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Morphological variation in the Cerralvo Island pocket mouse *Chaetodipus siccus* from the Baja California Peninsula, México

Sergio Ticul Álvarez-Castañeda[1]*

[1]Centro de Investigaciones Biológicas del Noroeste. Av. Instituto Politécnico Nacional 195, Playa Palo Santa Rita Sur, 23096. La Paz, Baja California Sur, México. Email: sticul@cibnor.mx (STAC).
*Corresponding author: https://orcid.org/0000-0002-2689-8758.

Chaetodipus siccus is a microendemic species with a restricted distribution and two geographically isolated populations, one on Cerralvo Island and its counterpart on the Baja California Sur peninsula, each associated with dissimilar environmental conditions. The hypothesis to test is that each population is adapted to its distinct environment and has its own evolutionary trend that can be used to differentiate them. The analysis of the skull shows that each population has a differential development of the region associated with chewing muscles. The statistical analyses of the Procrustes (shape) and Mahalanobis (size) distances confirm these differences statistically ($P < 0.05$). The set of differences in skull shape associated with the chewing muscles, craniodental measurements, external morphological traits, genetic isolation, and association with a different environment support the hypothesis that each population has its own evolutionary tendency.

Chaetodipus siccus es una especie microendémica de distribución restringida con dos poblaciones aisladas geográficamente, en la isla Cerralvo y a su contraparte en la península de Baja California Sur y cada una se asocian a condiciones ambientales disimiles. La hipótesis para probar es que cada una de las poblaciones se ha adaptado a su propia condición específica y tiene su propia tendencia evolutiva que puede usarse para distinguirlas. Los análisis del cráneo muestran que cada una de las poblaciones tiene un desarrollo de una región diferencial asociada a los músculos de la masticación. Los análisis estadísticos de las distancias Procrustes (forma) y Mahalanobis (talla) confirman estas diferencias de manera estadística ($P< 0.05$). El conjunto de diferencias en la forma del cráneo asociada a la musculatura usada para masticar, medidas craniodentales, características morfológicas externas, aislamiento genético y asociación a ambiente diferente, permiten considerar que cada una de las poblaciones tiene su tendencia evolutiva propia.

Keywords: *Chaetodipus*; Baja California Peninsula; endemic; México; new subspecies; Rodentia.

Introduction

A revision of *Chaetodipus arenarius* specimens collected across the geographic range of this species demonstrates that it is a species complex that includes three species endemics to the Baja California Peninsula (Álvarez-Castañeda and Rios 2011; Hafner 2016). The three species share very similar morphological characteristics, including the skull, measurements, fur pattern, and external traits; before the study of Álvarez-Castañeda and Rios (2011), these were considered a single species (Lackey 1991; Williams *et al.* 1993; Patton and Álvarez-Castañeda 1999). The three species can only be differentiated from one another through direct comparison by a specialist with solid experience in the subfamily Heteromyinae, based primarily on morphological characteristics such as rump bristle width and length and fur texture; however, an easier methodology is genetic analyses (Álvarez-Castañeda and Rios 2011). *Chaetodipus arenarius* and *C. ammophilus* (*sensu* Rios and Álvarez-Castañeda 2013) are sympatric in a small area within their distribution range. *C. arenarius* lives from La Paz isthmus to the USA-México border, including Magdalena Island; *C. ammophilus* thrives from the Magdalena plains to the cape region, including Margarita Island (Hafner 2016). *C. siccus* is parapatric with the other two species and its range is restricted to Los Planes Basin and Cerralvo Island (Álvarez-Castañeda and Rios 2011). These three species can be considered the *C. arenarius* species complex.

The Cerralvo Island Pocket Mouse, *Chaetodipus siccus*, can be differentiated from the other two species within the *C. arenarius* complex by being larger than *C. arenarius* (not statistically significant) and with very weak or rarely present rump bristles (Álvarez-Castañeda and Rios 2011). The cranium is markedly larger and heavier; the mastoids are somewhat larger (not significant) and have broad ascending branches of the supraoccipital ridge (Osgood 1907; Álvarez-Castañeda and Rios 2011); no measurements differ significantly and, thus, cannot be used to separate the species.

Chaetodipus siccus can be considered a microendemic species of the Baja California peninsula. It was originally described from Cerralvo Island as a subspecies of *C. penicillatus* (Osgood 1907) and later as *C. arenarius* (Nelson and Goldman 1929). *C. siccus* has a very restricted distribution (~1.7 km^2) in Cerralvo Island and is seriously threatened by the presence of feral cats (Lorenzo *et al.* 2010). Genetic studies of the *C. arenarius* species complex (Álvarez-Castañeda and Rios 2011) found a second population of *C. siccus* inhabiting a small basin (Los Planes basin) in front of the Cerralvo Island, a population that was unknown within the *C. arenarius* distribution range (~200 km^2). The two known populations of *C. siccus* are associated with different environmental conditions based on the local vegetation, being considered two different regions (Reimann and Ezcurra 2007).

Associated with different environments that can produce a differential adaptive effect between populations, the variation in the bite force provided by the masticatory apparatus, including the zygomatic arch (masseter muscle, mandible elevation) and braincase (temporalis muscle, bite force; Becerra *et al.* 2014; Cox *et al.* 2012) is considered to comprise elements that provide functional information on the variation between populations (Gomes Rodrigues *et al.* 2023).

Since *C. siccus* was recognized as a different species (Álvarez-Castañeda and Rios 2011), Álvarez-Castañeda has surveyed the whole distribution range (~202 km^2) in both the mainland and Cerralvo Island to understand its distribution, genetic structure, geographic boundaries, and ethology (Aguilera-Miller 2011; Aguilera-Miller et al 2018a, b; Aguilera-Miller and Álvarez-Castañeda 2019).

Los Planes is a U-shaped basin that drains into the Gulf of California, characterized by flat sandy lowlands with deep soils (average depth >100 cm), sedimentary rocks, Regosols with a high organic matter content (León de la Luz *et al.* 2000; INEGI 2010). The local vegetation is a sarcocaulescens shrubland with a very dense cactus forest (*Pachycereus pringlei*), in addition to *Jatropha cinerea, Cylindropuntia cholla, Prosopis articulata, Stenocereus gummosus, Parkinsonia microphyllum, Fouquieria diguetii,* and *Cyrtocarpa edulis* (León de la Luz *et al.* 2000; León de la Luz in lit.). Los Planes basin is surrounded by rocky slopes that are not suitable habitats for *C. siccus*; consequently, this mouse thrives only in the basin lowlands where it can be found in sympatry with *C. rudinoris* and *C. spinatus* (Aguilera-Miler 2016).

At Cerralvo Island, *C. siccus* has been found only in the small sandy areas of the western central portion, including the coastal plain and the sandy bed of streams. The rocks are igneous intrusive and the main soil types are Leptosoil (mean depth >15 cm) and Eutric Arenosol with a low organic matter content (Carreño and Helens 2002; Hernandez Ramirez 2004; INEGI 2010). These sandy areas originated from the accumulation of sand with a different granulometry as a result of sea waves and ocean currents (Hernandez Ramirez 2004) and in stream beds due to erosion. There are no large suitable areas for the species in the rest of the island. The vegetation is a sarcocaulescens shrubland composed mainly of *Pherocactus diguetii, Olneya tesota, Cyrtocarpa edulis, Jatropha cuneata, Lysiloma candida, Fouquieria diguetii, Acaciella goldmanii, Mimosa xanti, Euphorbia leucophylla,* and *Pachycereus pringlei*, and with at least one endemic species, *Mammillaria cerralboa* (Blazquez *et al.* 1997; León de la Luz *et al.* 2000). A large part of the island has very steep slopes and is stony (> 90 %). Only two other native mammals are known from the island: *Peromyscus avius*, which is endemic to the island, and *Lepus californicus*, introduced to the islands by fishers as a source of fresh meat (Lorenzo *et al.* 2010), in addition to two endemic reptiles (Teiidae: *Aspidoscelis ceralbensis*, and Colubridae: *Chilomeniscus savagei*; Case *et al.* 2002).

The original revision of the *C. arenarius* species complex using genetic data focused primarily on differences at the species level, and no detailed analyses within the *C. siccus* species were conducted (Álvarez-Castañeda and Rios 2011). *C. siccus* is a species with two isolated populations in two areas with different environmental conditions and with no genetic flow between them because the Gulf of California acts as an effective barrier. Under these conditions, the hypothesis is that each population has adapted to its particular environment, with skull modifications related to variations of the chewing muscles. Each species has its own distribution range and evolutionary trend, which can be used to differentiate them. The alternative hypothesis is that as the species has a discontinuous distribution between the two known populations, the geographic variations will involve only size, which can be statistically significant, but not the morphology as an adaptation to the local environment. This study aimed to describe the disparities between the two populations in the study area and whether these reflect geographically defined patterns of character variation.

