The LINNEAN SOCIETY of London
ZOOLOGICAL Journal of the Linnean Society

Zoological Journal of the Linnean Society, 2010. With 5 figures

Revision of *Chaetodipus arenarius* (Rodentia: Heteromyidae)

SERGIO TICUL ÁLVAREZ-CASTAÑEDA* and EVELYN RIOS

Centro de Investigaciones Biológicas del Noroeste, Mar Bermejo 195, Col. Playa Palo de Santa Rita, La Paz, Baja California Sur, 23090, México

Received 16 March 2008; accepted for publication 14 September 2009

Chaetodipus arenarius is an endemic species of the Baja California Peninsula. It has undergone taxonomic changes in the last few years. Today, two species, *C. arenarius* and *Chaetodipus dalquesti*, are formally recognized with an unknown range for each. However, genetic analysis showed the possible presence of a third species. The objectives of this study were to use molecular data (cytochrome *b* and cytochrome *c* oxidase subunit III genes) to determine how many genetic groups are present in *C. arenarius* in the Baja California Peninsula; if these groups have morphological characteristics that could be used to distinguish them; if the genetic groups have limited distributions; identify taxonomic implications; and establish if there are any associations amongst genetic groups and different habitats. Bayesian inference, maximum parsimony, maximum likelihood, distance optimality criteria, and minimum spanning network indicated three monophyletic groups with high genetic differences (5.54–13.59%). These groups are morphologically diagnosable based on pelage and morphometric characters and geographical range. The three genetic groups correspond to three taxa previously described as subspecies or species. Based on our results, these should be considered to be different species: *C. arenarius* occupies the most extreme habitats with hot summers; *C. dalquesti* occupies the moistest coastal areas in the southern part of the peninsula, and *Chaetodipus siccus* is restricted by mountain ranges to the isolated Los Planes Basin and Cerralvo Island.

doi: 10.1111/j.1096-3642.2009.00630.x

ADDITIONAL KEYWORDS: Baja California Peninsula – distribution – ecology – endemic – genetic structure – Mexico – molecular phylogenetics – mtDNA – rodents.

INTRODUCTION

The pocket mice *Chaetodipus arenarius* Merriam (1894) and *Chaetodipus dalquesti* Roth (1976) (Heteromyidae) were formally recognized (Patton, 2005) as endemic to the Baja California Peninsula of Mexico. However, the distribution of both species is not clear and has not been completely defined. For many years, *C. arenarius* was the only small species of the genus *Chaetodipus* lacking stiff bristles or spines and ranged widely on the peninsula (Hall & Kelson, 1959; Williams, Genoways & Braun, 1993; Patton & Álvarez-Castañeda, 1999) until *C. dalquesti* was described by Roth (1976: 562) from specimens found 6.4 km south-east of Migriño at the south-western tip of the Baja California Peninsula. The range of *C. dalquesti* has never been clearly defined but is considered sympatric with *C. arenarius* (Roth, 1976); both species have been recorded in the same localities (Pescadero, Tres Pachitas; Hall, 1981).

The diagnostic characteristics of *C. dalquesti* said that are larger in sizes than in *C. arenarius*, tail longer, dark, and distinctly crested; possessing numerous weak spine bristles in the rump; pelage grizzled; bullae moderately inflated; posterior palatal pits small; nasal bones long (Roth, 1976). However, the karyotypes of *C. dalquesti* and *C. arenarius* do not show differences (Hafner & Hafner, 1983). Hence, in the compilation of the taxonomy of the Heteromyidae family, *C. dalquesti* was considered a junior synonym

---

*Corresponding author. E-mail: sticul@cibnor.mx of *C. arenarius,* based on the karyotypes and the absence of morphological characteristics that could be used to differentiate it from *C. arenarius* (Williams *et al.*, 1993). Since then, many authors working in this area have not accepted *C. dalquesti* as a valid species (Lackey, 1991; Patton, 1993; Álvarez-Castañeda, 1998; Patton & Álvarez-Castañeda, 1999).

A genetic analysis of *C. arenarius* showed the possibility that two different species could be present on the peninsula (Riddle *et al.*, 2000) and that the second species could be *C. dalquesti*. As a species, it was added to the revision of the *Mammal Species of the World* (Patton, 2005). However, only a few specimens have been found, and no distribution pattern has been described.

Over many years of field research in the Baja California Peninsula, specimens in the *C. arenarius* complex were collected in coastal areas with high humidity and epiphytic plants that had morphological characteristics that seemed to be different from *C. arenarius* (S. T. Álvarez-Castañeda, pers. observ.); however, it was difficult to make quantitative evaluations. Additionally, two populations of pocket mice east of the Sierra de La Giganta were found where the species was previously unknown. A review of specimens of *C. arenarius* covering all of the peninsula and adjacent islands in the Gulf of California and Pacific Ocean was undertaken to compare specimens found in the foggy scrubland from the Pacific and the Gulf side of the peninsula with specimens from sandy and dryer habitats.

The goals of the work described here were to use molecular data (cytochrome *b* and cytochrome *c* oxidase subunit III genes) to determine how many genetic groups are present in *C. arenarius* of the peninsula. Whether the differences amongst groups are related at the species level using phylogenetic and genetic species concepts, if those genetic groups have morphological characteristics that could be used to distinguish them, and if the genetic groups have restricted distribution ranges. Additionally, we evaluated taxonomic implications and whether any genetic group is limited to the foggy scrubland.

MATERIAL AND METHODS

FIELD SURVEY AND SPECIMEN COLLECTION

The specimens were collected from 1994 to 2008 from the Baja California Peninsula and adjacent islands (Table 1; Fig. 1) as part of a general survey as well as several projects (1547 specimens, 710 tissues). Transects containing 40 live traps each (Sherman traps, H. B. Sherman Co., Tallahassee, Florida) were set and baited with rolled oats. In all instances, handling of animals was performed according to the recommendations of the American Society of Mammalogists (Gannon *et al.*, 2007). Identification, sample size, catalogue numbers, and localities are listed in the Appendix. Voucher specimens were deposited in the Centro de Investigaciones Biológicas del Noroeste (CIB) mammal collection, La Paz, B.C.S., Mexico.

INFERENCE OF PHYLOGENY

Laboratory procedures

Genomic DNA was extracted in the laboratory from liver tissues preserved in 95% ethanol, using the DNeasy kit DNA (QIAGEN, Valencia, California). The first part of the cyt *b* gene (~800 bp) was amplified for the minimum spanning network with primer pairs MVZ05/MVZ16 and the second part of the cyt *b* (~600 bp) for phylogenetic analyses with MVZ127/MVZ14 (primer sequences given in Smith & Patton, 1993; Smith, 1998). The addition of both fragments gave the 1140 bp of the complete cyt *b* gene. A 690-bp fragment of the cytochrome *c* oxidase subunit III (COIII) gene was amplified with primer pairs L8618/H9323 described by Riddle (1995).

The following conditions for initial double-strand amplifications were used for the two genes: 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) deoxyribonucleotide triphosphate, 0.5 μL (3 mM) $MgCl_2$, 0.125 μL Taq polymerase, and 1× Taq buffer to a final volume of 25 μL. Amplification conditions consisted of 3 min initial denaturation at 94 °C followed by 37 cycles of denaturation at 94 °C for 45 s, 1 min annealing at 50 °C, and 1 min extension at 72 °C. Amplified products were purified using the QIAquick PCR Purification Kit (QIAGEN).

The templates were cycle-sequenced with MVZ05/MVZ16, MVZ127/MVZ14, and MVZ45/MVZ14 for cyt *b* amplifications and L8618/H9323 for COIII (reverse strand MVZ16, MVZ14, and H9323 sequenced in ten representative subsets of haplotypes to check for accuracy) using the Taq FS Kit (Applied Biosystems, Foster City, California) and run on an ABI 377 automated sequencer (Applied Biosystems). The haplotypes included in Table 1 were deposited in GenBank (accession numbers: GQ241420–GQ241441, GQ241463–GQ241540 for cyt *b*; GQ241442–GQ241462 for COIII). A sequence of cyt *b* from *C. arenarius* from GenBank (AY926400) was included in the analyses. We used four species as outgroups, following Alexander & Riddle (2005): *Chaetodipus spinatus* and *Chaetodipus californicus* from the same clade and *Chaetodipus baileyi* and *Chaetodipus rudinoris* from a different clade (Table 2).

Table 1. Localities ($N = 34$) of the species of the *Chaetodipus arenarius* complex

