

VARIATION IN KANGAROO RATS (GENUS *DIPODOMYS*)
OF THE *HEERMANNI* GROUP IN
BAJA CALIFORNIA, MEXICO

TROY L. BEST

ABSTRACT.—Variation in skin and skeletal measurements of kangaroo rats (genus *Dipodomys*) was evaluated using 265 specimens from 11 localities in Baja California, Mexico. Cluster analyses were utilized to verify field identification at the two localities where *D. gravipes* and *D. agilis* were sympatric and to examine each of the other nine collecting sites for possible sympatric forms. Sexual dimorphism occurred in two external, three skull, and nine postcranial measurements. Males were significantly larger than females in all of these characteristics. Significant interOTU variation occurred in 41 of the 42 characters analyzed. Using correlation analyses the 19 least correlated characters were selected from the original 42. *Dipodomys gravipes* was readily separable from the other taxa. The data indicate that there are only two species of kangaroo rats (*D. agilis* and *D. gravipes*) of the *heermanni* group in Baja California.

Kangaroo rats (genus *Dipodomys*) of the *heermanni* group occupy most of Baja California from the mountains of the north through the desert areas that cover most of the peninsula (Huey, 1951). Kangaroo rats in Baja California have been studied by Villa R. (1941), Alvarez (1960), Huey (for example, 1925, 1927, 1951, 1962, 1964), Stock (1974), and Best and Schnell (1974). Lidicker (1960) discussed *D. merriami* and *D. insularis*, and Lackey (1967) examined kangaroo rats of the *heermanni* group, though he was primarily interested in *D. stephensi* and *D. cascus* in southern California. In addition I have analyzed bacular variation of *D. agilis* and *D. gravipes* as well as relationships between morphological and ecological variation of the populations of *D. agilis* discussed herein (Best, manuscripts submitted for publication).

Using univariate and multivariate statistical techniques, I have identified some patterns of variation in morphologic variables associated with kangaroo rats in Baja California. My purposes were to investigate the following: (1) degree of sexual dimorphism; (2) amount and pattern of interlocality variation within each character; (3) phenetic relationships between the populations; (4) taxonomic relationships of the populations.

MATERIALS AND METHODS

Kangaroo rats were collected at 11 localities in Baja California during June and July 1972 (Table 1). Specimens were divided into 13 Operational Taxonomic Units (OTUs), because at two of the collecting sites, two taxa of kangaroo rats of the *heermanni* group occur sympatrically—*D. gravipes* and *D. agilis* (Table 1, OTUs 2, 3, and 5, 6). Prior to this report the taxonomic designations (from range maps in Hall and Kelson, 1959, unless otherwise indicated) of the OTUs were as follows: (OTU 1) *D. agilis martirensis*; (2) *D. agilis simulans*; (3) *D. gravipes*; (4) *D. agilis simulans*; (5) *D. agilis plectilis*; (6) *D. gravipes*; (7) *D. peninsularis pedionomus*; (8) *D. paralius*; (9) *D. antiquarius* (Huey, 1962); (10) *D. peninsularis eremoecus*; (11 and 12) *D. peninsularis peninsularis*; (13) *D. peninsularis australis*. For the present analyses I have treated these as populations because their systematics are not fully understood (Lackey, 1967; Stock, 1974; Best, manuscript submitted for publication).

Specimens were aged according to the criteria of Best and Schnell (1974). The following external measurements, accurate to the nearest mm, were taken on freshly collected specimens before they were prepared as standard museum study skins and skeletons: total length; tail length; hind foot length; ear length from notch; body length was calculated by subtracting tail length from total length. The 37 skeletal measurements (Fig. 1) were taken to the nearest 0.1 mm with the same dial calipers. All specimens are deposited in the collection of Recent mammals at the Stovall Museum of Science and History, University of Oklahoma.

