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# TAXONOMIC REVISION OF *THOMOMYS BOTTAE* IN THE BAJA CALIFORNIA SUR LOWLANDS

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The populations of *Thomomys bottae* in the southern part of the Baja California peninsula have been assigned to several subspecies, mainly because they are isolated and show some morphological differences. In order to assess the status of *T. bottae* in Baja California, we conducted a survey in all the possible habitats in lowlands of the southern part of the peninsula by collecting specimens and obtaining tissues for genetic analyses. From the 6 subspecies of *T. bottae* present in Baja California Sur, 560 specimens were collected from 42 localities. A continuous geographical distribution among all the previously described isolate subspecies was confirmed and analysis of variance, analysis of molecular variance, and phylogentic analyses do not show morphologic or genetic differences among groups of the subspecies *T. b. anitae*, *T. b. imitabilis*, *T. b. incomptus*, *T. b. litoris*, and *T. b. magdalenae* from the lowlands south of the Vizcaino Desert. Thus, we conclude that these are junior synonyms of *T. b. anitae*. *T. bottae russeolus* in the Vizcaino Desert is sufficiently morphologically, morphometrically, and genetically different to be considered as a distinct subspecies.

Key words: Baja California, México, morphology, phylogeny, rodents, *Thomomys bottae*

The Baja California peninsula contains a series of isolated populations of *Thomomys bottae*. Most populations are known from only a few specimens at the associated type locality (Hall 1981; Patton 1999), and each has been considered a different subspecies. Historically, subspecies were recognized based on morphological variation that resulted from geographic and temporal isolation within the range of 1 species. Thus, a revision of the taxonomy and nomenclature of the taxa is necessary.

The distribution of *T. bottae* in the state of Baja California Sur is associated with elevations lower than 220 m on the Pacific side of the peninsula, with the exception of a single population that is restricted to the highlands of the Sierra de la Laguna (Hall 1981). The lowlands in the Baja California peninsula are relatively homogeneous with regard to habitat and weather conditions. There are 2 kinds of soils: pale brown yermosol and grayish brown xerosol. The vegetation in most of the region is desert scrubland (INEGI 1995). Thus, at present, no obvious habitat or physiographic barriers occur in the lowland areas occupied by pocket gophers.

Six subspecies of *T. bottae* are recognized from the lowlands of Baja California Sur (Patton 1999; Ramírez-Pulido et al. 2005). The subspecies *T. b. anitae*, J. A. Allen, 1898, was described at the end of the 19th century, from Santa Anita; *T. b. magdalenae*, Nelson and Goldman, 1909, from Magdalena Island; *T. b. russeolus*, Nelson and Goldman, 1909, from San Ángel; *T. b. imitabilis*, Goldman, 1939, from La Paz; *T. b. incomptus*, Goldman, 1939, from San Jorge; and *T. b. litoris*, Burt, 1940, from Magdalena Bay. However, limited numbers of specimens, including juveniles, were used in the original descriptions, leading to questions regarding the robustness of these subspecific designations.

Recent studies using genetic markers such as cytochrome *b* support the monophyly of populations of pocket gophers in Baja California Sur relative to *T. b. bottae*. Compared to populations from the northern part of the peninsula and California, populations from the southern peninsula show little divergence among specimens currently considered to be different subspecies (Álvarez-Castañeda and Patton 2004). In short, examination of existing data does not reveal characteristics that can be used to clearly distinguish among subspecies. Thus, we wished to evaluate whether a continuous distribution of pocket gophers exists among the populations currently considered to be distinct subspecies or whether there is a morphological gradient or morphological or genetic breaks among these populations that are consistent with the current subspecific taxonomy for pocket gophers in the lowlands of Baja California Sur. To this end, we employ the subspecies concept of Lidicker (1962), which emphasizes homogeneity within but genetic, geographic, or other distinctions among subspecies.