Geographical group	Sp	State	Locality	Latitude	Longitude	Hap$_{\text{No.GenBank, No. spec.}}$
1	A	BC	San Felipe	30.93359	–114.76669	$1_{\text{AY926399, 2903, 6699-6702}}$
2	A	BC	San Quintín	30.34833	–115.81833	$2_{\text{GQ241420, 6802}}$, $3_{\text{GQ241463, 6803, 6804, 6806}}$, $4_{\text{GQ241464, 6805}}$
3	A	BC	El Rosario	30.09611	–115.66222	$5_{\text{GQ241465, 6808-6810}}$, $6_{\text{GQ241466, 6811}}$
4	A	BC	San Luis Gonzaga Bay	29.9575	–114.5025	$7_{\text{GQ241467, 2915, 2917}}$
5	A	BC	De Los Angeles Bay	28.87389	–113.53	$8_{\text{GQ241468, 6818}}$, $9_{\text{GQ241421, 6819}}$
6	A	BC	Santo Domingo	28.31811	–113.89489	$12_{\text{GQ241471, 10159, 10162}}$, $13_{\text{GQ241472, 10161}}$, $14_{\text{GQ241473, 11616}}$
7	A	BC	El Barril	28.29639	–112.87056	$10_{\text{GQ241469, 11632}}$, $11_{\text{GQ241470, 11633}}$
8	A	BCS	Guerrero Negro	28.26511	–113.91711	$12_{\text{GQ241471, 9331, 9332}}$, $15_{\text{GQ241474, 6857}}$, $16_{\text{GQ241422, 9330, 9333}}$, $17_{\text{GQ241475, 9334}}$
9	A	BCS	El Arco	28.20972	–113.51861	$12_{\text{GQ241471, 11626}}$, $18_{\text{GQ241476, 11619}}$, $19_{\text{GQ241477, 11621}}$, $20_{\text{GQ241478, 11622}}$, $21_{\text{GQ241479, 11624}}$
10	A	BCS	Vizcaíno	28.03333	–113.96667	$12_{\text{GQ241471, 9856}}$, $24_{\text{GQ241482, 9854}}$, $25_{\text{GQ241483, 9855}}$, $26_{\text{GQ241484, 9857}}$
11	A	BCS	Bahía Tortugas	27.78335	–114.69719	$22_{\text{GQ241480, 6839, 6840}}$, $23_{\text{GQ241481, 6842}}$
12	A	BCS	San Ignacio	27.29761	–112.89247	$12_{\text{GQ241471, 8710}}$, $27_{\text{GQ241423, 8711, 8712}}$, $28_{\text{GQ241485, 9004}}$, $29_{\text{GQ241486, 9005}}$
13	A	BCS	Punta Abreojos	27.00861	–113.43917	$30_{\text{GQ241487, 6891}}$, $31_{\text{GQ241488, 6873}}$
14	A	BCS	San Juanico	26.48278	–112.68722	$12_{\text{GQ241471, 9315, 9317}}$, $32_{\text{GQ241424, 9314}}$, $33_{\text{GQ241489, 9318}}$, $34_{\text{GQ241490, 9316}}$
15	A	BCS	La Purísima	26.4375	–112.76528	$32_{\text{GQ241424, 6724, 6726, 6729}}$, $33_{\text{GQ241489, 6725}}$, $35_{\text{GQ241491, 6723}}$
16	A	BCS	Comondú	26.07083	–111.84236	$36_{\text{GQ241425, 9325}}$
17	A	BCS	Loreto	25.99889	–111.34361	$37_{\text{GQ241426, 1301}}$, $38_{\text{GQ241492, 1323}}$, $39_{\text{GQ241493, 1324}}$
18	A	BCS	San Jorge	25.72611	–112.07417	$40_{\text{GQ241494, 6745}}$, $41_{\text{GQ241427, 6741}}$, $42_{\text{GQ241495, 6744, 6747}}$, $43_{\text{GQ241496, 6746}}$, $44_{\text{GQ241497, 7913}}$, $45_{\text{GQ241498, 7914}}$
19	A	BCS	Insurgentes	25.41972	–111.88333	$46_{\text{GQ241499, 6752}}$, $47_{\text{GQ241500, 6753, 6754}}$, $48_{\text{GQ241501, 6755}}$, $49_{\text{GQ241502, 6756}}$
20	A	BCS	López Mateos	25.18475	–112.05944	$40_{\text{GQ241494, 6227}}$, $50_{\text{GQ241503, 6228}}$, $52_{\text{GQ241504, 6223}}$, $53_{\text{GQ241505, 6224}}$
20	D	BCS	López Mateos	25.18475	–112.05944	$51_{\text{GQ241428, 6222}}$, $54_{\text{GQ241506, 6225}}$
21	D	BCS	Constitución	25.03861	–111.65247	$51_{\text{GQ241428, 6262}}$, $55_{\text{GQ241429, 6264}}$
22	D	BCS	San Evaristo	24.89333	–110.71722	$56_{\text{GQ241430, 8714-8716}}$
23	A	BCS	San Carlos	24.77417	–112.07889	$57_{\text{GQ241507, 6242}}$, $58_{\text{GQ241431, 6243}}$, $59_{\text{GQ241508, 6244}}$, $60_{\text{GQ241509, 6246}}$, $61_{\text{GQ241510, 6247}}$
24	D	BCS	San Juan de la Costa	24.63917	–110.74028	$62_{\text{GQ241511, 6907, 6921}}$
25	A	BCS	Magdalena Island	24.63894	–112.14086	$63_{\text{GQ241432, 149}}$
26	A	BCS	Medano	24.53778	–111.5025	$61_{\text{GQ241510, 6269}}$, $64_{\text{GQ241433, 5559}}$, $65_{\text{GQ241512, 6739}}$
26	D	BCS	Medano	24.53778	–111.5025	$50_{\text{GQ241503, 6267}}$, $66_{\text{GQ241513, 6740}}$
27	D	BCS	Margarita Island	24.43892	–111.82581	$67_{\text{GQ241514, 5957-5959}}$, $68_{\text{GQ241515, 5960}}$
28	A	BCS	El Mogote, La Paz	24.16667	–110.35	$69_{\text{GQ241516, 158}}$, $70_{\text{GQ241517, 159}}$, $71_{\text{GQ241518, 160}}$, $72_{\text{GQ241519, 161}}$
29	S	BCS	Cerralvo Island	24.16111	–109.86389	$73_{\text{GQ241434, 230; GQ241440, 235.}}$
30	D	BCS	La Paz	24.13758	–110.46736	$74_{\text{GQ241520, 1840}}$, $75_{\text{GQ241521, 1841}}$, $76_{\text{GQ241522, 1842}}$, $77_{\text{GQ241523, 1843}}$, $78_{\text{GQ241524, 1844}}$, $79_{\text{GQ241525, 1926}}$
30	A	BCS	La Paz	24.13758	–110.46736	$80_{\text{GQ241526, 1905}}$
31	S	BCS	Ensenada de Muertos	23.99922	–109.82694	$81_{\text{GQ241527, 5600}}$, $82_{\text{GQ241435, 5601}}$, $83_{\text{GQ241528, 5604}}$; $84_{\text{GQ241529, 5602}}$, $85_{\text{GQ241530, 5603}}$
32	D	BCS	Tres Pachitas	23.74	–110.20056	$86_{\text{GQ241436, 6766}}$, $87_{\text{GQ241531, 6767}}$, $88_{\text{GQ241532, 6768}}$
33	D	BCS	Todos Santos	23.71625	–110.23331	89_{AY926400}
34	D	BCS	Migriño	23.3525	–110.18917	$90_{\text{GQ241533, 6281}}$, $91_{\text{GQ241532, 6282}}$, $92_{\text{GQ241437, 6284}}$, $93_{\text{GQ241535, 6290}}$, $94_{\text{GQ241536, 6291}}$, $95_{\text{GQ241537, 6292}}$, $96_{\text{GQ241538, 6294}}$, $97_{\text{GQ241539, 6296}}$, $98_{\text{GQ241540, 6288}}$
Outgroups						
Chaetodipus baileyi						AY926393
Chaetodipus rudinoris						AY926397
Chaetodipus spinatus						AY926398
Chaetodipus californicus						AY926401

The columns contain: geographical group numbers as used in Figure 1, species designation (Sp; A, *C. arenarius*; D, *C. dalquesti*; S, *C. siccus*); state (BC, Baja California; BCS, Baja California Sur); and haplotype (cytochrome *b*) number (Hap) used in Figures 2 and 3; the subscripts are the GenBank accession and voucher numbers of specimens with the haplotype for the locality.

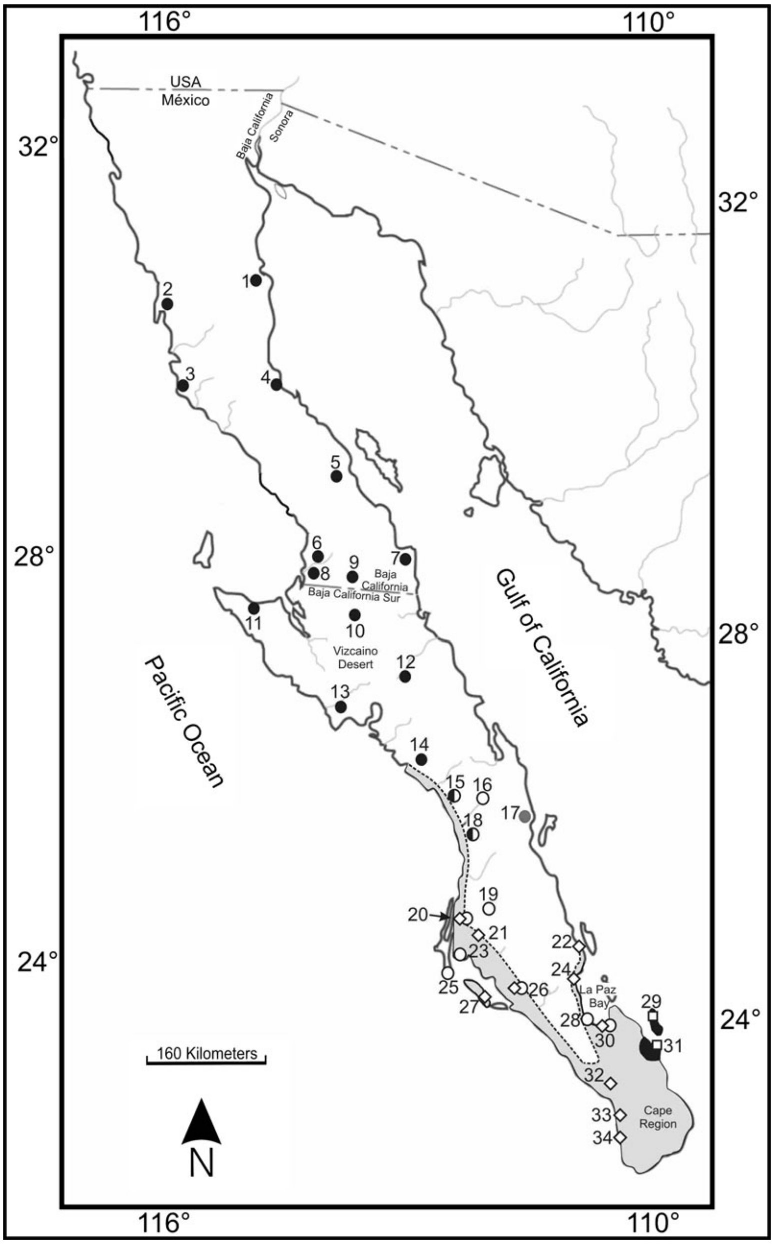

Figure 1. Location of *Chaetodipus arenarius* specimens examined for sequencing. Black-filled circles are the Northern subnetwork, open circles the Southern subnetwork, and grey-filled circles the Gulf of California subnetwork of *C. arenarius*. The localities with half-filled circles have specimens from all subnetworks. Rhomboids are the locations of *Chaetodipus dalquesti* and squares are the locations of *Chaetodipus siccus*. The distributions of the three species are shaded in different colours: white for *C. arenarius*, grey for *C. dalquesti*, and black for *C. siccus*. The specimens and geographical groups are listed in Table 1. The dashed line shows the hypothetical borders between species.