Material and methods

The specimens studied were collected between 1991 and 2014 from Los Planes Basin (mainland) in the Baja California Peninsula and Cerralvo Island (Figure 1). In all cases, animals were handled according to the recommendations of the American Society of Mammalogists (Sikes *et al.* 2016) and the Norma Oficial Mexicana NOM-126-ECOL-2000 (NOM 2001). Voucher specimens were deposited in the Collection of Mammals at Centro de Investigaciones Biológicas del Noroeste (CIB), La Paz, B.C.S., México (Appendix 1). To explore potential differences between the two disjoint populations of *C. siccus*, we examined 129 specimens collected throughout the distribution range of the species in the Baja California Peninsula and Cerralvo Island.

Age criteria. We categorized age classes using the numerical scores defined by Genoways (1973) based on molar wear. Only adult specimens were included in the analyses (Álvarez-Castañeda and Rios 2011).

Non-geographic variation. To examine sexual dimorphism, we performed generalized least-squares analyses of ventral and lateral views of specimens from each population. *P*-values for the Procrustes and Mahalanobis distances were tested for 1,000 permutations in the MorphoJ program. As a result, sexes were pooled in all analyses.

Cranial shape analyses. Two cranium views were photographed, and only complete craniums with no apparent damage were digitized for each view: ventral surface (n = 129) and lateral surface (n = 129; Figure 2). Photographs were captured with a Canon EOS 50D camera by the same photographer (Carmen Gutierrez) using standard settings (Canon EF 50 F/1. 8 STM), at the same lens-to-cranium distance (15 cm) and including a scale bar in all photographs to estimate the centroid size based on a scale factor. Most

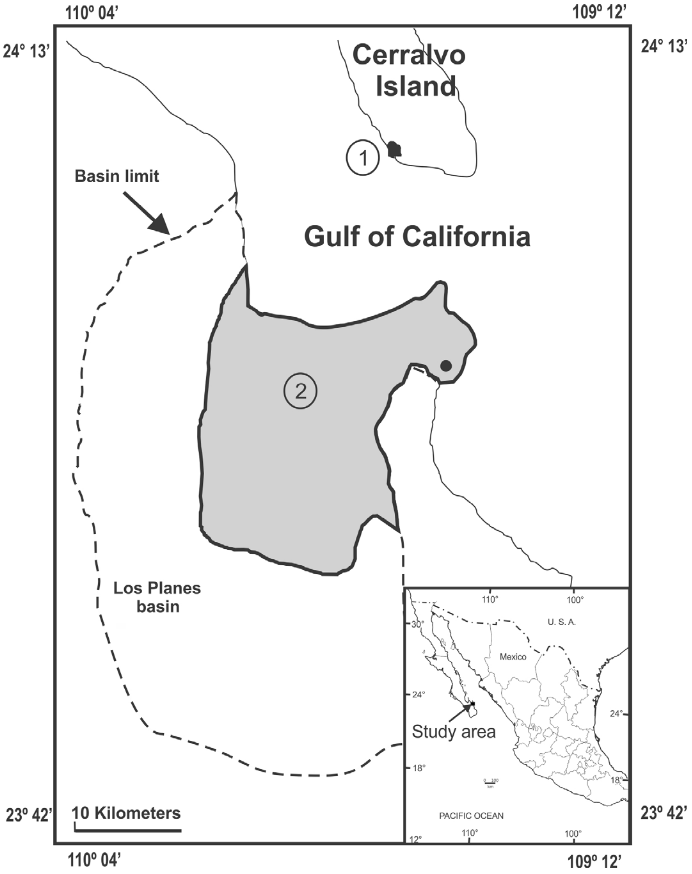

Figure 1. Distribution of *Chaetodipus siccus* in Cerralvo Island (1) and Los Planes Basin (2), Baja California Sur, México.

landmarks were Type 1 (where the intersection of bony sutures is locally defined) or Type 2 (by the tip of a structure; Bookstein 1991).

Nineteen ventral landmarks were used, as follows: 1, posterior most point of the occipital and interorbital suture; 2, posteriormost point of the occipital condyle; 3, outermost point of the auditory meatus; 4, outermost point of the mastoid; 5, posteriormost inner point of the zygomatic arch; 6, innermost point of the interorbital breadth; 7, posteriormost point of the rear of the last molar; 8, outermost point of the first molar; 9, innermost point of the first molar; 10, anteriormost point of the premolar alveolus; 11, anteriormost point of the zygomatic arch at the level of the inner margin of the zygomatic arch; 12, joint of the zygomatic and maxillary suture; 13, uppermost point of the incisor alveolus; 14, anteriormost point of both incisors; 15, anteriormost point of the incisive foramen; 16, posteriormost point of the palatal; 17, anteriormost point of the auditory bulla; 18, posteriormost point of the auditory bulla; 19, anteriormost point of the foramen magnum.

The 14 landmarks in the lateral cranium are as follows: 1, posteriormost point of the occipital; 2, uppermost point of the braincase at the level of the auditory meatus anterior margin; 3, dorsal extremity of the joint of the frontal and parietal suture; 4, dorsal extremity of the joint of the frontal and nasal suture; 5, anteriormost point of the suture between the nasal and the premaxilla; 6, anterior tip of the nasal; 7, anteriormost point of the premaxillary; 8, uppermost point of the incisor alveolus; 9, lowermost point of the incisor alveolus; 10, anteriormost point of the premolar alveolus; 11, posteriormost point of the rear of the last molar; 12, outermost point of the mastoid; 13, posteriormost point of the zygomatic arch; 14, posteriormost point of the occipital condyle.

Landmarks were digitized from images using TPSDig 2.16 (Rohlf 2010) and superimposed using Procrustes to remove the effects of rotation, translation, and size; these were then projected into a Euclidean tangent space (Rohlf and Slice 1990). With the landmarks, a wireframe diagram was drawn and used to compare the differences in cranium shape. Procrustes coordinate residuals (PC) were calculated by subtracting the mean or consensus shape, after which a Principal Component Analysis (PCA) was performed on the covariance matrix of the residuals (Dryden and Mardia 1998). Shape variation was analyzed with a PCA based on the covariance matrix of symmetric and asymmetric components in the entire dataset for females and males. Cross-validation was performed with a CVA used to calculate partial deformation scores and uniform components, extracting the canonical variations of such scores to generate a plot of the distribution of points. Changes in cranium shape between groups were visualized with a relative deformation grid in MorphoJ 1. 6d (Klingenber 2011).

Cranium size analysis. The size variable used was centroid size, a geometrically based measure of size calculated as the square root of the sum of the squared distances of the landmarks to their centroid (Bookstein 1991). Centroid size is independent of the variability in landmark shape (in the absence of allometry), so it can serve as a primary size variable (Yazdi and Alhajeri 2018).

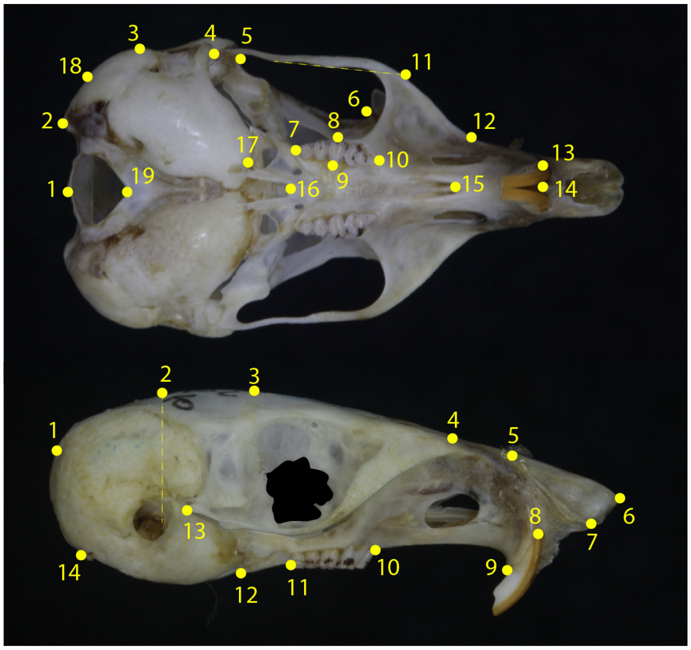

Figure 2. Morphological landmarks defined for A) ventral and B) lateral views of the cranium of *Chaetodipus siccus* (CIB 5616).