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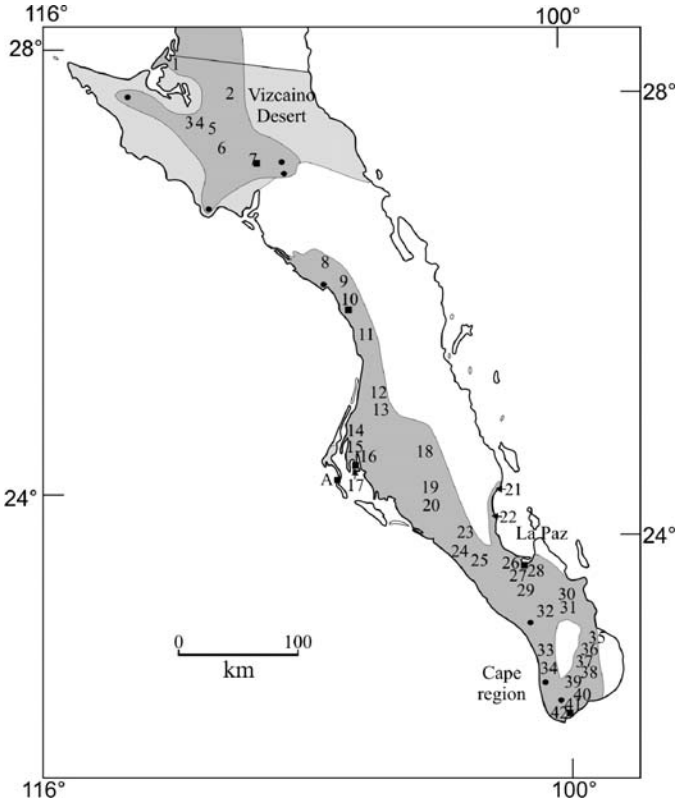


**Fig. 1.**—Distribution of localities in Baja California Sur where specimens of *Thomomys bottae* were collected. The populations sampled were: A) Guerrero Negro (localities 1–7), B) Francisco Villa (8–13), C) San Carlos (14–17), D) Constitución (18–20), E) La Paz (21–29), F) El Triunfo (30–32), G) Todos Santos (33 and 34), H) Santiago (35–39), and I) Santa Anita (40–42). Black squares represent the type localities; black dots represent localities from which specimens are juvenile and were not used for the analysis. The dark shaded area represents a habitat that is considered adequate for the species, and the light shaded the Vizcaino Desert. The *A* represents the population of the subspecies *T. b. magdalenae*.

## Materials and Methods

A total of 560 specimens from 6 subspecies of *T. bottae* were collected at 42 localities; these localities included all lowland areas in the Baja California peninsula from the cape region to Guerrero Negro (Fig. 1). All localities were assigned to 1 of 9 groups according to the range of each subspecies (Patton 1999). Some subspecies are represented in more than 1 group because their ranges include areas with differences in physiographical characteristics (Table 1). Specimens (Appendix I) were collected using pocket gopher trap sets, in croplands as well as in desert scrubland vegetation. Because the study focuses on the lowlands of the southern Baja California peninsula, *T. b. alticolus* from the highland of La Sierra de la Laguna was not considered. We followed the recommendations of the American Society of Mammalogists (Animal Care and Use Committee 1998) for handing the specimens.

*Morphological analysis*.—Only females identified as adults ($n = 169$) using a cranial suture score of 4.5 or greater (Daly and Patton 1986) were included in the morphometric analyses (Appendix I). *T. bottae* is sexually dimorphic; because of the small number of specimens collected, adult males were not included in these analyses. To increase the consistency of morphological measurements, all morphometric data were collected by the 1st author. Topotypes of the 6 subspecies were examined and measured. The 4 external measurements taken (total length, tail length, hind-foot length, and ear length) were recorded from specimen labels. Fourteen linear measurements were taken from cleaned skulls using dial calipers (0.01-mm resolution), following the protocol of Patton and Smith (1990). The measurements taken were occipitonasal length, basilar length Hensel, zygomatic width, mastoid breadth, least interorbital constriction, rostral length, nasal length, rostral width, diastema length, maxillary toothrow length, palatal length, bulla length, rostral depth, and cranial depth.

*Geographic variation*.—Geographic variation in cranial measurements from adult females was assessed by computing the taxonomical distance index (Sneath and Sokal 1973) among the 9 groups of collecting localities (Table 1); this was done with means generated by the unweighed pair-group method using arithmetic averages (UPGMA; NTSYS, version 2.2—Rohlf 1997). Principal component analyses were conducted using log-transformed linear measurements of skull shape and size (Statistica, version 5.0; StatSoft, Inc., Tulsa, Oklahoma); projections of each group of collecting localities were plotted on the first 3 components. Residuals obtained from the regression of each original craniodental variable on principal component (PC) I and PC II scores were used to conduct analyses of variance and a posteriori Duncan tests were performed to evaluate size and shape differences between groups of collecting localities.

*Color analysis*.—Pelage color was determined for 361 animals (both sexes) by comparing the dorsum, sides, rump, and venter of specimens. Juvenile and molting specimens were not used for the analysis. The hue and chroma of each area was recorded using Munsell soil color charts (Kollormogen Corporation 1975) following the methodology of Carraway and Verts (2002). Color data were analyzed with a principal component analysis. No color differences were found between specimens captured in summer and winter ($P < 0.05$) and thus all specimens were used, regardless of capture date.