Sequence alignments and haplotype determination

Nucleotide sequences were aligned using Sequencher ver. 3.1 software (Gene Codes, Ann Arbor, Michigan). This was visually checked and translated into amino acids for confirmation of alignment. Initially, we obtained a set of 146 sequences of a 656-bp fragment of cyt *b*; the TCS ver. 1.18 program (Clement, Posada & Crandall, 2000) was used to identify 98 unique haplotypes. From these haplotypes, we selected 21 haplotypes that correspond to representative specimens of the geographical groups. The geographical groups were selected based on possible contact areas amongst species (geographical groups 14 to 27, with the exception of 19 and 24) and those that are repre-

Table 2. Genetic distances (%) obtained from the concatenation of the cytochrome *b* (1140 bp) and cytochrome *c* oxidase subunit III (690 bp) genes amongst (upper and lower matrices) and within (diagonal, bold) the proposed species of the *Chaetodipus arenarius* complex examined here

	Chaetodipus arenarius	*Chaetodipus dalquesti*	*Chaetodipus siccus*	*Chaetodipus rudinoris*	*Chaetodipus baileyi*	*Chaetodipus spinatus*
Chaetodipus arenarius	**3.68**	12.87	13.28	23.97	24.64	20.06
Chaetodipus dalquesti	13.14	**0.53**	5.48	24.22	24.61	20.21
Chaetodipus siccus	13.59	5.54	**0.22**	24.31	24.63	20.04
Chaetodipus rudinoris	23.77	23.93	24.01	**0.00**	12.70	24.60
Chaetodipus baileyi	24.37	24.27	24.29	13.01	**0.00**	24.19
Chaetodipus spinatus	19.69	19.78	19.59	24.25	23.87	**0.00**

The lower-left matrix was generated using the general time reversible model with invariable sites and gamma-distributed amongst-site rate variation best model of evolution. Distances in the upper-right matrix and on the diagonal (bold) were generated using the Kimura-2-parameter model to allow comparison to traditional estimates of genetic distance in small mammals. *Chaetodipus spinatus*, *C. baileyi*, and *C. rudinoris* were used as the outgroup.

sentative of one species, such as: *C. arenarius* (2, 5, 8, and 12), *C. dalquesti* (33 and 34), and *C. siccus* (29 and 31). For this subset of specimens, the complete cyt *b* gene (1140 bp) was sequenced. To increase the number of characters available for the concatenated analysis, we then sequenced the COIII gene (690 bp) from the same 21 specimens from which we obtained the complete cyt *b* gene.

Two separate analyses were conducted. First, a minimal spanning network was performed based on the 656-bp fragment of cyt *b* from 146 specimens. Second, a phylogenetic analysis was performed. Initially we analysed the sequence data for the two genes separately and found a general concordance. Both revealed the major lineages identified by the network. We then concatenated the data for the 21 representative specimens (1140 bp of cyt *b* and 690 bp of the COIII gene). To estimate haplotypic and nucleotide variations within the groups, we used ARLEQUIN vs. 2.001 software (Schneider, Roessli & Excoffier, 2000).

Phylogenetic analyses

The general time reversible model with invariable sites and gamma-distributed amongst-site rate variation (GTR + I + G; Tavaré, 1986) was shown to be the most appropriate model for this dataset, using the MrModeltest ver. 2 model-comparisons software (Nylander, 2004) with the Akaike information criterion for the concatenated complete cyt *b* and COIII fragments. The frequency of bases was: A = 0.288, C = 0.266, G = 0.112, and T = 0.332.

A Bayesian analysis was performed using MrBayes ver. 3.1.1 software (Ronquist & Huelsenbeck, 2003). Four separate runs were performed with Markov chain Monte Carlo simulations starting from a random tree. Each run was conducted with 5 000 000 generations and sampled at intervals of 1000 generations. The first 2000 samples of each run were discarded as burn-in and all the remaining sampled trees were analysed to find the posterior probability of clades. A consensus tree was generated with the 50% majority-rule algorithm in PAUP ver. 4.0b10 software (Swofford, 2000) and the percentage of samples recovered in a particular clade was assumed to be that clade's posterior probability.

Maximum parsimony (MP) and maximum likelihood (ML) analyses were implemented in PAUP ver. 4.0b10 (Swofford, 2000). For MP analysis, all characteristics were weighted equally and heuristic searches were performed with 1000 random additions of sequences and tree-bisection reconnection (TBR) algorithm for branch swapping. For all the analyses that resulted in multiple, most parsimonious trees, consensus trees were constructed using the 50% majority rule. The GTR + I + G was the best model for the cyt *b* and COIII fragments and was then used for ML searches consisting of 100 random replicates with TBR branch swapping. Bootstrap values ≥ 50% are reported for branch support. The following sequences were extracted from GenBank to use as outgroups: *C. baileyi* (cyt *b* = AY926393 and COIII = AY009310), *C. rudinoris* (cyt *b* = AY926397 and COIII = AY009267), *C. californicus* (cyt *b* = AY926401 and COIII = AY009259), and *C. spinatus* (cyt *b* = AY926398 and COIII = AY009263).

Genetic distances were calculated using the GTR + I + G, the most appropriate model, and the Kimura 2 parameter, which is the most commonly used model for comparing levels of divergence amongst studies (Baker & Bradley, 2006). A neighbor-joining analysis was conducted in PAUP ver. 4.0b10 (Swofford, 2000). Support for nodes was assessed with bootstrap analyses, including a fast heuristic procedure with 1000 pseudoreplicates.

Genetic structure

Intraspecific cyt *b* gene genealogies were implemented in the program ARLEQUIN ver. 2.001 software (Schneider *et al.*, 2000). This program allows the estimation of phylogenetic relationships when there are low levels of divergence and provides a 95%-plausible set for all haplotype connections. A minimal spanning network was obtained showing the relationship amongst haplotypes.

MORPHOLOGY

Pelage characteristics

Pelage characteristics were considered as diagnostic in the original description of *C. dalquesti* to distinguish it from *C. arenarius* (Roth, 1976: 562). We examined the pelage characteristics of individuals to observe presence or lack of the weakly developed rump spines by direct observation and with a stereoscopic microscope (Leica 626).

Morphometric analysis

Morphometric analyses were limited to 223 adult specimens defined as having complete adult dentition, with all teeth showing some wear, and the auditory bullae revealing some translucence. The specimens were placed in one of three groups defined by the result of the phylogenetic analysis: (1) peninsular, includes specimens from the type locality of *C. arenarius,* the State of Baja California and north-central part of State of Baja California Sur (*N* = 97); (2) the Cape Region, from the type locality of *C. dalquesti*, the Cape Region and the coastal areas of Baja California Sur (*N* = 60); (3) the Cerralvo, on Cerralvo Island, the type locality of *C. arenarius siccus* Osgood, 1907 and the Los Planes Basin that faces the island (*N* = 60).

Nineteen measurements of each cranium were taken with callipers (0.01 mm resolution; all measurements in the text expressed in mm). Skull measurements were: GLS, greatest length; OBL, occipitobasal length; PL, palatal length; PIL, palatinal length, NL, nasal length; PPL, postpalatal length; ML, mandible length; MTR, mandible tooth row length; MXR, maxillar tooth row length; ANW, anterior nasal width; PNW, posterior nasal width; BW, bulla width; MW, mastoidal width; M1W, first upper molar width; WM1, width across first upper molar; DL, diastema length; IW, interparietal width; IL, interparietal length; SD, skull depth. Specimens did not show any systematic sex ratio bias; sexes were combined for these analyses.

Measurements of the three groups of specimens were analysed by one-way ANOVA of individual characters and Tukey's *post hoc* test (Table 3). The 19 measurements were used in a discriminant function analysis. The three groups tested in the analysis were defined based on the genetic data (Table 4). The statistical tests were applied with STATISTICA ver. 5.0. software (StatSoft, Inc., Tulsa, Oklahoma).

RESULTS

PHYLOGENETIC RELATIONSHIPS

Bayesian inference (four replicates) of the molecular data of the concatenated cyt *b* and COIII genes converged on essentially identical tree topologies with the MP, ML, and neighbor-joining analysis (Fig. 2). This result shows three monophyletic clades (100% support): Clade I represents the samples from the Peninsula that occupy the noncoastal areas of the southern part of the peninsula, from the Vizcaino Desert northward and all the sandy habitats for the species. This clade includes specimens from San Jorge, the type locality of *C. arenarius.* Clade II contains specimens from coastal areas on the Pacific side of the central peninsula, Margarita Island, and the south-western part of the Gulf side. This clade included specimens from Migriño (4 miles south-east of Migriño), which is the type locality of *C. dalquesti*. Clade III includes specimens from Cerralvo Island and the basin facing the island. The clade includes specimens from the island that is the type locality of *C. a. siccus.* No internal structure was found in this clade.

The ML analysis with the GTR + I + G evolution model produced one tree (score = 7589.0, Fig. 2B). The MP analysis yielded four trees (length = 1160, consistency index = 0.689, retention index = 0.858). The consensus tree is shown in Figure 2C. The GTR + I + G was the best-fit model of nucleotide substitution (A = 0.288, C = 0.266, G = 0.112, and T = 0.332, invariable sites = 0.591, and gamma distribution = 2.589).