Morphological analyses. We obtained four conventional external measurements from specimen labels (total length [ToL], tail length [TaL], hindfoot length [LHF], ear length [LE]), and weight (WG). Also, we recorded 18 linear measurements of cleaned skulls (*sensu* Best 1978) from adult specimens (*sensu* Genoways 1973) of the two populations using digital calipers (to the nearest 0.01 mm). Craniodental characters included greatest skull length (GLS), occipitobasal length (OBL), palatal length (PL), palatinal length (PIL), postpalatal length (PPL), mandibular length (MTR), maxillar tooth row (MXR), nasal length (NAL), anterior nasal width (ANW), posterior nasal width (PNW), bulla width (BW), mastoidal width (MW), M1 width (M1W), width across M1 (WM1), diastema length (DL), interparietal width (IW), interparietal length (IL), and cranium depth (CD).

Differences between the two geographic groups (Figure 1) were explored with a two-sided unequal variance Student's *t*-test (Welch's *t*-test) between the two independent geographic regions (mainland versus island) for each of the 18 cranial variables using JMP™ (ver. 3.1.6.2; SAS Institute Inc. 1997). The data were tested for normality and homoscedasticity with the Shapiro-Wilk and Bartlett's tests, respectively.

A multivariate principal component analysis (PCA) and a canonical variate analysis (CVA) were performed to distinguish specimens belonging to each physiographic region. The statistical significance of the principal components was assessed using the broken-stick method (Peres-Neto *et al.* 2005). The independence of the variables was evaluated with a correlation analysis; in those pairs of variables with a correlation greater than 0.8, one was excluded from the analyses. Both multivariate analyses were implemented using log-transformations of the original variables in Statistica (StatSoft Inc. 1984–1998 ver. 6) or SAS ver 8.2 (SAS Institute Inc. 1997). We excluded external measurements from our multivariate analyses because an unknown proportion of their variance is due to differences in measuring methods.

Discriminant function analyses. These analyses were used to evaluate the similarity in the cranial shape between the different species. Each analysis separated pairs of species for each view. The results are reported as the percentage of specimens of one species that can be considered of the other species. The analyses were carried out using only the Procrustes coordinates. For the conventional cranium measurements, the Wilk´s lambda discriminant function analysis was used and the percentage of misidentifications for each group was recorded.

Pelage coloration pattern. Four areas of the specimens were sampled: the mid-dorsal surface of the nape, the central part of the back, the belly, and the dark line at the back of the tail; these were evaluated with two different methodologies. The first was recorded through a direct visual comparison with Munsell Soil Color Charts (Munsell Color Co., 1975) under uniform light conditions. We used the color names and keys in the charts. For each color, we noted the chart, hue, and chroma (*i. e.*, 10YR 8/4, chart hue/chroma). The second was the same area used by Rios and Álvarez-Castañeda (2012). The pelage color of the specimens was determined with an X-Rite Digital Swatchbook spectrophotometer (X-Rite, Inc., Grandville, MI, USA); data were compared to the Commission Internationale d'Eclairage (International Commission on Illumination) with the standard Illuminant F7 for fluorescent illumination, which represents a broad-band daylight fluorescent lamp (6500 K). This standard was used because all the measurements were performed indoors under fluorescent ambient lighting. The instrument provides the reflectance spectrum (390 nm–700 nm) of the object being measured, plus tristimuli color scores (CIE X, Y, and Z). Color was measured on each form; five separate measurements were recorded and averaged. The sample area of the X-Rite Digital has a 3 mm-diameter port. Only adult specimens of both sexes were analyzed ($n = 246$).

The variation in pelage was evaluated by adding the three-color scores (CIE X, Y, and Z). When brightness is represented by the sum of the three variables, pelage of very different colors (hue) may produce the same brightness. A Student's *t*-test was used to test for differences in pelage brightness between localities. The analyses were carried out with Statistica™ ver. 5.0 (StatSoft, Inc., Tulsa, OK, USA).

Nomenclature statement. A life science identifier (LSID) number was obtained for the new subspecies *Chaetodipus siccus* detain: urn:lsid:lsid:zoobank.org:pub:7AE730F4-95C2-4ADD-B3D1-7E25AE9FA8A4.

Results

The analyses performed on the two landmark sets of the *Chaetodipus siccus* cranium yielded similar results. The ventral and lateral cranium datasets did not show significant differences between sexes in overall morphological variability (shape) and size (centroid). Consequently, the data for both sexes were pooled for subsequent analyses. The two views show that the marked variations in the skull between the two populations are related to the zygomatic arch, the dorsal area of the braincase and the occipital region.

Cranium shape analysis. The PCA showed significant differences (as per the broken-stick test) between the island and mainland populations in the first two principal components of the ventral view (PC1 = 16.7 %; PC2 = 10.6 %) and lateral view (PC1 = 19.1 %; PC2 = 13.8 %; Figure 3, Table 1).

In the ventral view, the PC1 shows differences between Cerralvo Island and Los Planes Basin specimens in the braincase width and the anterior area of the nasal and rostrum. The PC2 also shows significant differences (as per the broken-stick test); the greatest difference between the skulls refers to the proportion in the extension of the zygomatic arches in the Cerralvo Island population relative to Los Planes. In

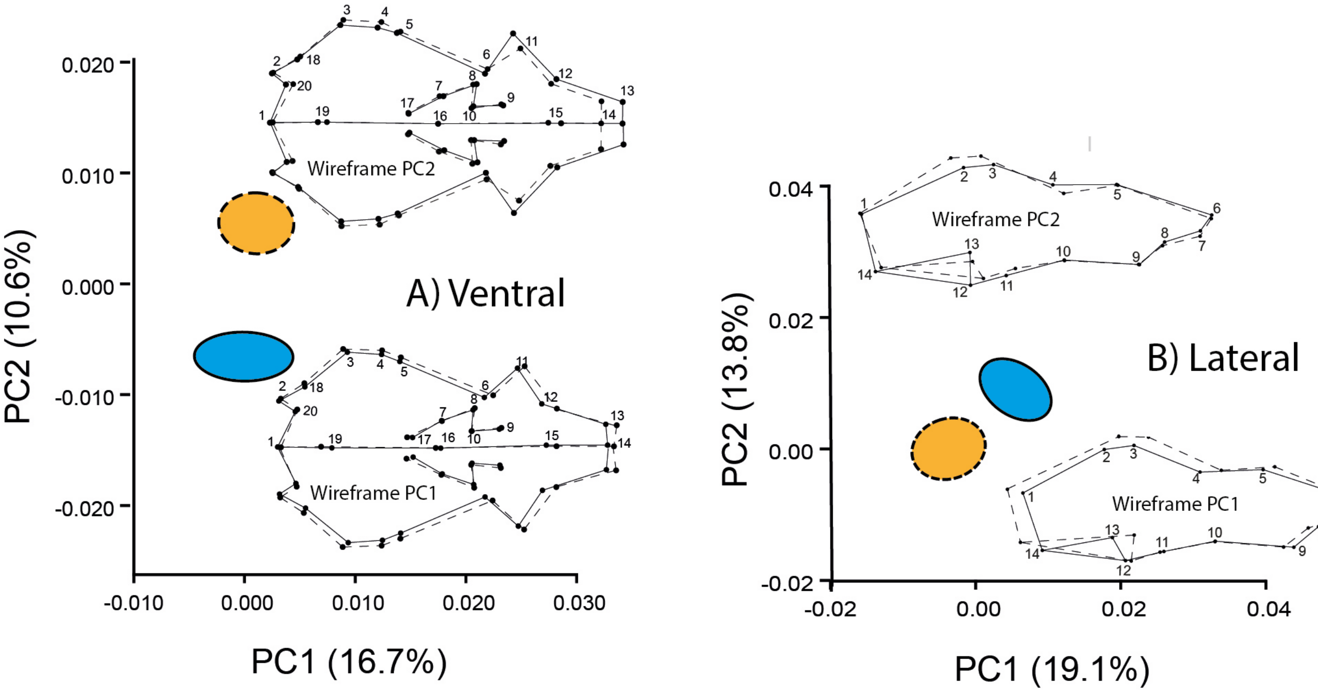

Figure 3. Principal Component Analyses for the ventral and lateral views. The wireframe diagram depicting areas of ventral and lateral cranial differentiation highlighted comparing specimens from the mainland at Los Planes Basin (dask line, orange) and Cerralvo Island (solid line, blue). A) Ventral view and B) lateral view.

the lateral view, the PC1 shows that Los Planes has a higher braincase, a more developed occipital region, and a different landmark 13 (posterior area of the zygomatic arch). In the PC2, the differences are related to braincase depth and the position of the back part of the arch with a displacement towards the center of the skull (Figure 3). Combining the wireframe of the two views of the two populations, there are differences in the muscle insertion areas associated with the chewing process, mainly the temporalis and masseter muscles. Los Planes population has a higher upper part of the braincase, which accommodates a larger temporal muscle, while in the Cerralvo Island population, the insertion areas of the masseter muscle are more developed. These results point to a differential bite-force capacity, in which the Los Planes population would be stronger than the Cerralvo Island population. The statistical analyses of Procustes and centroid distances for both populations yield significant differences as per the broken-stick test (Table 2).