*Molecular genetic procedures*.—Genomic DNA was extracted from liver tissue using the DNAeasy kit (Qiagen Inc., Valencia, California). The first 500 base pairs (bp) of the cytochrome-*b* gene was amplified with primer pairs MVZ05/MVZ16 and MVZ69/MVZ16, and the 2nd half of the cytochrome-*b* gene with MVZ45/MVZ14 (primer sequences given in Smith [1998]). We used the following conditions for the initial double-strand amplifications: 12.5 μl of template (10 ng), 4.4 μl of double-distilled $H_2O$, 2.5 μl of each primer (10 μM concentration), 0.474 μl of (0.4 μM) deoxynucleoside triphosphates, 0.5 μl of (3 μM) $MgCl_2$, 0.125 μl of (5 U/μl) Taq polymerase, and 1x Taq buffer to a final volume of 25 μl. Amplification conditions consisted of 3 min of initial denaturation at 94°C followed by 37 cycles of denaturation at 94°C for 45 s, 1 min of annealing at 50°C, and 1 min of extension at 72°C. Double-stranded poly-

**Table 1.**—This table lists the letter for the group used in all the figures (N), name of the group (Name), numbers of the localities of the group used in Fig. 1, nominal subspecific name (Subspecies), and latitude (Lat) and longitude (Long) of the group. Also given are the number of individuals morphometric studies (M) and color analysis (C), number of specimen sequences (G), number of haplotypes per group (H; some groups share haplotypes), and GenBank accession number for 1 sequence of 1,140 bp of 1 representative specimen per group; those with an asterisk (*) are topotypes.

| N | Name | Locality | Subspecies | Lat | Long | M | C | G | H | GenBank |
|---|---|---|---|---|---|---|---|---|---|---|
| A | Guererro Negro | 1–7 | *T. b. russeolus* | 27°36′N | 113°35′W | 39 | 122 | 12 | 4 | |
| B | Francisco Villa | 8–3 | *T. b. incomptus* | 25°48′N | 112°01′W | 13 | 40 | 20 | 5 | AY589039* |
| C | San Carlos | 14–17 | *T. b. litoris* | 24°46′N | 112°03′W | 16 | 12 | 14 | 7 | AY589036 |
| D | Constitución | 18–20 | *T. b. litoris* | 25°02′N | 111°39′W | 24 | 41 | 15 | 8 | AY589031* |
| E | La Paz | 21–29 | *T. b. imitabilis* | 23°44′N | 109°43′W | 20 | 48 | 17 | 18 | AY589037* |
| F | El Triunfo | 30 to 32 | *T. b. anitae* | 23°48′N | 110°10′W | 31 | 46 | 6 | 7 | AY589033 |
| G | Todos Santos | 33 and 34 | *T. b. anitae* | 23°26′N | 110°13′W | 7 | 15 | 12 | 7 | AY589025 |
| H | Santiago | 35–39 | *T. b. anitae* | 23°27′N | 109°43′W | 9 | 16 | 13 | 16 | AY589018 |
| I | Santa Anita | 40–42 | *T. b. anitae* | 23°10′N | 109°43′W | 10 | 21 | 18 | 1 | AY589021* |

merase chain reaction products were cleaned using the QIAquick PCR Purification kit (Qiagen); this template was cycle-sequenced with primers MVZ05, MVZ69, and MVZ127 using dRhodamine and Bigdye terminator kits, and then run on an ABI 377 automated sequencer following manufacturer protocols. Representative haplotypes generated during this study have been deposited in GenBank (accession numbers are given in Table 1).

*Sequence analyses*.—Nucleotide sequences were aligned and edited using Sequencher, version 3.1, software (Gene Codes Corp., Ann Arbor, Michigan), and translated into amino acids for confirmation of alignment. Missing data were coded with a question mark. To examine among-population genetic differentiation, we used cytochrome-*b* sequences from 127 individuals from the 9 groups of collecting localities, which encompassed the 6 recognized subspecies (Fig. 1; Table 1). Table 1 summarizes the number of individuals sequenced per locality and the distribution of all specimens used in this portion of the study. Samples from 1 to 5 individuals per group were sequenced; voucher specimens were deposited in Centro de Investigaciones Biológicas del Noroeste.

All nonredundant haplotypes (Collapse, version 1.1, http://darwin.uvigo.es) from each group of collecting localities were used for the phylogenetic analyses. Maximum parsimony and maximum likelihood were implemented using PAUP, version 4.0b10 (Swofford 2001). For maximum-parsimony analyses, all characters were equally weighed, and heuristic searches were performed with 1,000 pseudoreplicates, random addition of sequences, and tree-bisection reconnection branch swapping. For all analyses, trees were made using the 50% majority rule consensus algorithm. For maximum-likelihood analyses, the Tamura–Nei (TrN+I +G—Tamura and Nei 1993) model was selected using the Akaike information criterion module of Modeltest 3.06 (Posada and Crandall 1998). Two searches of 10 replicates each, with maxtrees = 100 and swapping according to the tree-bisection reconnection algorithm, were implemented. Bootstrap values $\geq$ 50% were considered. The number of steps required to generate each tree, the consistency index (CI), and the retention index (RI) were used to identify the most-parsimonious tree arrangement.