The neighbor-joining analysis showed that clade I has three subclades with strong geographical relationships. Clade Ia includes specimens northward to the Vizcaino Desert; Clade Ib contains specimens southward to the Vizcaino Desert and Magdalena Island; and Clade Ic contains specimens from the Loreto area on the Gulf side in the middle part of the State of Baja California Sur (Fig. 2D). The specimens from the Cape Region and Cerralvo Island have 13.14 and 13.59% sequence divergence, respectively, from specimens from the Peninsula (Table 2).

PHYLOGEOGRAPHY

The minimal spanning network obtained from the cyt *b* sequences showed the relationship amongst 98 unique haplotypes of cyt *b* (Table 1). Of these, 92 haplotypes (94%) were apparently limited to a single locality. Five of the six haplotypes found at more than

Table 3. Values of measured characters, mean ± standard deviation (max – min) from the three groups of specimens

Trait	Cape region (*Chaetodipus dalquesti, N* = 60)	A	Peninsular (*Chaetodipus arenarius, N* = 97)	B	Cerralvo Island (*Chaetodipus siccus, N* = 60)	C
GLS	24.91 ± 0.72 (26.15–22.42)	**	22.93 ± 0.71 (24.11–21.42)	**	25.00 ± 0.72 (27.06–23.49)	NS
OBL	22.07 ± 1.35 (23.65–12.96)	**	20.25 ± 0.69 (21.52–18.19)	**	22.02 ± 1.25 (24.28–14.32)	NS
PL	13.30 ± 0.62 (14.38–10.48)	**	11.90 ± 0.55 (13.20–10.62)	**	13.32 ± 0.58 (15.06–12.24)	NS
PIL	10.17 ± 0.66 (13.51–8.43)	**	9.29 ± 0.43 (10.50–8.02)	**	10.11 ± 0.39 (11.08–9.33)	NS
NL	9.71 ± 0.39 (10.71–8.77)	**	9.06 ± 0.50 (10.06–7.59)	**	9.90 ± 0.54 (11.32–8.89)	*
PPL	6.97 ± 0.29 (7.76–6.38)	**	6.54 ± 0.54 (7.73–5.34)	**	6.88 ± 0.52 (8.18–4.13)	NS
ML	10.72 ± 0.41 (11.45–8.59)	**	9.90 ± 0.43 (10.93–8.83)	**	10.57 ± 0.39 (11.53–9.72)	NS
MTR	3.00 ± 0.16 (3.55–2.66)	**	2.83 ± 0.20 (3.48–2.41)	**	3.13 ± 0.22 (3.63–2.79)	**
MXR	3.23 ± 0.18 (3.76–2.88)	**	3.06 ± 0.24 (3.66–2.45)	**	3.32 ± 0.21 (3.86–2.64)	*
ANW	1.71 ± 0.15 (2.23–1.28)	**	2.03 ± 0.26 (2.58–1.48)	**	1.81 ± 0.16 (2.11–1.36)	*
PNW	2.16 ± 0.18 (2.51–1.82)	*	2.11 ± 0.19 (2.68–1.55)	NS	2.18 ± 0.20 (2.76–1.75)	NS
BW	3.93 ± 0.17 (4.29–3.52)	**	3.49 ± 0.19 (3.91–3.00)	**	3.90 ± 0.19 (4.33–3.58)	NS
MW	13.08 ± 0.37 (13.84–12.13)	**	11.84 ± 0.39 (12.65–10.68)	**	13.00 ± 0.35 (14.01–12.22)	NS
M1W	1.03 ± 0.04 (1.17–0.96)	NS	1.01 ± 0.06 (1.19–0.66)	**	1.05 ± 0.06 (1.30–0.89)	*
WM1	2.22 ± 0.12 (2.51–1.92)	**	2.00 ± 0.16 (2.25–1.51)	**	2.21 ± 0.17 (2.66–1.76)	NS
DL	6.12 ± 0.24 (6.60–5.54)	**	5.51 ± 0.28 (5.99–4.44)	**	6.03 ± 0.25 (6.63–5.59)	NS
IW	7.11 ± 0.41 (7.94–5.82)	**	6.74 ± 0.36 (7.46–5.86)	**	6.93 ± 0.39 (7.71–6.06)	*
IL	3.79 ± 0.30 (4.74–3.27)	**	3.48 ± 0.34 (4.07–2.67)	NS	3.55 ± 0.28 (4.29–2.98)	**
SD	8.42 ± 0.26 (9.02–7.73)	**	7.98 ± 0.45 (9.54–7.01)	**	8.30 ± 0.16 (8.77–7.98)	NS

A, significance level between Cape Region (*Chaetodipus dalquesti*) and Peninsular (*Chaetodipus arenarius*); B, significance level between Peninsular (*C. arenarius*) and Cerralvo Island (*Chaetodipus siccus*); and C, significance level between Cape Region (*C. dalquesti*) and Cerralvo Island (*C. siccus*).

GLS, greatest length; OBL, occipitobasal length; PL, palatal length; PIL, palatinal length, NL, nasal length; PPL, postpalatal length; ML, mandible length; MTR, mandible tooth row length; MXR, maxillar tooth row length; ANW, anterior nasal width; PNW, posterior nasal width; BW, bulla width; MW, mastoidal width; M1W, first upper molar width; WM1, width across first upper molar; DL, diastema length; IW, interparietal width; IL, interparietal length; SD, skull depth.

**Significantly different ($P < 0.01$); *Significantly different ($P < 0.05$); NS, no significant differences.

one locality were present at only two localities. The remaining haplotype was present at six localities (Table 1). The majority of the haplotypes were found either at the tips or only one step away from a tip in the network (Fig. 3). However, the most common haplotype (no. 12) was present at six localities that span nearly the entire sampled area of the Peninsula-*arenarius* clade northward of San Ignacio (localities 6, 8–10, 12, 14; see Fig. 1). We found that the maximum number of mutational steps between haplotypes, allowing parsimonious connections, was 18 steps ($P > 0.95$). Using MP within these limits, three disjointed networks were obtained: the Peninsula, Cerralvo Island, and the Cape Region. These were separated by a minimum of 71 and 38 mutational steps, respectively (Fig. 3), well beyond the confidence limits for parsimony. Specimens of two disjointed networks were found only in three areas: López Mateos (locality 20 in Fig. 1), El Medano (26), and La Paz (30).

The Peninsula network (65 haplotypes) covers a large geographical area and is related to the *C. arenarius* clade in the phylogenetic analysis. Haplotype 12 was the most widespread, covering a geographical range that extends > 210 km, the most likely ancestral haplotype. This network has three subnetworks. The first covers the area between San Juanico and La Purísima to the north (localities 15 and 18, Fig. 1). The second covers the area to the south. The third is mainly on the Gulf of California side of the peninsula in the Loreto area. At localities 15 and 18, specimens from the north and south subnetwork were found. The Cerralvo Island network (six haplotypes) covers a small geographical area with two geographical subgroups, Cerralvo Island (haplotype 75) and the coastal basin (haplotypes 80–84) that faces the island (Fig. 3). The Cape Region network (27 haplotypes) covers the Pacific and Gulf southern coastal zones (Fig. 3). No haplotype was widespread. However, at the type locality for *C. dalquesti*, each of the ten specimens had a different haplotype (89–98). The values for haplotype diversity, nucleotide diversity, and mean number of pairwise differences obtained for cyt *b* for sampled populations are shown in Table 5.

Table 4. Underlying statistics (variable coefficients and correlations, eigenvalues, and cumulative variance of canonical variations) of discriminant function analyses with 19 variables (see Fig. 5), illustrating craniometric differentiation amongst the three groups

	Standardized coefficients		Correlations	
Variable	CV1	CV2	CV1	CV2
GLS**	0.828	–0.691	0.593	–0.262
OBL	0.075	0.132	0.384	–0.010
PL	0.020	0.059	0.411	–0.175
PIL	0.056	0.101	0.340	–0.046
NL**	–0.353	–0.458	0.326	–0.435
PPL*	0.013	0.496	0.400	0.084
ML	–0.047	–0.236	0.197	–0.365
MTR	–0.130	–0.183	0.154	–0.306
MXR**	–0.660	0.382	0.138	0.192
ANW**	–0.210	–0.576	–0.094	–0.284
PNW	–0.052	–0.166	0.115	–0.202
BW**	0.520	–0.012	0.475	0.003
MW**	0.553	–0.062	0.680	–0.070
M1W	–0.141	–0.076	0.045	–0.240
WM1	–0.109	0.011	0.204	0.096
DL	–0.134	0.427	0.439	0.046
IW*	0.274	0.146	0.139	0.192
IL	–0.043	0.363	0.091	0.244
SD**	0.370	0.169	0.269	0.126
Eigenvalue	6.415	0.431		
Cumulative variance	0.937	1.000		

**Significant at $P < 0.01$, *significant at $P < 0.05$.

GLS, greatest length; OBL, occipitobasal length; PL, palatal length; PIL, palatinal length, NL, nasal length; PPL, postpalatal length; ML, mandible length; MTR, mandible tooth row length; MXR, maxillar tooth row length; ANW, anterior nasal width; PNW, posterior nasal width; BW, bulla width; MW, mastoidal width; M1W, first upper molar width; WM1, width across first upper molar; DL, diastema length; IW, interparietal width; IL, interparietal length; SD, skull depth.

MORPHOLOGY

Pelage characteristics

Analyses of the specimens showed two main groups that were very easy to distinguish. The first includes all the specimens of the Northern and Central groups whose pelage is very soft. However, they have a few long hairs in the rump, but these are not stronger than those considered to be spine bristles (Fig. 4A).

The second group includes specimens from the Cape Region, Cerralvo Island, and the Los Planes Basin; these have a harsh pelage. Cape Region specimens have some small spine bristles in the rump, but these are not very long and are not easy to see in skin specimens (Fig. 4B). Specimens from Cerralvo Island and Los Planes Basin do not have spine bristles and the pelage is harsher than those of the first group (Fig. 4C).