Canonical Variate Analysis. The morphological variability of *Chaetodipus siccus* across the whole sample was explored with CVA analyses, which are highly sensitive to differences between populations. The CVA analysis to evaluate the variation in shape showed that the island and mainland populations show a low overlap in both views. The results of the CVA are consistent with those of the PCA.

Table 1. Loadings of the first three components of a Principal Component Analysis of 15 measurements of *Chaetodipus siccus* from Cerralvo Island and Los Planes Basin in the Baja California Peninsula. Specimen classes 4 and 5. Trait abbreviations are provided in the text.

	Principal Component			
Character	**1**	**2**	**3**	**4**
OBL	-0.846	0.162	-0.058	0.014
PL	-0.632	0.297	0.144	0.138
PIL	-0.603	0.181	0.176	0.055
PPL	-0.595	0.288	-0.067	0.046
MTR	-0.760	-0.014	-0.048	-0.020
MXR	-0.172	-0.651	0.242	0.247
ANW	-0.034	0.190	-0.762	0.103
PNW	-0.563	-0.135	-0.056	0.378
BW	0.016	-0.850	-0.168	-0.121
MW	-0.759	-0.382	-0.130	-0.173
M1W	-0.524	0.047	0.293	-0.571
WM1	-0.751	-0.029	0.251	0.105
IW	-0.274	0.232	-0.607	0.099
IL	-0.138	-0.442	-0.041	0.568
SD	-0.328	-0.435	-0.395	-0.492
Eigenvalues	4.379	2.021	1.428	1.198
% of Variance	4.380	2.022	1.428	1.198
Cumulative %	0.292	0.135	0.095	0.080

Table 2. Statistical analyses of Procustes and centroid distances observed from the analyses of mainland and Cerralvo island specimens.

	Ventral	**Lateral**
	Procustes distances	
Ms	398,158	134,100
F	38.55	28.37
P	0.001	0.001
	Centroid distances	
Ms	0.001	0.0003
f	6.32	4.49
p	0.001	0.001
Mainland *n*	73	72
Island *n*	56	57

Cranial disparity between populations. Differences in ventral and lateral cranial shape are illustrated in Figure 3, a biplot of PC variate scores for the first two axes. To the right and left of these plots, we display the wireframe diagrams that compare the resulting differences in shape between the mainland and Cerralvo Island populations, with most disparate samples aligned on the CP2 axis. Figure 3a shows the variation in the ventral view, and Figure 3b in the lateral view.

The first two CV axes of the Procrustes coordinates combined explain 89.8 % of the variances in the ventral view, with Mahalanobis distances of 2.68 ($P < 0.001$) and Procrustes distances of 0.0149 ($P < 0.001$). The lateral view explains 72.5 % of the variances, with Mahalanobis distances of 2.08 ($P < 0.001$) and Procrustes distances of 0.0158 ($P < 0.001$). The combination of CV1 scores and the centroid size ($\log_n$CS; Figure 4) cleanly separates the mainland population from the island population, with significant differences (predicted: 3.96 %; $P < 0.02$) in the ventral view but not in the lateral view.

Morphological analyses. Los Planes Basin specimens showed smaller values than Cerralvo Island specimens in all the craniodental and somatic measurements. The *t*-test showed statistically significant differences at α = 0.05 or α = 0.01 for one somatic and 15 craniodental traits (Table 3), with similar variances and a standard normal distribution.

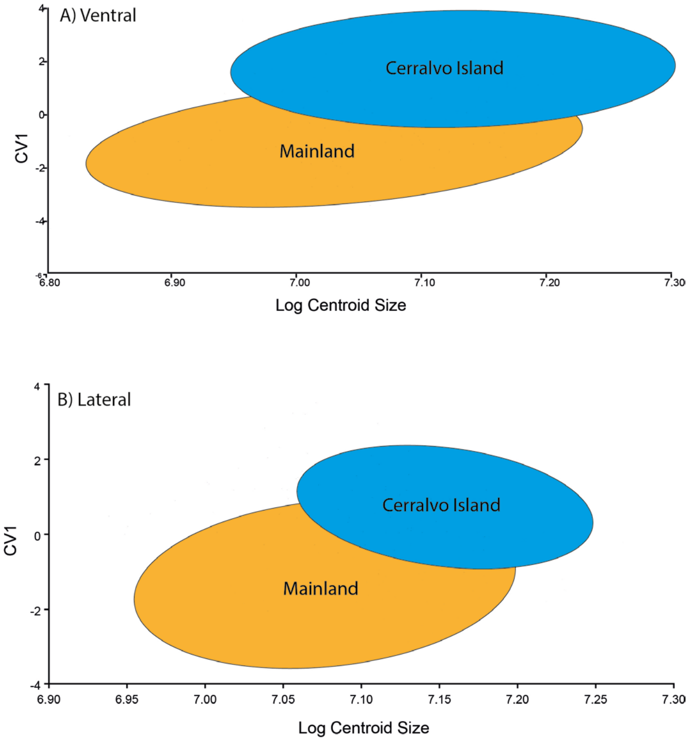

Figure 4. Linear regression of canonical variable (CV1) scores on log centroid size ($\log_n$CS). Crosses indicate mean values. Mainland at Los Planes Basin (orange) and Cerralvo Island (blue). A) Ventral view and B) lateral view.

Table 3. Mean values for four external and 18 craniodental characters for the holotype, followed by values for the characters of each of the two geographic groups: specimens from the mainland and from Cerralvo Island. *P*-values and significance levels for comparisons between samples using the Student's *t*-test are shown. *n* = sample sizes, μ = population average, and SD = standard deviation. (*$P < 0.05$; **$P < 0.01$).