We used a Tamura and Nei algorithm (Tamura and Nei 1993) based on a model of minimal molecular evolution to calculate genetic distance. Those distances were used to construct a neighbor-joining tree (Saitou and Nei 1993). Support for nodes was assessed with bootstrap analyses, including a fast heuristic procedure with 1,000 pseudoreplicates. The trees were rooted with sequences from *T. bottae bottae* (U65253).

Bayesian inference was performed using MrBayes 3.1.1 (Ronquist and Huelsenbeck 2003) using the Hasegawa Kishino Yano + G (Hasegawa et al. 1985) model selected by MrModeltest, version 2.2 (Nylander 2004) with Akaike information criterion. Four 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 1,000 generations. The first 5,000 samples of each run were discarded as burn-in; all remaining samples were analyzed to estimate the posterior probability of clades. A consensus tree was generated with the 50% majority-rule algorithm in PAUP, version 4.0b10 (Swofford 2001), and the percent of samples recovered in a particular clade was assumed to be that clade's posterior probability. Fu's Fs test and analysis of molecular variance (AMOVA) routines were performed in Arlequin 2.000 (Schneider et al. 2000). The 1st test was used to detect departure from neutrality caused by evolutionary forces such as hitchhiking, population size expansion, background selection, or selective sweep (Fu 1997). The AMOVA was used for determining the hierarchical apportionment of haplotypes among designated groups of collecting localities or taxonomic units (following Patton 1999).

*Comparison of phylogenetic and morphological data*.—Nine sequences of cytochrome *b* (1,140 bp) from topotype specimens were used to compare genetic and morphological trees using a Kishino–Hasegawa test (Kishino and Hasegawa 1989). Morphological trees were obtained from the taxonomical index (NTSYS 2.02); maximum-parsimony trees were generated with PAUP, version 4.0b10 (Swofford 2001). The results were tested at $P < 0.01$ to evaluate the differences between the 2 analyses.

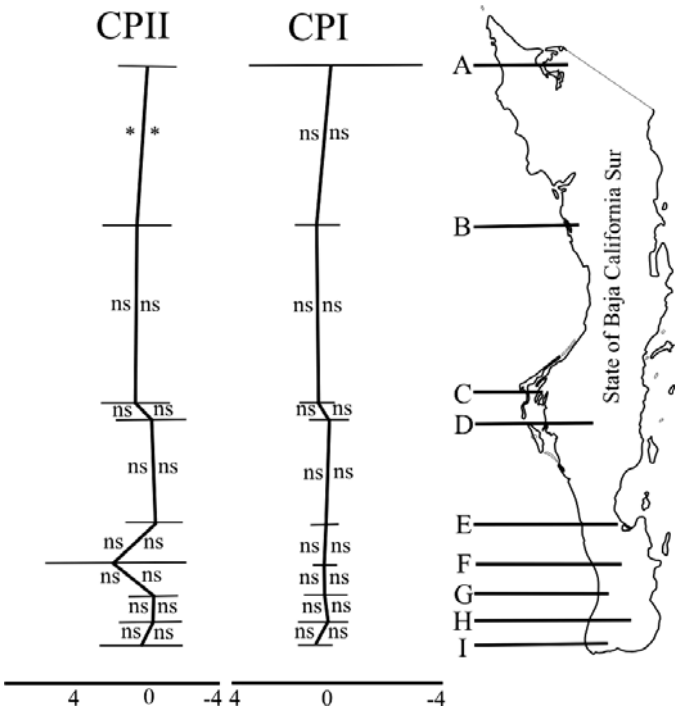


**Fig. 2.**—The lines represent the mean of the residuals from the log-transformed data from the principal component analysis. The explained variation from the log-transformed data is PC I = 41.2% and PC II = 10.0%, and from linear data PC I = 52.59% and PC II = 9.59%. A statistical analysis was made with the residuals obtained from the regression of each PC I and PC II scores from both principal component analyses, using ANOVA with a posteriori Duncan test among groups. The right side of the chart shows the log-transformed data, and the left side the linear data (ns = not significant, * = $P < 0.05$).

## Results

Collecting localities from the lowlands of Baja California Sur revealed a continuous distribution area of *T. bottae* along over a 600-km distance, from the southern tip of the cape region to southern end of the Vizcaino Desert (Pacific side of peninsula) and to the city of La Paz (Gulf side of peninsula). This distribution of pocket gophers is consistent with the area that has been considered to be adequate habitat for the species (Fig. 1). Therefore, all subspecies previously considered isolated are included in the current range. The density of pocket gophers is greater in regions with agricultural activities and lower in those with natural desert scrubland vegetation.