Morphometry

Specimens from the Cape Region had 11 of the largest skull measurements; those from Cerralvo Island had seven and the Peninsular specimens had only one. For the other 18 skull measurements, the Peninsular specimens were the smallest. One-way ANOVA of adult cranial measurements indicated significant differences amongst the three groups of specimens (Table 3).

In the discriminant function analysis (Wilks' lambda: 0.09424; $F_{(38,308)} = 18.297$; $P < 0.001$), nine measurements were significant (Table 4). The greatest length (GLS) and bulla width (BW) at the positive side and maxillar tooth row length (MXR) and nasal length (NL) at the negative side were the most weighted characters based on discriminant function coefficients of canonical 1 variables (CV1). Postpalatal length (PPL) and diastema length (DL) at the positive

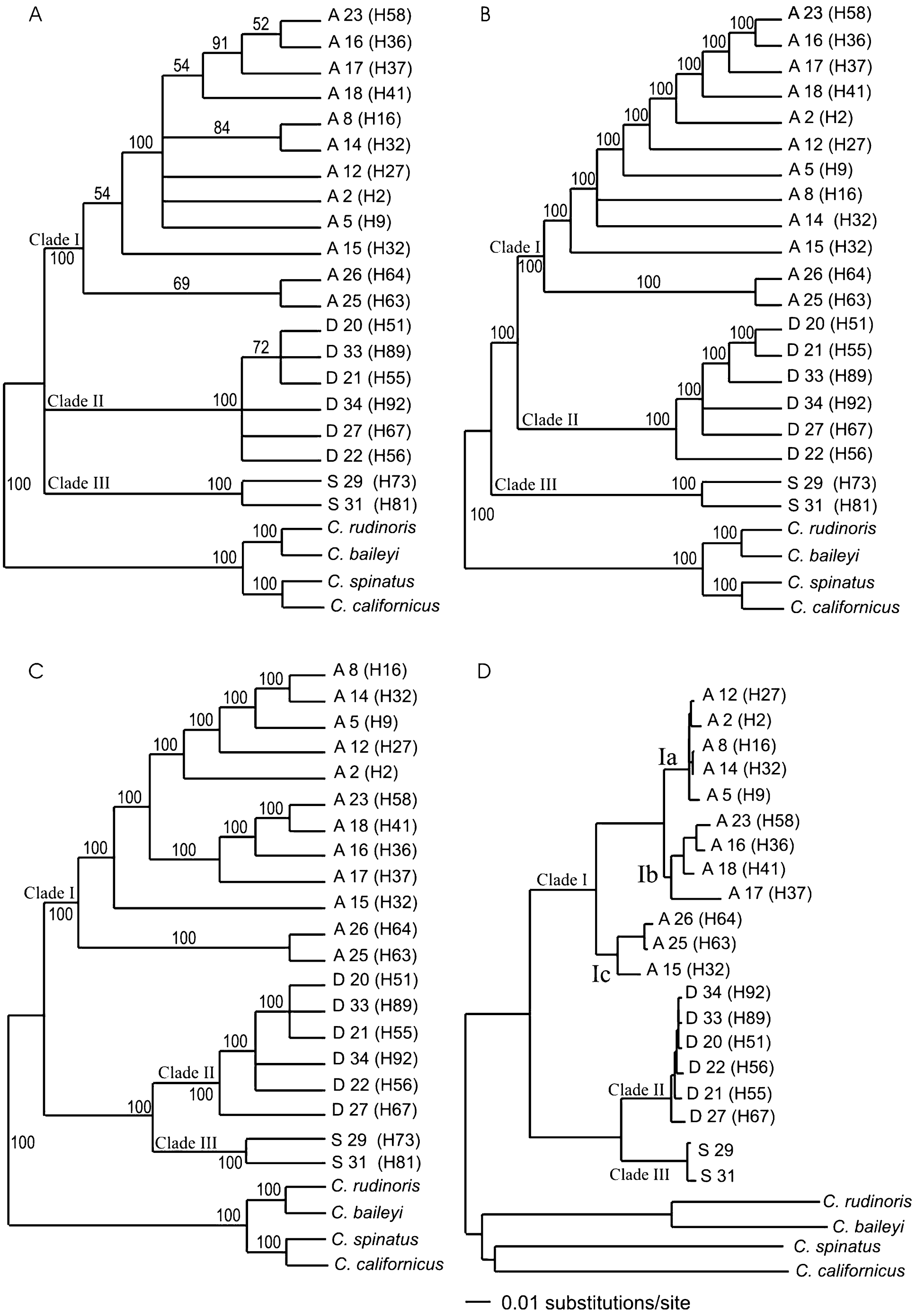

Figure 2. Phylogenetic relationships amongst 21 specimens of the concatenated cytochrome *b* and cytochrome *c* oxidase subunit III gene sequences of the *Chaetodipus arenarius* complex. The main topology was the same as the one used for the Bayesian inference analyses (A), maximum likelihood (B), maximum parsimony, consensus of four trees (C) and bootstrap of the neighbor-joining (D). The three groups are monophyletic. Clade I contains specimens of *C. arenarius* and has three subclades (indicated in D) with strong geographical relationships. (Ia) includes specimens northward to the Vizcaino Desert; (Ib) contains specimens southward to the Vizcaino Desert and Magdalena Island; and (Ic) contains specimens from the Loreto area bordering the Gulf of California. Clade II contains specimens of *Chaetodipus dalquesti* and Clade III contains specimens of *Chaetodipus siccus*. The acronym for each species is at the tip of each branch (A, *C. arenarius*; D, *C. dalquesti*; S, *C. siccus*), the locality numbers are as shown in Figure 1 and the haplotype (H) numbers listed in Table 1 are shown in parentheses. The values at the nodes are branch support for each of the analyses.

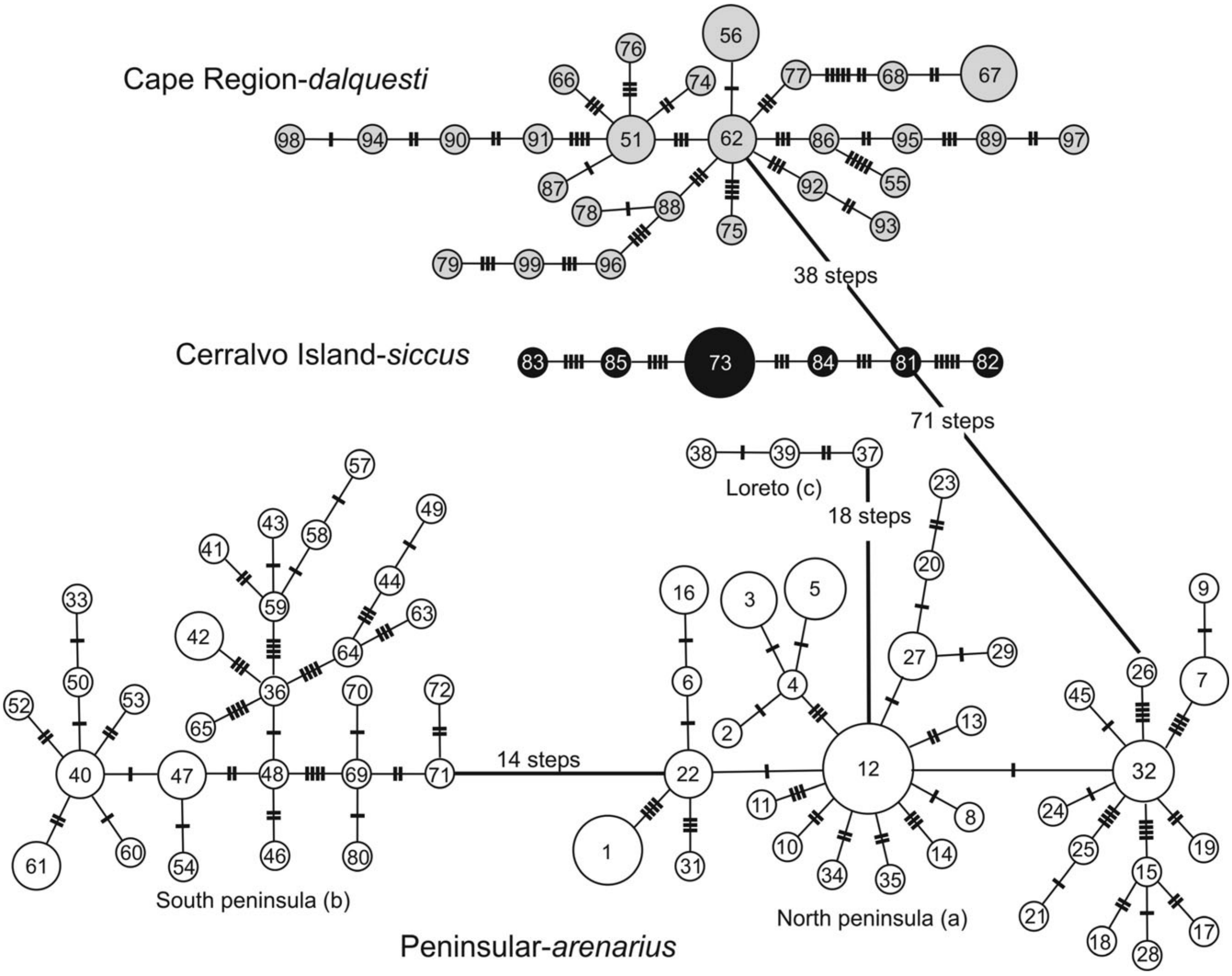

Figure 3. The minimum spanning network for the 656-bp cytochrome *b* data set includes populations from the Baja California Peninsula. Each perpendicular hash mark across the line between adjacent haplotypes in the network represents a single-base substitution. The key for the haplotypes is shown in Table 1; some of the haplotypes are present in more than one population. The peninsular-*Chaetodipus arenarius* minimum spanning network has three subnetworks: Northern peninsula (a), Southern peninsula (b), and Loreto (c).