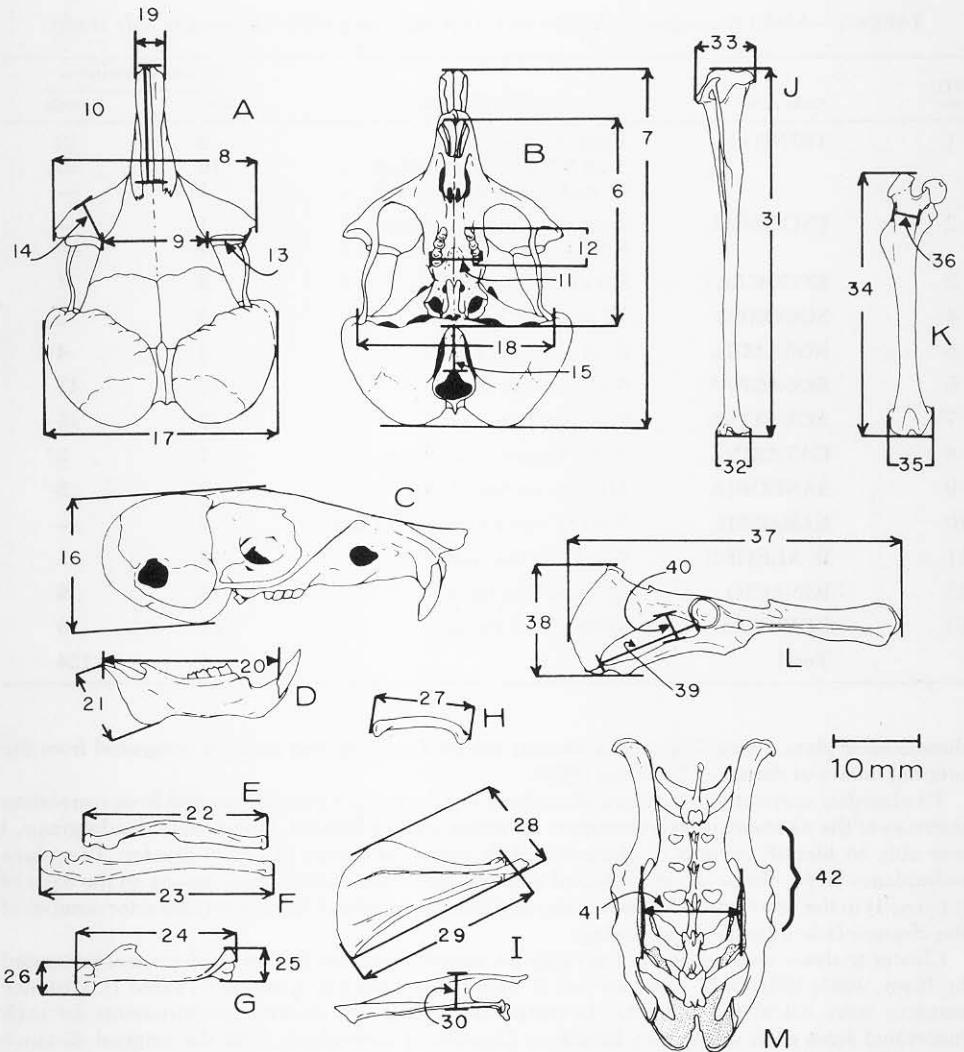


FIG. 1.—Skeletal elements of *Dipodomys gravipes* illustrating the 37 skeletal measurements taken. A, skull, dorsal view; B, skull, ventral view; C, skull, lateral view; D, mandible, lateral view; E, radius, lateral view; F, ulna, lateral view; G, humerus, anterior view; H, clavicle, anterior view; I, scapula, dorsal and lateral views; J, tibia, posterior view; K, femur, posterior view; L, pelvis, lateral view; M, pelvic girdle, dorsal view. Numbers correspond to the characters listed in Table 2.

Several statistical techniques were used in data analysis. The mean and standard deviation were calculated for each character for each OTU and are presented in Appendix I of Best (1976). I tested interOTU heterogeneity of each character with a one-way analysis of variance, and used a sums of squares simultaneous test procedure (SS-STP; Gabriel and Sokal, 1969) to determine the maximally nonsignificant subsets of OTUs.

