C. arenarius*, *C. californicus*, *C. dalquesti*, and *C. spinatus* as outgroups. I) Northern clade; II) Central clade; and III) Southern clade. At the end of each branch the locality is indicated in a capital letter and the current subspecies are indicated. The values in the nodes are branch support for each of the analyses.

al. (1993). Moreover, all analyses place this population as sister to populations of the adjacent Vizcaíno Desert (T–V) apart from all other *C. fallax*. Three geographic and evolutionary groups are generally consistent across analyses (see later in text) but do not correspond to currently recognized subspecies. Subspecies recognition should be based on characters of the nuclear DNA (e.g., direct sequence data or encoded characters such as morphology). If nuclear characters eventually are found to be concordant with mitochondrial DNA (mtDNA) patterns described herein, for example as was found by Hafner et al. (2008) for 2 species of *Cratogeomys*, each genetic group should be considered a different subspecies.

Three regional groups identified in the AMOVA (Northern = A–D; Central = E–R; and Southern = S–V) also were recognized in the minimum spanning network, Bayesian inference analysis, and maximum-likelihood analysis, except that population A (Los Angeles Basin) was not included within the Northern group in the maximum-likelihood analysis. In contrast, only the Central and Southern groups were identified in the SAMOVA, with the northernmost 2 populations of the Central group (E and F) separated and the Northern group broken into 3 groups. This difference likely results from SAMOVA considering both geographical and genetic distances: the genetic difference among geographically close populations in California is relatively larger. Gene flow among these northern populations may be lower, perhaps reflecting local topographic and edaphic filter-barriers to dispersal (see below).

Hafner and Riddle (2005) and Riddle and Hafner (2006) identified 3 putative vicariant events that might have impacted the distribution and genetic structure of *C. fallax*: the Vizcaíno Desert of the central Baja California Peninsula; Mesa Huatamote (~30°N latitude), which marks the northern margin of the peninsular regional desert (Hafner and Riddle 1997; Riddle et al. 2000b); and the Salton Sea–San Gorgonio Constriction (sensu Murphy 1983), along the Salton Trough. No evidence exists for any impact of a Mesa Huatamote event in mtDNA patterns of *C. fallax*, but the Vizcaíno Desert marks the southern boundary of the species, and the Salton Trough may be coincident with the transition between Northern and Central groups.

TABLE 3.—Genetic distances (%) among representative haplotypes (650 base pairs) from the geographic areas and subspecies. The upper-right portion of the matrix was generated with the Jukes–Cantor model of evolution. Distances in the lower-left matrix were generated with the Kimura 2-parameter model to compare traditional estimates of genetic distance in small mammals. Genetic distances within current subspecies are enclosed in a thin-lined square.