Measurements	**Type**	**Cerralvo Island (*n* = 33)**		**Los Planes Basin (*n* = 48)**				
		μ ± SD	**max - min**	**μ ± SD**	**max - min**	***t*-value**	***P***	
Greatest length	24.77	25.49 ± 0.68	(27.06 - 24.20)	24.75 ± 0.48	(25.87 - 23.92)	6.415	0.01	**
Occipitobasal length	21.49	22.68 ± 0.64	(24.28 - 21.11)	21.98 ± 0.54	(22.97 - 20.92)	1.934	0.06	
Palatal length	12.44	13.62 ± 0.47	(14.56 - 12.40)	13.18 ± 0.47	(13.81 - 12.24)	5.753	0.01	**
Palatinal length	10.16	10.35 ± 0.37	(11.08 - 9.55)	9.99 ± 0.32	(10.59 - 9.33)	5.070	0.01	**
Nasal length	10.05	10.34 ± 0.46	(11.32 - 9.51)	9.72 ± 0.30	(10.19 - 9.04)	7.951	0.01	**
Postpalatal length	6.8	7.10 ± 0.26	(7.76 - 6.64)	6.83 ± 0.24	(7.25 - 6.35)	2.723	0.01	**
Mandibular length	10.29	10.78 ± 0.40	(11.53 - 10.11)	10.47 ± 0.34	(11.11 - 9.72)	4.565	0.01	**
Maxillar tooth row	2.87	3.10 ± 0.13	(3.53 - 2.95)	3.11 ± 0.25	(3.52 - 2.79)	3.164	0.01	**
Anterior nasal width	1.93	1.82 ± 0.12	(2.03 - 1.56)	1.84 ± 0.12	(2.06 - 1.67)	5.455	0.01	**
Posterior nasal width	2.06	2.26 ± 0.13	(2.58 - 2.05)	2.13 ± 0.14	(2.37 - 1.88)	2.137	0.04	*
Bulla width	4.03	3.84 ± 0.18	(4.19 - 3.59)	3.96 ± 0.18	(4.33 - 3.65)	4.297	0.01	**
Mastoidal width	13.3	13.14 ± 0.36	(14.01 - 12.54)	12.97 ± 0.29	(13.58 - 12.49)	5.084	0.01	**
M1 width	1.01	1.07 ± 0.03	(1.14 – 1.00)	1.02 ± 0.05	(1.11 - 0.89)	3.967	0.01	**
Width across M1	2.18	2.29 ± 0.14	(2.66 - 2.08)	2.12 ± 0.08	(2.31 - 1.96)	3.293	0.01	**
Diastema length	6.22	6.20 ± 0.23	(6.63 - 5.61)	5.93 ± 0.19	(6.40 - 5.59)	3.772	0.01	**
Interparietal width	7.2	7.06 ± 0.42	(7.71 - 6.06)	6.81 ± 0.35	(7.63 - 6.16)	-3.697	0.01	**
Interparietal length	3.49	3.57 ± 0.23	(4.01 - 3.22)	3.52 ± 0.21	(3.88 - 3.16)	1.570	0.12	
Cranium deep	8.53	8.30 ± 0.15	(8.77 - 7.99)	8.29 ± 0.15	(8.53 - 7.98)	0.857	0.39	
Total length	167	177.20 ± 8.03	(190 - 158)	167.20 ± 6.06	(177 - 157)	1.617	0.11	
Tail length	99	96.30 ± 4.92	(107 - 85)	91.21 ± 3.25	(99 - 85)	2.316	0.02	*
Hind foot length	21	22.70 ± 1.18	(24 - 20)	20.60 ± 1.17	(23 - 19)	1.391	0.17	
Ear length	8	9.32 ± 0.68	(10 - 8)	7.92 ± 0.72	(9 - 7)	0.541	0.59	
Weight	15	14.96 ± 1.77	(20.0 - 11.5)	14.55 ± 1.72	(18.0 - 10.0)	1.165	0.25	

The first three principal components of the cranial measurements in the PCA explained 51.37 % of the total variation (Figure 5). The loadings of the variables analyzed along components 1, 2, and 3 are shown in Table 1. All variables showed a positive loading on the first axis (except BW), thus indicating a general variation in size, where OBL, BW, and ANW had relatively large loadings. Meanwhile, LIF, DI, and DL (positives) on the second axis and BZP (negative) on the third axis had relatively large loadings. GLS, LN, and PL were excluded from the PCA and CVA because these measurements showed a correlation greater than 0.8 with other measurements. Individual scores for the components (PC1 and PC2) are plotted in Figure 5. Two major groups of specimens can be identified, one clustering individuals from Cerralvo Island and the other grouping specimens collected in Los Planes Basin. Both groups overlap marginally (Figure 5).

Discriminant analyses. The differences in the ventral and lateral views between means using Procrustes and Mahalanobis distances between the Cerralvo Island and mainland populations were statistically significant ($P < 0.001$; Table 3). For cranium measurements, the discriminant function analysis revealed a significant variation between the Los Planes Basin and Cerralvo Island populations (Wilk´s lambda = 0.28; $P < 0.0001$) and showed a clear separation between them (Figure 3b). The first discriminant function accounted for 63.9 % of the variance. The most influential variables for the first and second functions were WM1 and MXR, respectively. The percentage of misidentifications was zero (0) for each group.

Pelage coloration pattern. Specimens from the mainland and Cerralvo Island populations have a noticeably distinct coloration. The specimens from Los Planes showed darker greyish shades, while those of Cerralvo Island were lighter in brownish shades. The underparts, particularly the belly, display a somewhat different but still very similar coloration that cannot be used to differentiate between specimens from any of these areas (Table 4). In mainland specimens, the dorsal and lateral pelage is grizzly, very dark greyish brown (10YR 3/2) mixed with very pale brown (7.5YR 8/1); a very dark gray (7.5YR 3/1) dorsal part of the tail, and light gray (7.5YR 3/1) underparts. On the other hand, the specimens inhabiting Cerralvo Island have a black (7.5YR 2.5/1) upper and lateral pelage mixed with brown (7.5YR 5/3); dark brown (7.5YR 3/2) tail dorsum, and pink (7.5YR 7/3) underparts.

The pelage color using the X-Rite Digital Swatchbook spectrophotometer shows significant differences between Cerralvo Island and Los Planes populations in all the color measurements: nape ($P < 0.01$), back ($P < 0.05$), and tail strip ($P < 0.01$; Table 4). No significant differences were found in the ventral coloration.

Discussion

Non-geographic variation. The analyses between sexes did not show statistically significant differences in shape in any cranial views. However, significant differences between the mainland and Cerralvo Island populations were found in size, cranium shape, and fur color. In addition, the genetic analyses revealed that the Cerralvo Island population is

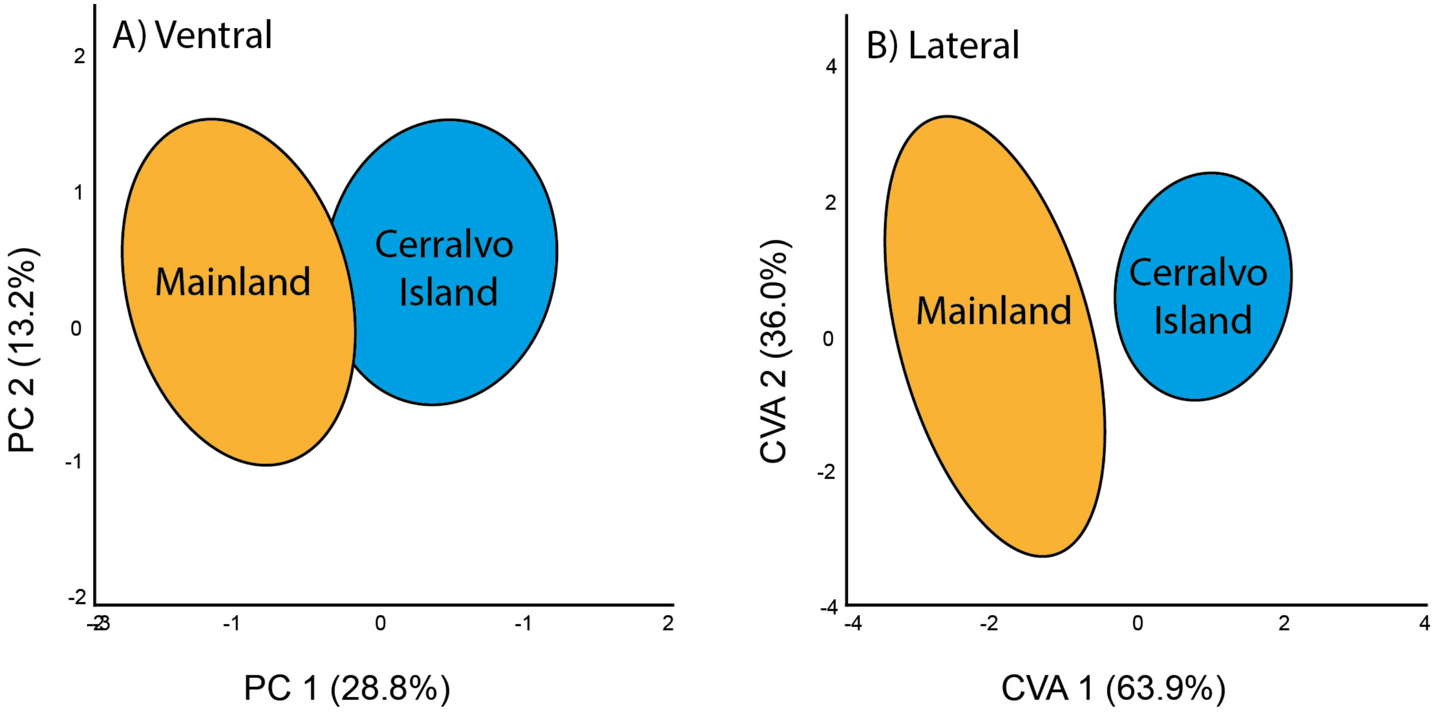

Figure 5. Specimen scores of 18 craniodental measurements of adult individuals of *Chaetodupus siccus*. Specimens from the mainland at Los Planes Basin (orange) and Cerralvo Island (blue). A) For Principal Components 1 and 2 generated from the correlation matrix and B) for Canonical Variants extracted from a discriminant function analysis. The percentage of the total variation explained by each axis is indicated.

within the *C. siccus* clade and has unique haplotypes that differ from those of *C. siccus* inhabiting Cerralvo Island (Álvarez-Castañeda and Rios 2011).