Table 5. Genetic parameters of the specimens from the different physiographical areas considered in the revision of the *Chaetodipus arenarius* complex

Species	N_{ind}	N_{hap}	Haplotype diversity	Mean no. of pairwise differences	Nucleotide diversity
Chaetodipus arenarius	94	64	0.983 ± 0.005	12.18 ± 5.55	0.018 ± 0.009
Chaetodipus dalquesti	35	28	0.984 ± 0.011	10.76 ± 5.01	0.016 ± 0.008
Chaetodipus siccus	10	6	0.911 ± 0.062	4.86 ± 2.59	0.007 ± 0.004

Data are based on the 656 bp fragment of the cytochrome *b* gene.
N_{ind}, sample size; N_{hap}, numbers of haplotypes.

side and greatest length (GLS) and anterior nasal width (ANW) at the negative side were the most weighted characters of the canonical 2 variables (CV2, Table 4). The Peninsular-*C. arenarius* specimens were correctly classified for all specimens; however, some individuals from the Cape Region-*C. dalquesti* (85.1%) and Cerralvo Island-*C. siccus* (82.5%) were classified amongst its nominal species.

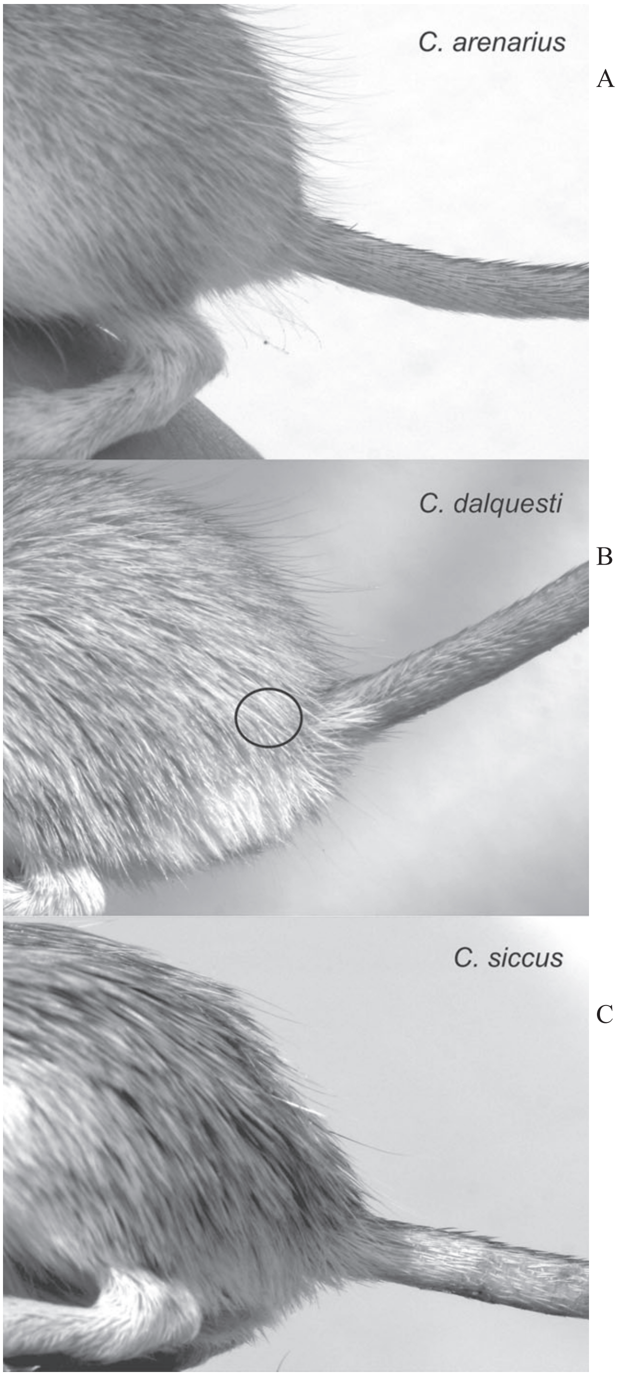

Figure 4. Photos of the rump pelage from three representative live animals: A, Peninsular-*Chaetodipus arenarius* (CIB 15534). B, Cape Region-*Chaetodipus dalquesti* (CIB 15535), and C, Cerralvo Island-*Chaetodipus siccus* (CIB 15536).

The Peninsular-*C. arenarius* group did not overlap with the other two groups along the CV1; however, Cape Region-*C. dalquesti* and Cerralvo Island-*C. siccus* did have overlaps (Fig. 5).

DISCUSSION

GENETIC GROUPS

In the following discussion, we use the concepts of genetic species level differences (Bradley & Baker, 2001) and phylogenetic species (Cracraft, 1997) based on mtDNA. We used the morphological analyses and pelage characteristics as a phenotype expression of nuclear genes to distinguish amongst groups.

All analyses (Bayesian inference, MP, ML, and neighbor-joining analysis) of the concatenated cyt *b* and COIII genes display similar topologies. Bayesian analysis (Fig. 2A) was used as a reference for discussing relationships amongst taxa.

The phylogenetic analyses identified three reciprocally monophyletic clades, each one in relation to a specific geographical area of the Baja California Peninsula: (1) coastal areas of southern Baja California; (2) interior areas of southern Baja California and areas north of the Vizcaino Desert; and (3) Cerralvo Island and the Los Planes Basin that faces the island.

Morphological analyses show differences in size amongst the three groups. The Peninsular group has smaller specimens ($P < 0.05$) than the Cerralvo Island and Cape Region groups. The specimens of Cerralvo Island are significantly larger ($P < 0.05$). Morphometrical characteristics can be used to distinguish the Peninsula group from the other two groups. The differences between the Cerralvo Island and Cape Region groups are not easy to observe by using this measurement. However, the groups are not sympatric, which reduces the possible confusion. Discriminant function analysis also supports the difference between the Peninsula group and the two other groups; however, the analysis did not discriminate between the Cerralvo Island and Cape Region groups.

The pelage, in combination with morphology, could be used with live animal species identification. North Peninsula specimens are smaller in size and the pelage is very soft, similar in texture to the specimens of the genus *Perognathus*, which do not have spines, but have a few long hairs in the rump. Cape Region specimens have the typical harsh pelage compared to other species of the genus *Chaetodipus*, with very few small spine bristles on the rump. The spine bristles are not conspicuous and are very small compared to those of *C. spinatus*, *C. fallax*, and *C. nelsoni*. Cerralvo Island specimens have the harsher pelage of the genus *Chaetodipus* and they are the harshest of the three groups; no spine bristles are obvious on the specimens.

Figure 4 shows photographs of live animals of the three groups, in the same position. It shows differences in hair texture, with a gradient in harshness of the pelage from the North Peninsula to Cerralvo Island. The Cape Region group is the only one that

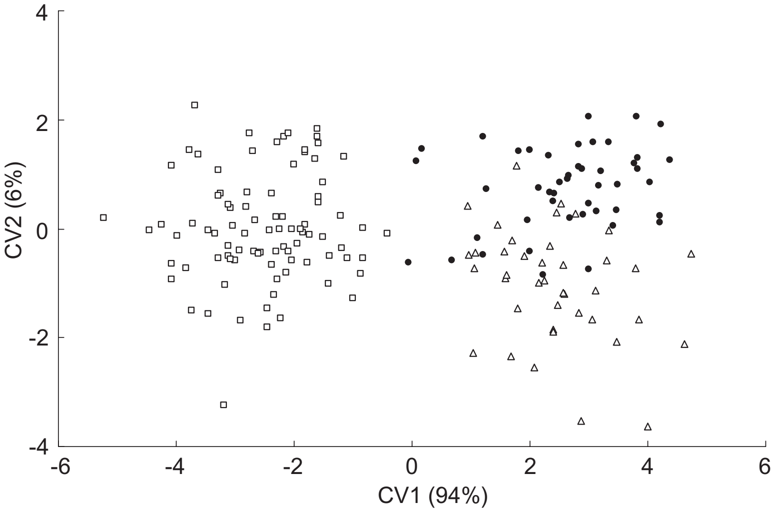

Figure 5. Projection of individual scores on discriminant roots 1 (canonical variable 1, CV1) and 2 (CV2) for 19 craniodental measurements (Table 4). The specimens were grouped into three representative groups: Peninsular-*Chaetodipus arenarius* (open square), Cape Region-*Chaetodipus dalquesti* (filled circle), and Cerralvo Island-*Chaetodipus siccus* (open triangle).

has bristles, but they are not easy to see; in the photograph, they are marked with a circle. Geographical and habitat differences amongst the three groups are indicated. The Cerralvo Island group occupies a small area in the south-eastern part of the peninsula, which includes Cerralvo Island and the Los Planes Basin that faces the island (Fig. 1).

The Cape Region group occupies moister coastal areas in the southern part of the peninsula. The habitats have fog during many months of the year. The characteristics that could be diagnostic of the habitats used by the Cape Region group are: the subtropical deciduous forest in the Cape Region and coastal areas with epiphytic plants, mainly *Rocella* sp. and *Tillandsia recurvata.* The climate in the coastal and foggy sarcocaulescent scrubland is wetter and cooler than interior areas of the peninsula (Secretaría de Programación y Presupuesto, 1981).

The Peninsula group occupies the most extreme habitats with hot summers. In the southern part of the peninsula, these are interior areas with no fog. The only exception is the large sand bar called El Mogote at the southern end of the La Paz Bay, which has a slightly moister habitat, but sparser vegetation and no epiphytes. In the State of Baja California (northern half of the peninsula), the species is found on all the sandy habitats, including those with moister and cooler winters.

The minimum spanning network shows that the Peninsula group is expanding in all of its range, but mainly in the northern part of its distribution. The Cape Region and Cerralvo Island groups seem to be stable. This difference in the results could be related to habitat; in the case of the Cape Region group, the specimens were found in all possible habitats in the southern part of the peninsula, the moister areas in the coastal plain. The range of the Cerralvo Island group is very well defined by physiographical borders and cannot expand. However, until the geographical separation of Cerralvo Island and the mainland groups do not show significant differences between populations.