Subspecies	Locality	B	C	E	A	D	F	G	H	J	K	L	M	O	R	P	T	U	V	S
pallidus	B Pioneertown	**0.0**	0.5	3.6	0.9	1.1	4.3	3.5	3.3	3.5	4.0	4.3	3.6	3.8	3.5	5.5	3.0	3.0	3.0	2.7
	C Morongo	0.5	**0.0**	3.8	1.1	1.2	4.4	3.6	3.5	3.6	4.1	4.4	3.8	4.0	3.6	5.6	3.1	3.1	3.1	2.8
	E Borrego	3.7	3.8	**0.0**	3.3	3.8	0.9	0.2	0.5	0.6	0.8	1.1	0.5	0.9	0.3	2.2	3.8	3.8	3.8	3.5
fallax	A Etiwanda	0.9	1.1	3.3	**0.0**	1.1	4.0	3.1	3.0	3.2	3.6	4.0	3.3	3.5	3.1	5.1	2.7	2.7	2.7	2.3
	D Riverside	1.1	1.3	3.8	1.1	**0.0**	4.4	3.6	3.5	3.6	3.8	4.1	3.8	4.0	3.6	5.6	3.1	3.1	3.1	2.5
	F Jacumba	4.3	4.5	0.9	4.0	4.5	**0.0**	0.8	1.1	1.1	1.4	1.4	1.1	1.1	0.9	2.7	4.1	4.1	4.1	3.8
	G Rosarito	3.5	3.7	0.2	3.2	3.7	0.8	**0.0**	0.3	0.5	0.6	0.9	0.3	0.8	0.2	2.1	3.6	3.6	3.6	3.3
	H Ojos Negros	3.3	3.5	0.5	3.0	3.5	1.1	0.3	**0.0**	0.2	0.6	0.9	0.3	0.8	0.2	2.1	3.8	3.8	3.8	3.5
majusculus	J Colonet	3.5	3.7	0.6	3.2	3.7	1.1	0.5	0.2	**0.0**	0.8	1.1	0.5	0.9	0.3	2.2	4.0	4.0	4.0	3.6
	K El Rosario	4.0	4.2	0.8	3.7	3.8	1.4	0.6	0.6	0.8	**0.0**	0.6	0.3	1.1	0.5	2.4	4.1	4.1	4.1	3.8
xerotrophicus	L San Fernando	4.3	4.5	1.1	4.0	4.2	1.4	0.9	0.9	1.1	0.6	**0.0**	0.6	1.1	0.8	2.7	4.1	4.1	4.1	3.8
	M Cataviña	3.7	3.8	0.5	3.3	3.8	1.1	0.3	0.3	0.5	0.3	0.6	**0.0**	0.8	0.2	2.1	3.8	3.8	3.8	3.5
	O Chapala	3.8	4.0	0.9	3.5	4.0	1.1	0.8	0.8	0.9	1.1	1.1	0.8	**0.0**	0.6	2.5	3.6	3.6	3.6	3.3
	R Prieta	3.5	3.7	0.3	3.2	3.7	0.9	0.2	0.2	0.3	0.5	0.8	0.2	0.6	**0.0**	1.9	3.6	3.6	3.6	3.3
inopinus	P San José	5.5	5.7	2.2	5.2	5.7	2.7	2.1	2.1	2.2	2.4	2.7	2.1	2.5	1.9	**0.0**	5.6	5.6	5.6	5.3
	T Tortugas	3.0	3.2	3.8	2.7	3.2	4.2	3.7	3.8	4.0	4.2	4.2	3.8	3.7	3.7	5.7	**0.0**	0.3	0.3	0.9
	U Asunción	3.0	3.2	3.8	2.7	3.2	4.2	3.7	3.8	4.0	4.2	4.2	3.8	3.7	3.7	5.7	0.3	**0.0**	0.0	0.9
	V Abreojos	3.0	3.2	3.8	2.7	3.2	4.2	3.7	3.8	4.0	4.2	4.2	3.8	3.7	3.7	5.7	0.3	0.0	**0.0**	0.9
anthonyi	S Isla Cedros	2.7	2.9	3.5	2.4	2.5	3.8	3.3	3.5	3.7	3.8	3.8	3.5	3.3	3.3	5.4	0.9	0.9	0.9	**0.0**

Recent ecological, in addition to past vicariant, mechanisms could explain the distribution and genetic structure of *C. fallax* in the Vizcaíno Desert. Separation of the Central and Southern groups might be related to the most recent hypothesized Vizcaíno seaway (1 million years ago [mya]—Hafner and Riddle 2008; Riddle and Hafner 2006). However, *C. fallax* does not occur south of the Vizcaíno Desert, unlike other species that show a local genetic discontinuity; for example, *Dipodomys merriami* (Álvarez-Castañeda et al. 2009), *Thomomys umbrinus* (Álvarez-Castañeda and Patton 2004; Trujano-Álvarez and Álvarez-Castañeda 2007), *Ammospermophilus leucurus* (Whorley et al. 2004), and *Chaetodipus rudinoris* and *C. arenarius* (Riddle et al 2000b). Instead, the range of *C. fallax* matches the winter rain pattern of the central-northern region of the Baja California Peninsula (García and Mosiño 1968; Salinas-Zavala et al. 1998). As appears to be the case with *Perognathus longimembris* (Álvarez-Castañeda et al. 2001), the Vizcaíno Desert may pose an ecological barrier to the southward expansion of *C. fallax*.