Cerralvo Island populations (*C. siccus*) were isolated from mainland ones during the Pleistocene by a sea channel impassable for the vicariant *arenarius* complex (Carreño and Helens 2002; Álvarez-Castañeda and Rios 2011; Aguilera-Miller 2011). These barriers between islands and the mainland persisted in the Last Glacial Maximum (LGM), while land bridges connected many islands to the adjacent mainland until about 18,000 years ago, when the sea level was 120 m lower than today (Fairbanks 1989). However, the least depth between the islands and the mainland is about 235 m (Case *et al.* 2002), so Cerralvo Island populations have remained isolated since the LGM and currently comprise one endemic species of mammals (*Peromyscus avius*, Cornejo-Latorre *et al.* 2017) and two of reptiles (*Aspidoscelis ceralbensis, Chilomeniscus savagei,* Case *et al.* 2002). Under these circumstances, insular populations of *C. siccus* have remained isolated from mainland ones. However, Cerralvo Island harbors species introduced by fishers, such as jackrabbits (*Lepus californicus*), cats (*Felis sylvestris*), and goats (*Capra aegagrus*), for use as sources of fresh meat in the islands during the fishing season (Lorenzo *et al.* 2010).

The results show that the specimens from populations inhabiting Los Planes basin (mainland) and Cerralvo Island differ in external characteristics, including the coloration pattern and size. The skull shape is different in both populations, each showing areas associated with the main chewing muscles with differential development. The Cerralvo Island population has more developed zygomatic arches (where masseter muscles are attached) and near to the central axes of the skull. This position to the center of the skull allows for a greater distance with the jaw and a stronger muscle. On the other hand, Los Planes specimens have a higher braincase related to a stronger temporal muscle (bite force). These conditions have been recorded in relation to the bite force in species of the superfamily Geomyoidea (Lessa and Stein 1992; Cox *et al.* 2020). Both populations have been isolated without a generic flow at least from the LGM due to the presence of the Gulf of California. Each population inhabits a different environment (soil characteristics, vegetation composition, and physiography) and can be identified as geographic units with a sustained evolutionary divergence (*sensus* Patton and Smith 1990:107) with its own evolutionary tendency. Under these conditions, our findings support the hypothesis that each population has been adapted to its own habitat and has its own evolutionary tendency. Based on the skull anatomical differences associated with the chewing muscles, fur color, and size, each population can be considered taxonomically different at the subspecies level (Lidicker 1962); therefore, a new name is proposed for the currently unnamed subspecies inhabiting Los Planes Basin in the Baja California Peninsula.

Chaetodipus siccus (Osgood, 1907)

Perognathus penicillatus siccus (Osgood, 1907).

Perognathus arenarius siccus (Nelson and Goldman, 1929).

Chaetodipus siccus Álvarez-Castañeda and Rios (2011).

Holotype. U. S. National Museum, Biological Survey Collection 146,890 (USNM), an adult male collected by E. W. Nelson and E. A. Goldman on February 13, 1906, at Ceralbo [Cerralvo] Island, Lower California [Baja California Sur], México. The specimen consists of a stuffed museum study skin with accompanying cranium and mandibles.

Paratypes. 10 specimens (no catalog number is given).

Common name. Cerralvo Island Pocket Mouse, ratón de abazones de Isla Cerralvo.

Distribution. *Chaetodipus siccus* is known only from the southwestern part of Cerralvo Island in the Gulf of California, Baja California Sur, México. *C. siccus* inhabits only areas with deep sandy soil.

Diagnosis and description. From the original description (Osgood, 1907:20). Size larger than in *Perognathus arenarius* [*Chaetodipus arenarius*]; very weak rump bristles rarely present; color dimorphic, buff phase slightly darker than in *C. arenarius*; gray phase markedly different; cranium large and heavy; mastoids relatively large.

Comparisons. For a comparison between *C. siccus* from Cerralvo Island and the Los Planes population, refer to the description of the latter.

Ecology. *Chaetodipus siccus* is not abundant; it is only found in the southwestern part of the island and on the sandy bed of streams. The local vegetation where it thrives is sarcocaule scrubs, dominated by plants of the families Euphorbiaceae, Cactaceae, and Leguminosae (León de la Luz *et al.* 1996).

Remarks. From the original description (Osgood 1907:20), "Careful examination reveals a very weak rump bristle in several species of *siccus*, though they are not found in other members of the *penicillatus* (sensu *arenarius*; Nelson and Goldman 1929) series".

Etymology. From siccus/sicca/siccum, latin. Refers to the physical state of any object that lacks moisture, so it can be translated as "dry" or "arid". Pocket Mouse of arid land.

Conservation status. The species is listed as Threatened by the Mexican regulations based on its restricted distribution range.

***Chaetodipus siccus liaae,* new subspecies**

Holotype. CIB 5616, an adult male collected by Edgar Martínez-Agama (original number 106) on October 1, 2000, at Ensenada de Muertos, Baja California Sur, México, 23.9992° N, -109.8269° W; Figure 1). The specimen consists of a stuffed museum study skin with accompanying cranium and mandibles (Figure 6) housed at the Collection of Mammals of Centro de Investigaciones Biológicas del Noroeste (CIB).

Paratypes. CIB 5600-5615, 5617-5647.

Common name. Lia Pocket Mouse, ratón de abazones de Los Planes.

Distribution. *Chaetodipus siccus liaae* is currently known only from Los Planes Basin lowlands (*ca.* sea level to 250 m), 40 km south of La Paz, Baja California Sur. *C. s. liaae* inhabits only the basin lowlands, where the soil is sandy and deep; it is less abundant at slopes as the soil becomes stonier, where it coexists with *C. spinatus*. The latter is another pocket mouse likely endemic to Los Planes Basin but thriving mainly in slopes with stony soil.

Diagnosis. A member of the *C. arenarius* complex, *C. s. liaae* is characterized externally by a small body. The general pelage coloration is light gray; the dorsum and sides are grizzly, very dark greyish brown (10YR 3/2) mixed with white (7.5YR 8/1); lateral lines usually absent, very light when present; tail very dark gray (7.5YR 3/1) and crested dorsally, light gray (7.5YR 7/1) ventrally; a very dark gray ring around the eye (7.5YR 3/1); ears light brown (7.5YR 6/4) with a very dark gray edge (7.5YR 3/1); cheeks, neck, and underparts white (7.5YR 9/1); dorsal parts of feet white (7.5YR 8/1). Cranium: *C. s. liaae* has shortened face and nasal bones; smaller diastema; branch of the mandible relatively small; cheektooth relatively small and narrow; braincase flattened and relatively narrow; bulla elliptical.

Description and comparisons. *Chaetodipus siccus liaae* differs externally from *C. s. siccus* — a pocket mouse that inhabits Cerralvo Island. The former is restricted to Los Planes Basin by its smaller size (mean total length 163.7 mm for *C. s. liaae vs* 177.3 mm for *C. s. siccus*) and smaller somatic and cranium measurements (Table 1). The dorsal and lateral pelage is grizzly, very dark greyish brown (10YR 3/2) mixed with very pale brown (7.5YR 8/1) in *C. s. liaae vs* black (7.5YR 2.5/1) mixed with brown (7.5YR 5/3) in *C. s. siccus*; in addition, the dorsal part of the tail is very dark gray (7.5YR 3/1) in *C. s. liaae vs* dark brown (7.5YR 3/2) in *C. s. siccus*; ventrally, the pelage is light gray (7.5YR 3/1) in *C. s. liaae vs.* pink (7.5YR 7/3) in *C. s. siccus*; all other pelage areas are similar in color in these two subspecies.

Ecology. *Chaetodipus siccus liaae* is an abundant pocket mouse, frequently being the dominant species and the only *Chaetodipus* mouse in the basin lowlands and salty soils. Specimens were captured in large numbers in the basin lowlands, characterized by a slope <1.6 % and deep soils, and were absent in slopes where stony and shallow soils prevail. The dominant vegetation in the basin lowlands is sarcocaule scrub dominated by plants of the families Euphorbiaceae, Cactaceae, and Leguminosae (León de la Luz *et al.* 1996), including *Pachycereus pringlei* (cardón), probably the largest plant species thriving in the Baja California Peninsula. *Chaetodipus s. liaae* occurs in agricultural fields and a small area with salty soils near the coastline. Data from the samples shows that reproduction is seasonal with two peaks, the first in April-May and the second mostly from August to October, although the latter period may vary according to the precipitation pattern in the rainy season (hurricanes). Juveniles were collected in early March and from August to October.