TAXONOMIC IMPLICATIONS

The mtDNA genetic distance found amongst clades (6.9 to 15.7%) is higher than the results suggested for the genetic species concept-level differences (Bradley & Baker, 2001). Therefore, the three groups are monophyletic, following the phylogenetic species concept (Cracraft, 1997). Following the two species concepts, *C. arenarius* can be considered a species complex that includes more than one species, all endemic to the Baja California Peninsula. The morphological analyses support the differences amongst the three clades. To clarify which species are in each clade and morphological group, we included specimens from the type localities of *C. arenarius, C. dalquesti*, and *C. a. siccus.* All the haplotypes obtained from the topotype specimens were associated with one clade; given this condition, the specimens in Clade I are assigned to *C. dalquesti*, those in Clade II to *C. arenarius*, and those in Clade III to *C. siccus*.

The geographical relationships amongst the three species are different because *C. arenarius* and *C. dalquesti* can be found in sympatry in specific areas, whereas*C. siccus* is restricted to a geographical area, with no overlap with the other two species. Another interesting aspect is that *C. dalquesti* is not reciprocally monophyletic, and in its type locality (Migriño), there are no shared haplotypes. The *C. siccus* population was considered to be a population of *C. arenarius*; however, the phylogenetic analysis shows that it is a sister species of *C. dalquesti.* Therefore, the analyses support recognizing it as a distinctly separate species from *C. arenarius.*

The data from the specimens reveal overlap in two localities on the Magdalena Plains (geographical groups 20 and 26 in Fig. 1) between specimens of *C. arenarius* and *C. dalquesti*. In the La Paz area (geographical group 30), both species were sympatric. The Magdalena Plains need to be surveyed in more detail to determine the particularity of the microhabitats exploited by each species. No physical barriers were found between *C. arenarius* and *C. dalquesti*. We cannot determine whether hybrids or intergrades are or can be produced where they overlap; we only have a maternally inherited marker. For that reason, we recommend testing nuclear genes to check for the possibility of hybridization or intergradation.

We do not recommend changes in the subspecies taxonomy, only in the nomenclature of the species, because all subspecies of this group were defined originally by morphological characteristics, and their validity as recognized taxa must be evaluated, at least substantially, by detailed examination of those diagnostic characteristics. Our molecular analyses used specimens of the different subspecies and these specimens were also used for the designation of the species nomenclature.

The specimens that were analysed show that many of the subspecies previously considered to be part of *C. arenarius* need to be designated *C. dalquesti,* whereas others should remain *C. arenarius*.

CHAETODIPUS ARENARIUS

Distribution: The range of *C. arenarius* includes all of the State of Baja California (northern half of the peninsula) and the northern 80% of the State of Baja California Sur (from La Paz northward, including the driest areas) and Magdalena Island (geographical group 25). It does not include the coastal areas as previously considered by Hall (1981) and Patton & Álvarez-Castañeda (1999). *Chaetodipus arenarius* is not found in any localities with foggy desert scrubland.

Diagnosis: This is a moderately small species within the genus, with tail longer than the head and body, small ears, and the pelage relatively soft and usually lacking stiff bristles or spines; the lateral stripe is not clearly developed. The skull is short and broad, with somewhat vaulted braincase, slender and parallel zygomatic arches, the interparietal is more than twice as broad as it is long and is strap shaped to slightly pentagonal with slender nasals (Lackey, 1991).

In the field, the differences between *C. arenarius* and *C. dalquesti* were noted by simple comparisons. *Chaetodipus arenarius* is smaller, with a smaller, crested tail and is more light coloured dorsally. Rump spines are mainly absent in *C. arenarius* and present in *C. dalquesti,* but not as strongly developed as in *C. spinatus.* The fur is softer in *C. arenarius* than in *C. dalquesti.*

Subspecific taxonomy: Some of the subspecies previously considered as *C. arenarius* show genetic characteristics that are assigned to *C. dalquesti*. The only previous subspecies from the Cape Region that is still considered *C. arenarius* is *Chaetodipus arenarius ramirezpulidoi* (Álvarez-Castañeda & Cortés-Calva, 2004), which is restricted to El Mogote sand bar at the south-western end of Bahía de La Paz (geographical group 28). The population is surrounded by populations of *C. dalquesti*. Genetic analyses indicate that the population in the Loreto area (geographical group 17) is genetically different from all other specimens of *C. arenarius*.

Comments: Phylogenetic analyses show that the range of *C. arenarius* is separated into three geographical areas that could be related to discontinuous habitat characteristics: northern populations (Fig. 1, solid circles; Fig. 2D, subclade Ia); southern populations, including specimens from El Mogote (Fig. 1, open circles; Fig. 2D, subclade Ib); and Loreto (Fig. 1, grey circles; Fig. 2D, subclade Ic). The ranges of the subspecies follow Patton & Álvarez-Castañeda (1999).

The Loreto group (geographical group 17) is geographically isolated from other populations of *C. arenarius* and has a 3.6% genetic distance from specimens from the southern part of the peninsula; therefore, this group should be considered a different subspecies. However, because only a few specimens have been examined, there are no clear morphological characteristics to distinguish the Loreto population from other populations of *C. arenarius*.

The current subspecies included under *C. arenarius* are: *C. a. arenarius* (Merriam, 1894), which occurs in the inland areas of Baja California Sur from San Ignacio Lagoon (geographical group 12) southward to the north of the Isthmus of La Paz (geographical group 30). *Chaetodipus a. albescens* (Huey, 1926) is found on sandy eastern lowlands of the San Pedro Mártir Range in the vicinity of San Felipe (geographical group 1) in the State of Baja California. *Chaetodipus a. ambiguus* (Nelson & Goldman, 1929) is found in the south-central part of Baja California and north-western part of the Vizcaino Desert in Baja California

Sur. *Chaetodipus a. mexicalis* (Huey, 1939) occurs on sandy eastern lowlands of the Sierra de Juárez, including the area of Laguna Salada and the north-eastern coast of Baja California. *Chaetodipus a. paralios* (Huey, 1964) is found in the eastern lowlands of the Sierra de La Giganta from Bahía de los Ángeles (geographical group 5) to El Barril (geographical group 7) in Baja California. *Chaetodipus a. albulus* (Nelson & Goldman, 1923) is restricted to Magdalena Island (geographical group 25). *Chaetodipus a. helleri* (Elliot, 1903) is found from the San Quintín Plains (geographical group 2) to the coastal area southward from El Rosario (geographical group 3) and *C. a. ramirezpulidoi* (Álvarez-Castañeda & Cortés-Calva, 2004) is restricted to the El Mogote (geographical group 28) sand spit in the south-western end of Bahía de La Paz.

CHAETODIPUS DALQUESTI

Distribution: The original distribution of *C. dalquesti* was limited to the south-western tip of the Baja California Peninsula (Roth, 1976). The examined specimens placed the range of *C. dalquesti* from López Mateos (geographical group 20) on the Pacific side and the La Paz region (geographical group 30) on the Gulf side and southward to the Cape Region, with the exception of the El Mogote (geographical group 28) sand spit and the Los Planes Basin. The range of *C. dalquesti* also includes Margarita Island (geographical group 27) on the Pacific side of the peninsula.

Diagnosis: Following Roth (1976: 562), *C. dalquesti* is similar to *C. arenarius*; however, *C. dalquesti* is larger; the tail is longer, darker, and distinctly crested; has numerous somewhat weakly developed rump spines; ears are large and edged with white fur; pelage is grizzled; males are slightly larger than females. The bulla is moderately inflated; posterior palatal pits are small; nasal bones are long.

Subspecific taxonomy: The genetic analysis of specimens from different areas shows that the range of *C. dalquesti* includes some populations previously considered to be *C. arenarius*.

Comments: Analysis of genetic data of specimens from different localities on the peninsula shows that the species' range is larger than previously reported, including coastal areas on both sides of the peninsula and an island population (Fig. 1).

In the La Paz region (geographical group 30), *C. dalquesti* and *C. arenarius* are apparently present; for that reason the position of *C. a. sublucidus* (Nelson & Goldman, 1929) is not easy. However, *C. arenarius* occurs on the El Mogote sand spit and in the western coastal zone surrounding the Laguna de La Paz. By contrast, *C. dalquesti* is widely spread in the La Paz area, south and east of the Laguna de La Paz. The original vegetation of the La Paz area was palm and mesquite trees that are more closely related to the habitat characteristics of *C. dalquesti*. For those reasons, we tentatively assign *C. sublucidus* as a subspecies of *C. dalquesti*. However, a final assignment of this subspecies can only be made by an appropriate comparison of sequenced DNA from the holotype of *C. sublucidus*.

The range of *C. dalquesti* is restricted to moister areas on the coastal plain of the southern part of the Baja California Peninsula. These areas have some characteristics that make it a very particular habitat. The vegetation is a desert scrubland in an area subject to coastal fog and contains epiphytes, mainly *Rocella* and *Tillandsia recurvata*. Along the Pacific coast, these characteristics are special, containing many endemic plant species: *Gongylocarpus* sp., *Opuntia pycnacantha*, *Ferocactus santa-maria*, *Stenocereus eruca*, *Cyrtocarpa edulis* var. *glabra*, and *Harfordia macroptera* (Turner, Bowers & Burgess, 1995). The climate in the foggy desert scrubland is moister and cooler than inland areas of the peninsula.

The range of *C. dalquesti* seems to be discontinuous, probably related to the disjunctive characteristics of the habitats in the three areas: (1) the Pacific coastal area from López Mateos (geographical group 20) to Migriño (geographical group 34); (2) La Paz (geographical group 30); and (3) Margarita Island (geographical group 27, Fig. 1). Each group is considered a different subspecies. Between the Pacific coast and La Paz, the relatively narrow isthmus, mostly a rolling plain of geological origin, acts as a pathway that brings more moister and cooler breezes across the isthmus from the Pacific, for at least part of the year. During the Pleistocene, the lowland connection probably brought even more pronounced cool and moist air across the peninsula.