*Multivariable analysis*.—The phenogram showed 3 main groups of collecting localities: El Triunfo (F), La Paz (E), Santiago (H), and Guerrero Negro (A); Santa Anita (I), San Carlos (C), Constitución (D), and Francisco Villa (B); and Todos Santos (G; not shown). All branches contained specimens thought to belong to the same subspecies that were collected from the same geographical area (i.e., Santiago [H], Santa Anita [I], and Todos Santos [G]); these localities were characterized by large taxonomical index values (ti = 1.83). Conversely, localities assigned to different subspecies (i.e., La Paz [E] and El Triunfo [F]) were characterized by minimal taxonomic index differences (ti = 0.18).

*Principal component analysis*.—Collectively, PCs I, II, and III explained 69.4% (PC I 52.5%, PC II 9.5%, and PC III 7.2%) of the variation in linear skull measurements among groups of collecting localities; for the log-transformed data, this value was 59.4% (PC I 41.2%, PC II 10.0%, and PC III 8.2%). PC I had positive values for all factors, regardless of whether data were linear or log-transformed. For that reason, the analysis was heavily influenced by the size of the specimens (Fig. 2). Graphical analyses of PC I versus PC II, and PC II versus PC III (not shown) showed extensive overlap for all groups and, hence, these analyses could not be used to distinguish among groups of collecting localities.

Analyses of variance of the residuals from linear and log-transformed data revealed that, for all measurements considered, animals from the Guerrero Negro (A) group were significantly ($P < 0.05$) smaller than animals from all other groups. No significant differences in size were found among the 8 groups (B to I) located south of the Vizcaino Desert (Fig. 2).

*Color analysis*.—The dorsal color of all pocket gopher groups from south of the Vizcaino Desert was brown with a Munsell chart score of 7.5YR. In contrast, specimens from the Guerrero Negro group (A) were yellowish brown with a Munsell chart score of 10YR. Together, the first 3 PCs of the color analysis explained 76.5% (PC I 44.6%, PC II 22.0%, and PC III 9.7%) of the variation among groups of collecting localities. With the exception of animals from Guerrero Negro (A), all specimens from groups south of the Vizcaino Desert overlapped; specimens from Guerrero Negro (A) formed a distinct group.

The principal component analysis for pigmentation did not reveal any basis for distinguishing among groups from south of the Vizcaino Desert. For these groups, the most frequent color of the dorsal and lateral parts was brown to light brown (7.5YR 5/3 and 6/4), with a light yellowish brown venter (10YR 6/4), and brownish yellow rump (10YR 6/6).

*Genetic variation*.—Seventy-three haplotypes were detected; of these, 45 were present in only 1 individual. The most common haplotype was present in 11 individuals. One haplotype was present in 3 different groups, 13 were present in 2 groups, and 14 were present in only a single group. All shared haplotypes were shared among groups south of the Vizcaino Desert; only 1 haplotype was shared between the groups of Santa Anita (I) and Guerrero Negro (A).

Maximum-likelihood analyses were performed with the TrN+I+G substitution model using the following parameters: gamma distribution shape pattern G = 0.6749, proportion of invariable sites I = 0.4098, and proportions of bases: A = 0.2766, C = 0.2397, G = 0.1562, and T = 0.3275. For the analysis with 73 haplotypes, only 1 tree was found in the 1st island (−ln L 1,311.14; Fig. 3). The Bayesian inference analysis shows the same topology (not shown).

Neighbor-joining analyses with the Tamura–Nei parameter generated a tree (not shown) with similar topology to the maximum-parsimony tree. The percentage of differences

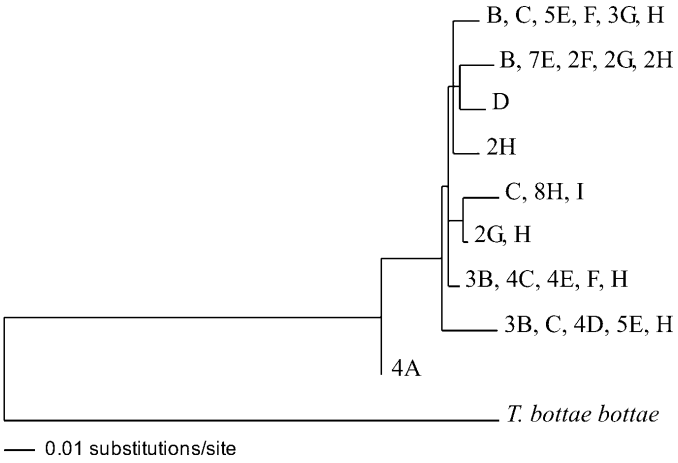


**Fig. 3.**—Phylogram of 73 haplotypes (500 bp) of the cytochrome-*b* gene, which was generated via maximum-likelihood analysis using substitution model TrN+I+G and parameters G = 0.6749 and I = 0.4098. Only the main structure of the phylogram is shown. The number represents the haplotypes and the letter the group (Table 1).