Remarks: The sequences of 153 specimens of *C. siccus* show 56 Cytochrome-b haplotypes, three being unique to *C. s. siccus* and 53 unique to *C. s. liaae*; only one of the most frequent haplotypes occurs in both subspecies (Aguilar Miler *et al.* 2011; Álvarez-Castañeda and Rios 2011, refer to Figure 3). Other small mammals collected at Los Planes Basin were *Notiosorex crawfordi, Thomomys nigricans anitae, Ammospermophilus leucurus extimus, Chaetodipus spinatus peninsulae, C. rudinoris extimus, Dipodomys merriami melanurus*, *Peromyscus eva eva,* and *Neotoma bryanti bryanti.*

Conservation status. The upper portion of Los Planes Basin is a currently inactive mining area; however, there are gold deposits across the area, so mining could be reactivated at any time. Agriculture is practiced in the basin lowlands, and coastal areas include tourist, recreational, and

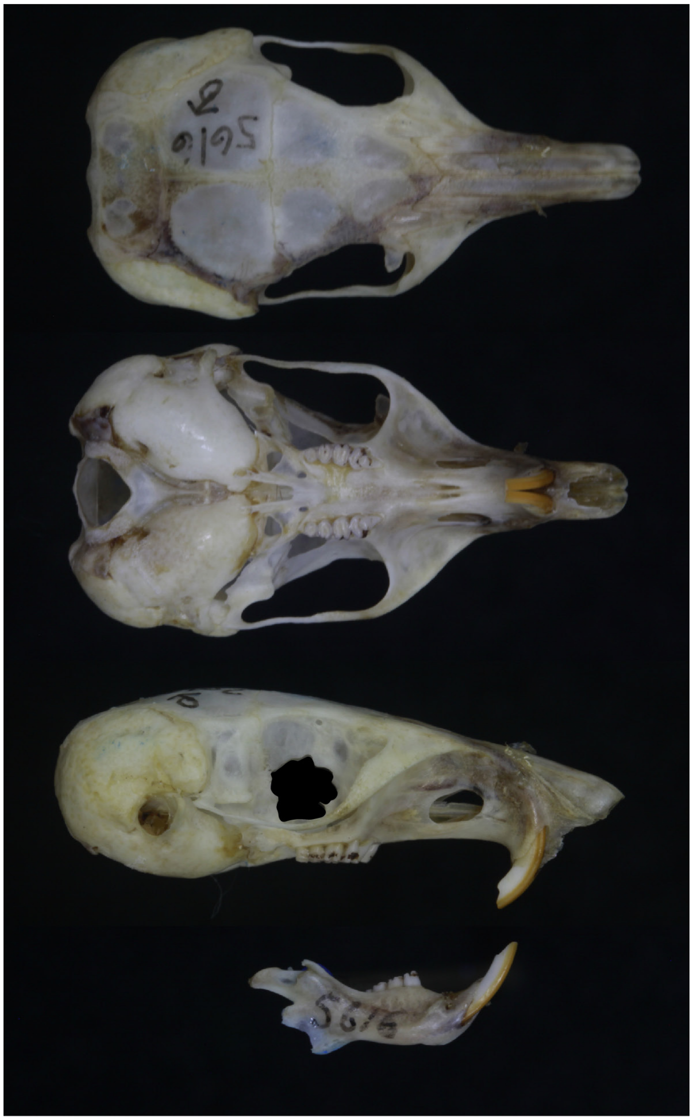

Figure 6. Dorsal, lateral, ventral, and mandibular views of the holotype skull of *Chaetodipus siccus liaae*. Adult male (CIB 5616) from Ensenada de Muertos, Baja California Sur, 23.9992° N, -109.8269° W.

residential uses. These conditions will involve growing conflicts with wildlife that are likely to increase in importance and magnitude because many parties with strong opinions clash over management objectives, with adverse impacts on wildlife (Delibes-Mateos 2015). Besides, climate change is likely to modify the habitat and distribution of microendemic species due to rising temperatures and changes in precipitation (Sántiz *et al.* 2016). The potential distribution range of this subspecies is 280 km^2, without considering areas with current human activities.

Etymology. The name proposed honors Lia C. Méndez Rodríguez, Ph. D., for her outstanding career in toxicology and mammalogy, and Lia Montserrat Álvarez Méndez, MSc. Both have provided invaluable support for decades.

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Literature cited

Aguilera-Miller, E. F. 2011. Análisis filogeográfico de *Chaetodipus siccus* de la cuenca de Los Planes, B.C.S. Master Thesis. Centro de Investigaciones Biológicas del Noroeste, S. C.

Aguilera Miller, E. F. 2016. Comportamiento agonístico asociado a filopatria como posible explicación de una estructura genética. PhD. Tesis. Centro de Investigaciones Biológicas del Noroeste, S. C.

Aguilera-Miller, E. F., and S. T. Alvarez-Castañeda. 2019. Review of philopatry and its strategy in xeric environments. Therya 10:39-44.

Aguilera-Miller, E. F., S. T. Álvarez-Castañeda, and R. W. Murphy. 2018a. Matrilineal genealogies suggest female-female aggression in a desert rodent. Journal of Arid Envioromental 152:28-36.

Aguilera-Miller, E. F., *et al*. 2018b. Dominance by extremely high aggressive behaviors in relation to genetic microstructure in matrilines. Mammalian Biology 89:1-6.

Álvarez-Castañeda, S. T., and E. Rios. 2011. Revision of *Chaetodipus arenarius* (Rodentia: Heteromyidae). The Zoological Journal of the Linnean Society 161:213-228.

Becerra, F. *et al*. 2014. Another one bites the dust: Bite force and ecology in three caviomorph rodents (Rodentia, Hystricognathi). Journal of Experimental Zoology 321:220–232.

Best, T. L. 1978. Variations in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, México. Journal of Mammalogy 59:160-175.

Blazquez, M. C., R. Rodriguez-Estrella, and M. Elibes. 1997. Escape behavior and predation risk of mainland and island Spiny-tailed Iguanas *(Ctenosaura hemdopha).* Ethology 103:990-998.

Bookstein, F. L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge University Press. New York, U.S.A.

Carreño, A. L., and J. Helenes. 2002. Geology and ages of the islands. In A new island biogeography of the Sea of Cortes (Case, T. J., M. L. Cody, and E. Ezcurra, eds). Oxford. Oxford, UK.

Case, T. J., M. L. Cody, and E. Ezcurra. 2002. A new island biogeography of the Sea of Cortes. Oxford. Oxford.

Cornejo-Latorre, C., P. Cortés-Calva, and S. T. Álvarez-Castañeda. 2017. The evolutionary history of the subgenus *Haplomylomys* (Cricetidae: *Peromyscus*). Journal of Mammalogy 98:1627-1640.

Cox, P. G., *et al*. 2012. Functional Evolution of the Feeding System in Rodents. Plos One 7:e36299.

Delibes-Mateos, M. 2015. Conservation conflicts involving mammals in Europe. Therya 6:123-137.

Dryden, I. L., and K. V. Mardia. 1998. Statistical analysis of shape. John Wiley and Sons. New York, USA.

Fairbanks, R. G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep ocean circulation. Nature 342:637-642.

Genoways, H. H. 1973. Systematic and evolutionary relationships of spiny Pocket mice, Genus *Liomys*. Special Publications, The Museum, Texas Tech University 5:1-368.

Gomes Rodrigues, H., *et al*. 2023. Digging up convergence in fossorial rodents: insights into burrowing activity and morpho-functional specializations of the masticatory apparatus. Pp. 37-63, *in* Convergent Evolution: Animal Form and Function. Springer International Publishing. Berlin, Germany.

Hafner, D. 2016. Handbook of the mammals of the world, Volume 6, Lagomorpha and Rodentia (Wilson, D. E., T. E. Lacher, Jr., and R. A. Mittermeier, eds.). Lynx Press. Barcelona, Spain.

Hernandez Ramirez, H. B. 2004. Diagnostico ambiental de Isla Cerralvo, B. C. S., México. Thesis Master. Centro de Investigaciones Biológicas del Noroeste. La Paz, México.

INEGI. 2010. Compendio de información geográfica municipal 2010. La Paz, Baja California Sur. https://www.inegi.org.mx/contenidos/app/mexicocifras/datos_geograficos/03/03003.pdf.