The current *C. dalquesti* subspecies include: *C. d. dalquesti* (Roth, 1976), which occupies the Pacific coastal area from López Mateos to all of the Cape Region of the State of Baja California Sur; *C. d. ammophilus* (Osgood, 1907), which is restricted to Margarita Island on the Pacific side of the Baja California Peninsula; and *C. d. sublucidus* (Nelson & Goldman, 1929), which occupies the coastal area near the Bahía de La Paz, with the exception of the El Mogote sand spit.

CHAETODIPUS SICCUS

Distribution: The original distribution of *C. a. siccus* was Cerralvo Island (geographical group 29), which is close to the south-eastern coast of the peninsula. However, specimens of the *C. arenarius* complex collected in the Los Planes Basin (geographical group 31) are genetically similar to the Cerralvo Island population. Los Planes Basin is surrounded by mountain ranges on three sides and opens to the Gulf of California facing Cerralvo Island, which is 11 km off the coast (Gastil, Minch & Phillips, 1983). The relatively high ridges isolate the population from other species in the *C. arenarius* complex (*C. dalquesti* and *C. arenarius*).

Diagnosis: Following Osgood (1907), *C. siccus* is similar to *C. arenarius*; however, externally it is decidedly larger than *C. arenarius*, with very weak or rarely present rump bristles. The skull is decidedly larger and heavier; the mastoids are somewhat larger and have broad ascending branches of the supraoccipital ridge.

Subspecific taxonomy: No genetic or morphological differences were found amongst the specimens from the basin and the island. The evidence does not support the designation of any subspecies as *C. siccus*.

Comments: The five specimens from Cerralvo Island have the same haplotype.

ACKNOWLEDGEMENTS

Appreciation is expressed to J. Patton for his helpful comments; M. De la Paz Cuevas and A. Gutiérrez-Ramos for their valuable assistance in the field, I. Leyva for some of the laboratory analyses, and to D. Dorantes and I. Fogel for their English editing and tutorial. Funding was provided by Consejo Nacional de Ciencia y Tecnología (CONACYT grant I25251N; 39467Q; SEMARNAT-2002-CO1-019).

REFERENCES

Alexander LF, Riddle BR. 2005. Phylogenetics of the new world rodents family Heteromyidae. *Journal of Mammalogy* **86:** 366–379.

Álvarez-Castañeda ST. 1998. Analysis of the nomenclature and taxonomy of the species of mammals of the Baja California Peninsula. *Journal of the Arizona-Nevada Academy of Sciences* **22:** 57–70.

Álvarez-Castañeda ST, Cortés-Calva P. 2004. A new subspecies of sand pocket mouse, *Chaetodipus arenarius* (Rodentia: Heteromyidae), from Baja California Sur, Mexico. In: Castro-Campillo A, Ortega J, eds. *Homenaje a la trayectoria Mastozoológica de José Ramírez Pulido*. Mexico City: Universidad Autónoma Metropolitana, Iztapalapa, 33–40.

Baker RJ, Bradley RD. 2006. Speciation in mammals and the genetic species concept. *Journal of Mammalogy* **87:** 643–662.

Bradley RD, Baker RJ. 2001. A test of genetic species concept: cytochrome-*b* sequence and mammals. *Journal of Mammalogy* **84:** 960–973.

Clement M, Posada D, Crandall K. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9:** 1657–1660.

Cracraft J. 1997. Species concepts in systematics and conservation biology – an ornithological viewpoint. In: Claridge MF, Dawah HA, Wilson MR, eds. *Species: the units of biodiversity*. London: Chapman and Hall, 325–340.

Elliot DG. 1903. Description of apparently new species and subspecies of mammals from California, Oregon, the Kenai Peninsula, Alaska, and Lower California, Mexico. *Field Columbia Museum, Publication in Zoology Series* **3:** 153–173.

Gannon WL, Sikes RS. and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **88:** 809–823.

Gastil G, Minch J, Phillips RP. 1983. The geology and ages of the island. In: Case TJ, Cody ML, eds. *Island biogeography in the Mar de Cortez*. Berkeley: University of California Press, 13–25.

Hafner JC, Hafner MS. 1983. Evolutionary relationships of heteromyid rodents. *Great Basin Naturalist Memoirs* **7:** 3–29.

Hall RE. 1981. *The mammals of North America*. New York: John Wiley and Sons.

Hall RE, Kelson KR. 1959. *The mammals of North America*. New York: Ronald Press.

Huey LM. 1926. The description of a new subspecies of *Perognathus* from Lower California with a short discussion of the taxonomic position of other peninsular members of this genus. *Proceedings of the Biological Society of Washington* **38:** 83–88.

Huey LM. 1939. A new *Perognathus arenarius* from near the U. S.-Mexican boundary in Lower California. *Transactions of the San Diego Society of Natural History* **9:** 57–58.

Huey LM. 1964. The mammals of Baja California, Mexico. *Transactions of the San Diego Society of Natural History* **13:** 85–168.

Lackey JA. 1991. *Chaetodipus arenarius*. *Mammalian Species* **384:** 1–4.

Merriam CH. 1894. Descriptions of four new pocket mice from Lower California, collected by Walter E. Bryan. *Proceedings of the California Academy of Sciences, Series 2* **4:** 457–462.

Nelson EW, Goldman EA. 1923. A new pocket mouse from Lower California. *Proceedings of the Biological Society of Washington* **36:** 159–160.

Nelson EW, Goldman EA. 1929. Six pocket mice from Lower California and notes on the status of several described species. *Proceedings of the Biological Society of Washington* **42:** 103–112.

Nylander JAA. 2004. *MRMODELTEST version 2.2*. Uppsala: Evolutionary Biology Center, Uppsala University.

Osgood WH. 1907. Four new pocket mice. *Proceeding of the Biological Society of Washington* **20:** 19–22.

Patton JL. 1993. Heteromyidae. In: Wilson DE, Reeder DM, eds. *Mammal species of the world. A taxonomic and geographic reference*. Washington, DC: Smithsonian Institution Press, 477–486.

Patton JL. 2005. Heteromyidae. In: Wilson DE, Reeder DM, eds. *Mammal species of the world. A taxonomic and geographic reference*. Baltimore: The John Hopkins University Press, 844–858.

Patton JL, Álvarez-Castañeda ST. 1999. Family Heteromyidae. In: Álvarez-Castañeda ST, Patton JL, eds. *Mamíferos del Noroeste de México*. La Paz, BCS: Centro de Investigaciones Biológicas del Noroeste, 351–443.

Riddle BR. 1995. Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): the Late Cenozoic Development of a North American aridlands rodent guild. *Journal of Mammalogy* **76:** 283–301.

Riddle BR, Hafner DJ, Alexander LF, Jaeger JR. 2000. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceeding of the American Academy of Science* **97:** 14438–14443.

Ronquist F, Huelsenbeck JP. 2003. MrBayes3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19:** 1572–1574.

Roth EL. 1976. A new species of pocket mouse (*Perognathus*: Heteromyidae) from the Cape Region of Baja California Sur, Mexico. *Journal of Mammalogy* **57:** 562–566.

Schneider S, Roessli D, Excoffier L. 2000. *Arlequin: a software for population genetics data analysis. Version 2.001*. Geneva: Genetics and Biometry Lab, Department of Anthropology, University of Geneva.

Secretaría de Programación y Presupuesto. 1981. *Carta de uso de suelo y vegetación 1:1,000,000*. México City: Secretaría de Programación y Presupuesto.

Smith MF. 1998. Phylogenetic relationships and geographical structure in pocket gophers in the genus *Thomomys*. *Molecular Phylogenetics and Evolution* **9:** 1–14.

Smith MF, Patton JL. 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of the Linnean Society* **50:** 149–177.

Swofford DL. 2000. *PAUP: phylogenetic analysis using parsimony, version 4.0b10*. Sunderland, MA: Sinauer Associates.

Tavaré S. 1986. Some probabilistics and stadistical problems in the analysis of DNA sequences. In: Miura RM, ed. *Some mathematical questions in biology – DNA sequence analysis*. Providence, RI: American Mathematics Society, 57–86.

Turner RM, Bowers JE, Burgess TL. 1995. *Sonora Desert plant and ecological atlas*. Tucson: University of Arizona Press.

Williams DF, Genoways HH, Braun JK. 1993. Taxonomy and systematics. In: Genoways HH, Brown JH, eds. *Biology of the Heteromyidae*. Special publications No. 10. American Society of Mammalogy, 38–197.

APPENDIX

SPECIMENS INCLUDED IN THE MORPHOMETRIC ANALYSES, WITH CORRESPONDING LOCALITY (SAMPLE SIZE AND SPECIMEN VOUCHER)

Chaetodipus arenarius (97): 70 km S, 18 km W San Ignacio (2, 6718, 6722); Batequi, 33 km N, 60 km W La Purísima (16; 6723–6738); San Jorge (10, 6741–6751); Poza Grande 54 km N, 32 km W Cd. Insurgentes (11; 6752–6762); El Mogote. 5 km N, 7 km W La Paz (58: 158–170, 172–183, 186–195, 197–199, 201–202, 204–207, 209–219, 223, 225, 227).

Chaetodipus dalquesti (60): 30 km N Todos Santos (11; 1648–1649, 1651–1659); 11 km N Todos Santos (4; 1661–1663, 1668); 3 km S Pescadero (10; 6288–6297); Tres Pachitas, 45 km S, 12 km E La Paz (35; 6764–6767, 6769–6774, 6776–6787, 6789–6801).

Chaetodipus siccus (60): Isla Cerralvo (7; 229–235); Playa Los Viejitos, Isla Cerralvo (27; 5563–5572, 5574–5575, 5577, 5579, 5581–5592); Ensenada de Los Muertos (26; 5600–5612, 5614, 5616, 5618, 5623, 5629, 5633, 5635–5639, 5642–5643, 5645, 5647).