TABLE 4.—Average distances in percentages (minimum and maximum) between the clades. JC = Jukes–Cantor model, K2P = Kimura 2-parameter model.

Clades	JC	K2P
Northern (I) versus Central (II)	3.9 (3.0–5.6)	3.9 (3.0–3.9)
Central (II) versus Southern (III)	3.9 (3.3–5.6)	4.0 (3.3–5.7)
Northern (I) versus Southern (III)	2.9 (2.3–3.1)	2.9 (2.4–3.2)

The historical geology of the southern California portion of the range of *C. fallax* is perhaps more complex, involving initial marine inundation of the Salton Trough (>5 mya), damming (and desiccation) by sediment from the Colorado River (4 mya), uplift of the Transverse Ranges (San Gabriel and San Bernardino Mountains, 5 mya), flooding of the Salton Trough to form Pleistocene Lake Cahuilla (most recently 10,000 years ago), and climatic oscillations and changing sea levels of the Pleistocene glacial–interglacial periods that were magnified by high regional topography (summarized in Bell et al. 2009). Although Hall (1981) indicates a continuous distribution of *C. fallax* around the Salton Sea, both museum records and the known habitat affinities of the species restrict it to the higher-elevation western margins of the Salton Trough (Fig. 1). Patton and Álvarez-Castañeda (1999) describe the habitat of *C. fallax* as rocky areas within shrub communities on desert slopes and the coast and stony soils above sandy desert fans. The relatively low level of genetic divergence between the Northern and Central groups (3.9%; Table 4) argues against a causative role of the initial Salton Trough marine inundation (at >5 mya) in effecting genetic isolation, as has been invoked for species of *Peromyscus* (subgenus *Haplomylomys*—Riddle et al. 2000a) and *Neotoma* (Patton et al. 2007). Instead, it is likely that Pleistocene events, such as Pleistocene Lake Cahuilla, isolated the Northern group into the southwestern margin of the Mojave Desert, and that relatively low gene flow and high genetic differentiation among the northern populations might have resulted from geographic fragmentation associated with Pleistocene climatic oscillations in this topographically diverse region.

Resumen

Se evaluó la sistemática y filogeografía de *Chaetodipus fallax*, especie restringida a la Península de Baja California y suroeste de California, usando secuencias del gen mitochondrial citocromo-*b* (*Cytb*). Una población isleña (Isla Cedros), *C. f. anthonyi*, fue descrita originalmente como especie separada, pero posteriormente fue considerada como subespecie; sin embargo, no se ha publicado algún análisis morfológico, genético o citogenético que lo soporte. Las relaciones genéticas fueron evaluadas entre las 6 subespecies reconocidas de *C. fallax* (incluyendo la población isleña) y considerando las 3 áreas geográficas que la especie ocupa, basadas en 650 pb del *Cytb* de individuos representativos de 22 poblaciones. Los análisis de varianza molecular, inferencia bayesiana, máxima parsimonia, máxima probabilidad, distancia y análisis de redes indicaron 3 clados: 1) las poblaciones del norte, al sur de el Desierto de Mojave y Los Angeles Basin, al norte del Salton Trough; (2) las poblaciones centrales desde el sur de Salton Trough y a través del estado de Baja California hacia; y (3) las poblaciones del sur, desde el oeste de El Desierto del Vizcaíno, en Baja California Sur, y la Isla Cedros. Todos los análisis claramente soportan la inclusión de *anthonyi* dentro de *C. fallax*. Tres grupos geográficos y evolutivos son delineados; estos no coinciden con las actuales subespecies reconocidas. Cada grupo evolutivo podría ser considerado como subespecies distintas; sin embargo, para aclarar la taxonomía de la especie se requieren análisis morfológicos o con DNA nuclear.

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APPENDIX I

Specimens of *Chaetodipus fallax* are presented in order from north to south with letter of the locality as in Fig. 1 and Table 1, with the specific locality, cytochrome-*b* haplotype found (H*n*), and catalog number in the mammal collection of the Centro de Investigaciones Biológicas del Noroeste (CIB) or Museum of the Vertebrate Zoology, University of California, Berkeley (MVZ). The sequence with AY initials was obtained from GenBank (accession number), and those with GQ were generated for this study.