among specimens from south of the Vizcaino Desert (B to I) was 1.78%. The percentage between south of the Vizcaino Desert versus Guerrero Negro (A) was 3.05%, and south of the Vizcaino Desert versus *T. b. bottae* was 18.67%.

Analyses of molecular variance revealed that most variation (54.13%) was contained among individuals within local populations, with little variation among groups of collecting localities or subspecies. The variation among individuals increased and the variation among subspecies decreased when the specimens from Vizcaino were discarded from the analysis (Table 2). The value of Fu's Fs test for the specimens south of the Vizcaino Desert was −24.56, indicating a balancing selection or population substructure. Maximum-parsimony analysis using the 9 haplotypes (1,140 bp) that represented each group were conducted with a heuristic search in PAUP (length = 228, CI = 0.90, RI = 0.52). The resulting tree contained 2 subclades: a clade with 4 groups (La Paz [E], El Triunfo [F], Santa Anita [I], and Santiago [H]), and a clade with 3 groups (Francisco Villa [B], San Carlos [C], and Constitución [D]). Todos Santos (G) and Guerrero Negro (A) joined subsequently; no geographical structure was found. All groups south of the Vizcaino Desert were monophyletic with respect to *T. bottae bottae*, with a bootstrap support of 100 to the group of the north (Fig. 4). Kishino–Hasegawa tests (Kishino and Hasegawa 1989) performed using the results of the maximum-parsimony and multivariate analyses (no outgroup) revealed that these trees are not identical.

## Discussion

All of the analyses completed revealed limited morphometric, morphological, and genetic variation among the localities and groups of localities to the south of the Vizcaino Desert. The differences within groups of the same subspecies are greater than those among groups thought to represent different subspecies. Only the group from Guerrero Negro (A) could

**Table 2.**—Result of the AMOVA using different arrangements in relation to the groups of the localities (Groups), and in relation to the subspecies following Patton (1999—ssp). Result of previous analysis (Álvarez-Castañeda and Patton 2004) for the same region (A-P), and the analysis for the population south of the Vizcaino Desert, without *Thomomys bottae russeolus* (SV).

| Hierarchical level | Groups | ssp | A-P | SV |
|---|---|---|---|---|
| Among populations | 29.72 | 24.44 | 26.54 | 13.64 |
| Among populations within groups | 16.15 | 23.06 | 24.12 | 26.58 |
| Within populations | 54.13 | 52.5 | 49.34 | 59.78 |

be distinguished from groups south of Vizcaino (B to I) by means of skull measurements. Groups from south of the Vizcaino Desert were similar, with no significant among-group variation (Fig. 2). Therefore, we found no geographical pattern (north–south, east–west) that could be used to differentiate among the southern subspecies. Only the group from Guerrero Negro (A) showed significant differentiation from the other subspecies considered.

The morphological similarities among groups may reflect adaptation to the similar vegetation, weather, soil, and slope conditions at these localities (INEGI 1995). Examination of our data suggests that only 1 form of *T. bottae* is present south of the Vizcaino Desert and the previously accepted subspecies were a result of an incomplete survey with small sample sizes or with juveniles included in the original descriptions. The pelage colors used in the original descriptions of many of the subspecies are relative to *T. b. anitae*. The authors of the original description only mention terms such as ''similar'' when comparing pelage coloration (Goldman 1939; Nelson and Goldman 1909); these contrasts are vague, and fail to discriminate between variations within versus among populations. Our analysis shows that the general coloration of the specimens could not be used as a reliable character for distinguishing

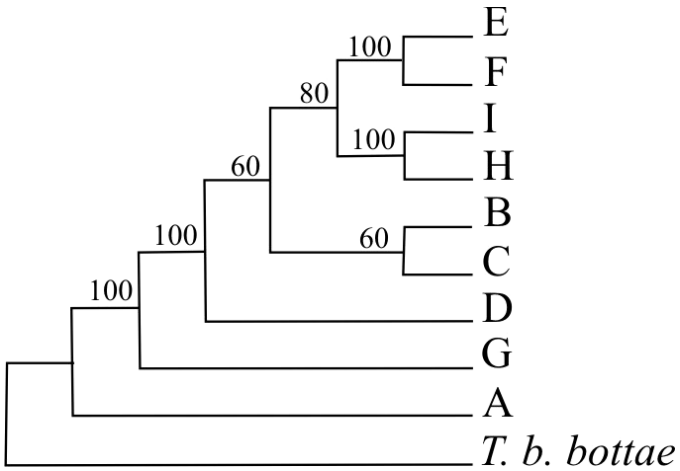


**Fig. 4.**—Majority-rule consensus tree (1,140 bp) obtained from 5 of the most-parsimonious trees generated using a heuristic search option of PAUP (Swofford 2001). The outgroup was established using *T. b. bottae*. This tree consisted of 228 steps in length (CI = 0.904, RI = 0.522, homoplasy index = 0.096).