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. Molecular Ecology Resources 11:353–357.

Lackey, J. A. 1991. *Chaetodipus arenarius*. Mammalian Species 384:1-4.

Lidicker, W. Z., Jr. 1962. The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Systematic Zoology 11:160-171.

León De La Luz, J. L., R. Coria-Benet, and M. Cruz-Estrada. 1996. Fenología floral de una comunidad arido-tropical de Baja California Sur, México. Acta Botánica Mexicana 35:45-64.

León de la Luz, J. L., J. J. Pérez Navarro, and A. Breceda. 2000. A transitional xerophytic tropical plant community of the Cape Region, Baja California. Journal of Vegetation Science 11:555-564.

Lessa E.P., and B. R. Stein. 1992. Morphological constraints in the digging apparatus of pocket gophers (Mammalia: Geomyidae). Biological Journal of the Linnean Society 47: 439–453.

Lorenzo, C., *et al*. 2010. Status of an invading mainland jackrabbit on Cerralvo island, Gulf of California. Western North American Naturalist 70:249-251.

Munsell, A. H. 1975. Munsell soil color charts. *Kollmorgen Corporation*. Baltimore, USA.

Nelson, E. W., and E. A. Goldman. 1929. Six new pocket mice from Lower California and notes on the status of several described species. Proceeding of the Biological Society of Washington 42:103-112.

NOM. 2001. NORMA Oficial Mexicana NOM-126-ECOL-2000, Por la que se establecen las especificaciones para la realización de actividades de colecta científica de material biológico de especies de flora y fauna silvestres y otros recursos biológicos en el territorio nacional. Diario Oficial de la Federación 20 de marzo 2001

Osgood, W. H. 1907. Four new pocket mice. Proceeding of the Biological Society of Washington 20:19-22.

Patton, J., and S. T. Álvarez-Castañeda. 1999. Family Heteromyidae. Pp. 351-443, *in* Mamíferos del Noroeste Mexicano (Álvarez-Castañeda, S. T., and J. L. Patton, eds.). Centro de Investigaciones Biológicas del Noroeste, S. C. La Paz, México.

Patton, J., and M. Smith. 1990. The evolutionary dynamics of the pocket gopher *Thomomys bottae*, with emphasis on California populations. University of California Publications in Zoology 123:1–161.

Peres-Neto, P. R., D. A. Jackson, and K. M. Somers. 2005. How many principal components? Stopping rules for determining the number of non-trivial axes revisited. Computational Statistics and Data Analysis 49:974-997.

Reimann, H., and E. Ezcurra. 2007. Endemic regions of the vascular flora of the peninsula of Baja California, Mexico. Jurnal of vegetation Science 18:3327-336.

Rios, E., and S. T. Álvarez-Castañeda. 2012. Pelage color variation in pocket gophers (Rodentia: Geomyidae) in relation to sex, age, and differences in habitat. Mammalian Biology 77:160-165.

Rios E., and S. T. Álvarez-Castañeda. 2013. Nomenclatural change of *Chaetodipus dalquesti*. Western North America Naturalist 73:399-400.

Rohlf, F. J. 2010. tpsDig v2.16. Free software available. Aug 2015. http://www.sbmorphometrics.org/ Accessed 22 Jun 2020.

Rohlf, F. J ., and D. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic biology 39:40–59.

Sántiz, E. C., *et al*. 2016. Effect of climate change on the distribution of a critically threatened species. Therya 7:147-159.

Sikes R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663-688.

Statistica ver. 5.0. software StatSoft, Inc., Tulsa, Oklahoma.

Williams, D. F., H. H. Genoways, and J. K. Braun. 1993. Taxonomy. Pp. 38-196, *in* Biology of the Heteromyidae (Genoways, H. H., and J. H. Brown, eds.). The American Society of Mammalogists. Special Publication 10.

Yazdi, F. T., and B. H. Alhajeri. 2018. Sexual dimorphism, allometry, and interspecific variation in the cranial morphology of seven *Meriones* species (Gerbillinae, Rodentia). Hystrix, the Italian Journal of Mammalogy 29:162.

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Appendix 1

Specimens Examined:

Chaetodipus siccus liaae (*n* = 596): 11.8 km S, 0.6 km E Los Planes (23.8598, -109.9300; *n* = 4); 11.5 km S, 8.7 km W Los Planes (23.8635, -110.0209; *n* = 1); 11 km S, 2.5 km E Los Planes (23.8674, -109.9113; *n* = 1); 10.8 km S, 3.7 km W Los Planes (23.8703, -109.9711; *n* = 1); 11 km S, 3.7 km W Los Planes (23.8703, -109.9711; *n* = 10); 10.4 km S, 5.5 km W Los Planes (23.8708, -109.9663; *n* = 22); 11 km S, 8 km W Los Planes (23.8712, -110.0136; *n* = 9); 10.4 km S, 6 km W Los Planes (23.8728, -109.9914; *n* = 21); 10.6 km S, 3 km W Los Planes (23.8729, -109.9906; *n* = 11); 10.3 km S, 7.4 km W Los Planes (23.8742, -110.0091; *n* = 20); 9.2 km S, 3.1 km W Los Planes (23.8828, -109.9663; *n* = 14); 9.1 km S, 2.9 km W Los Planes (23.8850, -109.9073; *n* = 2); 8.7 km S, 8 km W Los Planes (23.8893, -110.0183; *n* = 8); 7.4 km S, 8.6 km W Los Planes (23.8990, -110.0218; *n* = 5); 7.5 km S, 7.6 km W Los Planes (23.9005, -110.0121; *n* = 21); 7 km S, 8 km W Los Planes (23.9044, -110.0167; *n* = 9); 5.98 km S, 0.83 km E Los Planes (23.9130, -109.9272; *n* = 2); 6 km S, 2.8 km E Los Planes (23.9130, -109.9073; *n* = 31); 6 km S, 2.8 km W Los Planes (23.9130, -109.9073; *n* = 25); 5.7 km S, 8 km W Los Planes (23.9155, -110.0164; *n* = 15); 4.9 km S, 1.7 km W Los Planes (23.9232, -109.9535; *n* = 10); 5 km S, 1.6 km W Los Planes (23.9232, -109.9535; *n* = 17); 5 km S, 1.6 km W, Los Planes (23.9232, -109.9535; *n* = 12); 4.6 km S, 1.7 km E Los Planes (23.9248, -109.9170; *n* = 2); 4.5 km S, 1.9 km E Los Planes (23.9254, -109.9073; *n* = 18); 5.6 km S, 1.6 km W Los Planes (23.9254, -109.9170; *n* = 46); 4.3 km S Los Planes (23.9283, -109.9358; *n* = 55); 4.24 km S, 400 mts W Los Planes (23.9326, -109.9466; *n* = 4); 3.7 km S, 1 km E Los Planes (23.9334, -109.9480; *n* = 7); 3.1 km S, 4 km W Los Planes (23.9371, -109.8971; *n* = 3); 3 km S, 7 km W Los Planes (23.9440, -110.0060; *n* = 27); 2.5 km S Los Planes (23.9446, -109.9363; *n* = 1); 1.3 km S, 0.8 km W Los Planes (23.9549, -109.9278; *n* = 3); 1.2 km S, 1.7 km W Los Planes (23.9569, -109.9529; *n* = 7); 0.5 km S, 6.1 km W, Los Planes (23.9625, -109.9978; *n* = 4); 5 km S, 6 km W Los Planes (23.9625, -109.9978; *n* = 9); 3 km N, 2.6 km W Los Planes (23.9959, -109.9616; *n* = 10); Ensenada de Muertos (23.9992, -109.8269; *n* = 49); 1 km W Ensenada de Muertos (23.9993, -109.8371; *n* = 1); 5.3 km N Los Planes (24.0152, -109.9334; *n* = 18); 6 km N, 2 km E Los Planes (24.0207, -109.9175; *n* = 21); 6 km N, 8 km W Los Planes (24.0226, -110.0146; *n* = 19); 7 km N, Los Planes (24.0261, -109.934; *n* = 2); 8.1 km N, 6.3 km E Los Planes (24.0377, -109.8729; *n* = 4); Brisamar, 25 km W La Paz (24.1486, -110.5427; *n* = 5); 1.5 km S, 1.6 km W Los Planes (24.1694, -110.3714; *n* = 10).

Chaetodipus siccus siccus (*n* = 68): Isla Cerralvo (24.1554, -109.8692; *n* = 31); Playa Los Viejitos, Isla Cerralvo (24.1527, -109.8697; *n* = 37).