Specimens examined.—A) Etiwanda Wash: Etiwanda Wash, 2 mi N State Hwy. 30, H1 (MVZ 182929, GQ175230). B) Pioneertown: 1.2 mi E Pioneertown, H2 (MVZ 199944, GQ175231); H3 (MVZ 199945; GQ175232); H4 (MVZ 199946, GQ175233). C) Morongo Valley: E end Morongo Valley, H5 (MVZ 199941, GQ175234); H6 (MVZ, 199942, GQ175235); H7 (MVZ 199943, GQ175236). D) Banning, Riverside Co.: 1.5 mi S Banning, Riverside Co., H1 (MVZ 196189, GQ175237); H8 (MVZ 196186, MVZ 196187, GQ175238); H9 (MVZ 196188, GQ175239). E) Borrego Spring: 3.3 mi S Borrego Spring, H10 (MVZ 182932, GQ175240). F) Jacumba: 5 mi E Jacumba, H11 (MVZ 198445, GQ175241). G) Rosarito: 10.4 km SE Rosarito, H12 (CIB 8745, GQ175242); H13 (CIB 8744, CIB 8746, CIB 8748, GQ175243); H14 (CIB 8747, GQ175244). H) Ojos Negros: 2 km N, 9 km E Ojos Negros, H15 (CIB 7007, GQ175245); H16 (CIB 7008, GQ175246); H17 (CIB 7009, GQ175247); H18 (CIB 7010, GQ175248); H19 (CIB 7011, GQ175249). I) San Vicente: 9 km S, 7 km E San Vicente, H20 (CIB 7014, GQ175250); H21 (CIB 7016, GQ175251); H22 (CIB 7017, GQ175252). J) Colonet: 19.5 km S, 31.2 km E Colonet, H23 (CIB 10269, GQ175253); H24 (CIB 10270, GQ175254). K) El Rosario: 13.2 km N, 5.7 km W El Rosario, H25 (CIB 10276, CIB 10277, CIB 10278, GQ175255). 10.2 km N, 6.7 km W El Rosario, H26 (CIB 10297, GQ175256); H27 (CIB 10298, GQ175257). L) Misión San Fernando: Misión San Fernando, H28 (AY926402). M) Cataviña: Cataviña, H29 (CIB 2489, GQ175258); H30 (CIB 2490, GQ175259); H31 (CIB 2491, GQ175260). N) Pico Fernando: 23.2 km S, 3.5 km W Cataviña, H32 (CIB 10279, GQ175261). O) Laguna Chapala: 5 km S, 5 km W Laguna Chapala, H33 (CIB 2516, GQ175262); H34 (CIB 2517, GQ175263); H35 (CIB 2518, GQ175264). Laguna Chapala, H36 (CIB 2520, GQ175265). P) San José: 35.2 km N, 68 km W Punta Prieta, H37 (CIB 10287, GQ175266). Q) Punta Blanca: 23.5 km N, 54.7 km W Punta Prieta, H38 (CIB 10290, GQ175267); H39 (CIB 10291, GQ175268). R) Punta Prieta: Punta Prieta, H18 (CIB 2478, CIB 2524, CIB 2525, GQ175269). S) Isla Cedros: Isla Cedros, H40 (CIB 13044, CIB 13053, GQ175270; 13054); H41 (CIB 13045, GQ175271). T) Bahía Tortugas: 2.5 km N, 7.7 km E Bahía Tortugas, H42 (CIB 10262, GQ175272). U) Bahía Asunción: 13.7 km N, 11.6 km W Bahía Asunción, H43 (CIB 9499, GQ175273); H44 (CIB 9501, GQ175274). V) Punta Abreojos: 26.5 km N, 19.5 km W Punta Abreojos, H45 (CIB 9504, CIB 9505, CIB 9506, CIB 9508, GQ175275); H43 (CIB 9507, GQ175276).