among groups. The soils from throughout the study area are very similar in color and match the coloration of the pocket gophers. This observation is in accord with Krupa and Geluso (2000) and Patton (1973), who proposed that the color of the specimen is related to the color of the soil that it inhabited.

The haplotype analyses revealed that 28 cytochrome-*b* variants were shared among 8 groups. Maximum-likelihood analysis showed that all clades contained haplotypes from different groups; only the group from Guerrero Negro (A) was monophyletic with respect to locality. One haplotype was shared between Guerrero Negro (A) and Santa Anita (I), suggesting historical gene flow between these groups. Because of the current physical barriers and distances between the 2 populations containing this haplotype, this sharing may reflect the retention of ancestral polymorphism. The distance analysis with the Tamura–Nei parameter indicated a very small percentage of difference among the groups south of the Vizcaino Desert; similar genetic results for this area were obtained by Álvarez-Castañeda and Patton (2004) with other analyses.

The results of AMOVAs (Table 2) were generally consistent with those reported previously by Álvarez-Castañeda and Patton (2004). In both cases, approximately half of the total pool of variation was contained among individuals within local populations. However, when the subspecies south of the Vizcaino Desert were excluded from these analyses, the variation within the populations south of the Vizcaino increased relative to variation among different subspecies. We interpret this as evidence that genetic variation among different localities is greater than that between the previously designated subspecies.

Rejection of a neutral model for geographical differentiation was based on a significantly negative test (Nielsen and Weinreich 1999), which may have been caused by recent directional selection, a population bottleneck, recent population growth, or background selection of slightly deleterious alleles (Tajima 1989). The value of Fu's Fs test for the populations of pocket gophers from Baja California is negative (−24.5). These results and those obtained by Álvarez-Castañeda and Patton (2004) suggest that the most plausible explanation for rejecting the neutrality model could be a bottleneck for the isolated populations.

Thus, we postulate that the populations south of the Vizcaino Desert are experiencing or have experienced recent gene flow. Under this condition, none of the groups have their own phylogenetic history and cannot be distinguished from the others. This hypothesis is supported by the observation that haplotypes from this region are differentiated by an average of 1.90 mutation steps, as well as data suggesting high migration rates among these populations (Álvarez-Castañeda and Patton 2004).

We did not find similarities between trees constructed using morphological and genetic data. This suggests that morphological variation is not due solely to phylogenetic relationships among populations. The discrepancies between morphological and genetic data can be explained as follows: morphological variation and genetic differentiation are so limited that no contrasts are found among subspecies, gene flow between groups is greater than expected (for this reason, no genetic structure can be found among groups), or any morphometric characters unique to each population are absent. This hypothesis is supported by the reported plasticity of morphotypes in response to local ecological conditions and nutritional quality (Hadly 1997; Ingles 1950; Smith and Patton 1984). For example, larger specimens can be found in soft and deeper soils and lower altitudes (Davis 1938), and with better nutritional quality of the food (Patton and Brylski 1987); under the opposite conditions, the specimens become smaller. Alternatively, our data may reflect recent fragmentation of a continuous population as a result of the desertification process of the Baja California peninsula.

Morphological, morphometric, and genetic data cannot be used to distinguish among our groups of collecting localities from the lowlands south of the Vizcaino Desert. The continuous habitat among all groups suggests that they are not likely to be isolated by habitat barriers. We do not find any reason to retain *T. b. imitabilis*, *T. b. incomptus*, and *T. b. litoris* as different subspecies. Under these conditions and because *T. b. anitae* is the oldest name of all the subspecies, we propose that the other subspecific epithets should be junior synonyms of *T. b. anitae*.

In the case of *T. b. magdalenae*, only 7 specimens have been collected to date on Magdalena Island, where the population density is very low. These specimens seem to be similar in color, morphometry, and genetics to specimens from south of the Vizcaino Desert, but we do not have a sample size that is adequate to confirm this quantitatively. Therefore, after examining all other specimens from the lowlands of Baja California Sur, we believe that there are no strong differences between insular and mainland specimens, and *T. b. magdalenae* can be considered as *T. b. anitae*. The range of *T. b. anitae* includes all of the lowlands south of the Vizcaino Desert. Specimens from the Vizcaino Desert, *T. b. russeolus*, have morphological, morphometric, and genetic characteristics that are sufficiently distinct as to be considered a different subspecies.

### *Thomomys bottae anitae* J. A. Allen

*Thomomys bottae anitae* J. A. Allen, 1898:146. Type locality "Santa Anita, Lower California" [= Baja California Sur].

*Thomomys magdalenae* Nelson and Goldman, 1909:24–25. Type locality "Magdalena Island, Lower California" [= Baja California Sur].

*Thomomys bottae incomptus* Goldman, 1939:29–30. Type locality "San Jorge, near Pacific coast west of Poza Grande and about 25 miles southwest of Comondú, southern Lower California (altitude 50 feet)" [= Baja California Sur].

*Thomomys bottae imitabilis* Goldman, 1939:30–31. Type locality "La Paz, southern Lower California" [= Baja California Sur].

*Thomomys bottae litoris* Burt, 1940:1. Type locality "Stearns Point, Magdalena Bay (west side), Lower California" [= Baja California Sur].

*Distribution.*—The range of *T. b. anitae* includes all of the lowlands of the Pacific Ocean side of the southern part of

the Baja California Peninsula, from the San Ignacio Lagoon in the northern part to the Cape Region and from La Paz in the Gulf side to the south. Isolated populations of this subspecies can be found in the lower areas of the canyons of Sierra de la Giganta and Sierra de La Laguna. The subspecies is associated primarily with desert scrub, although some populations can be found in the tropical deciduous forest of the southern region of the peninsula.


## Resumen

Las poblaciones de *Thomomys bottae* en el sur de la península de Baja California se han asignado a diferentes subespecies debido a que se encuentran aisladas, y muestran algunas diferencias morfológicas. Se realizó un estudio de *T. bottae* en todos los hábitats localizados en las tierras bajas al sur de la península, con un total de 560 ejemplares colectados de 42 localidades ubicadas en el estado de Baja California Sur. Se obtuvieron las secuencias de 500 pb de 127 ejemplares y 1,140 pb de nueve ejemplares del gen del citocromo *b*. Se demuestra la existencia de una distribución continua entre las subespecies consideradas previamente como aisladas, y mediante análisis de análisis de varianza, análisis de varianza molecular y filogenéticos se observa que no existen diferencias morfológicas, morfométricas y genéticas entre las poblaciones localizadas en las tierras bajas del sur del Vizcaíno (*T. b. anitae*, *T. b. imitabilis*, *T. b. incomptus*, *T. b. litoris*, y *T. b. magdalenae*) por lo que se consideran como sinónimo de *T. b. anitae*. La subespecie *T. b. russeolus* localizada en el desierto del Vizcaíno presenta diferencias en los caracteres morfométricos, morfológicos y genéticos que nos llevan a considerarla como una subespecie diferente de las del sur del desierto del Vizcaíno.



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## APPENDIX I

List of the localities used for the morphological analysis, which were joined in 9 geographical groups. The list of specimens only includes adult females. Measurements were taken from specimens deposited at the Mammal Collection of Centro de Investigaciones Biológicas del Noroeste (CIBNOR).

A. Guerrero Negro (♀39): 1. Guerrero Negro, 2. Ejido Lagunero, 3. Santa Teresita, 4. Valladares, 5. Rancho el Vergel, 6. Emiliano Zapata, 7. San Evodio. B. Francisco Villa (♀13): 8. Loma Linda, 9. Las Jarillas, 10. Los Laureles, 11. Poza Grande, 12. 8.5 km N Cd. Insurgentes, 13. 19 km N Constitucion. C. San Carlos (♀16): 14. López Mateos, 15. 7 km N Puerto San Carlos, 16. 3 km E Puerto San Carlos, 17. San Buto. D. Constitución (♀24): 18. Constitución, 19. Arroyo Santa Rita, 20. El Médano. E. La Paz (♀20): 21. Punta Coyote, 22. Rancho el Potrero, 23. El Cien, 24. Punta Conejo, 25. Reforma Agraria, 26. El Centenario, 27. Chametla, 28. La Paz, 29. San Pedro. F. El Triunfo (♀31): 30. La Pimientilla, 31. El Triunfo, 32. El Carrizal. G. Todos Santos (♀7): 33. Todos Santos, 34. Migriño. H. Santiago (♀9): 35. La Ribera, 36. Las Cuevas, 37. Santiago, 38. Rancho la Misión Santiago, 39. Caduaño. I. Santa Anita (♀10): 40. 10 km N San José del Cabo, 41. San José del Cabo, 42. Santa Anita.