For multivariate procedures, the mean measurements for each OTU were used. These characters were standardized (so that each had a mean of 0 and SD of 1 across OTUs) and correlation and distance matrices (Sneath and Sokal, 1973) were calculated. Clusters of OTUs and characters were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a correlation matrix among characters, and projections of the OTUs were plotted on the first three components. On the resulting three-

TABLE 1.—*Skeletal samples of kangaroo rats from Baja California used in this study.*

OTU no.	Code name	Collecting localities	Number of specimens	
			Male	Female
1	TRINIDAD	Valle de Trinidad	9	13
		4 mi S Valle de Trinidad	10	15
		W end Valle de Trinidad	1	—
2	ESCOAGIL	2 mi E Colonia Guerrero	1	—
		8.5 mi N San Quintin	1	—
3	ESCOGRAV	8.5 mi N San Quintin	8	7
4	SOCORRO	12 mi N El Rosario	2	2
5	ROSAAGIL	6 mi E El Rosario	3	4
6	ROSAGRAV	6 mi E El Rosario	17	17
7	AGUSTINE	San Agustine	19	13
8	CATARINA	Santa Catarina Landing	7	3
9	SANBORJA	Mission de San Borjas	8	5
10	ELBARRIL	7 mi W San Francisquito Bay	2	—
11	R. ALEGRE	2.5 mi W Mesquital	18	17
12	IGNACIO	10 mi E San Ignacio	11	9
13	REFUGIO	4.5 mi N El Refugio	24	19
	Total		141	124

dimensional plots, I superimposed a shortest minimally connected network computed from the original matrix of distances between OTUs.

To elucidate correlations between characters, dendrograms were constructed from correlation matrices of the 42 standardized characters for males and for females. Using these dendrograms, I was able to identify groups of characters with intercorrelations of 0.9 or greater. To reduce redundancy in my character set I selected one character from each of these groups on the basis of it being 1) in the same group for both males and females, and/or 2) the lowest character number of the characters in a particular grouping.

Cluster analyses were performed to verify my visual separation (based on characters presented by Huey, 1925, 1951) of *D. gravipes* and *D. agilis* at localities 2, 3, and 5, 6 (Table 1). Distance matrices were calculated from the 42 standardized skin and skeletal measurements for each individual from each of the two localities. Clusters of individuals from the original distance matrices were obtained with the UPGMA. Similar examinations of the remaining nine localities were conducted in search of other sympatric forms.

Analyses were performed using the IBM 360 computer at the University of Oklahoma Computation Center. The programs UNIVAR (Power, unpublished manuscript) and NT-SYS (Rohlf et al., 1972) provided most of the analytic foundation for this study.

RESULTS

Using individual specimens as OTUs, cluster analyses were performed for each of the 11 localities. Results of two such analyses are shown in Fig. 2. Two distinct clusters appear in both dendrograms. The upper cluster in each includes all specimens identified in the field as *D. agilis*; the lower corresponds to specimens of *D. gravipes*. In subsequent analyses these clusters were treated as separate OTUs. Similar analyses for the other nine localities did not reveal a similar degree of heterogeneity, indicating that only one taxon was represented by the specimens collected at each site.

Of the 42 morphologic characters, 14 exhibit significant secondary sexual dimorphism in size (Table 2), with males being significantly larger than females. These include two external, three skull, and nine postcranial measurements. The dimorphism is

TABLE 2.—Secondary sexual dimorphism in size in 42 skin and skeletal characters of Baja California kangaroo rats (*Dipodomys*).

Character	Char. no.	Character-state means ³		Analysis of variance ¹	
		♂♂ (G = 13, N = 141)	♀♀ (G = 11, N = 124)	D.F.	F-ratio ²
Skin					
Total length	1	294.13	288.84	1,209	6.532*
Body length	2	120.13	124.99	1,263	0.514
Tail length	3	173.40	171.18	1,209	2.343
Hind foot length	4	43.38	42.41	1,263	8.406**
Ear length	5	17.30	17.08	1,263	1.145
Skull and mandible					
Basal length	6	22.03	21.89	1,254	2.274
Greatest length	7	39.95	39.34	1,231	5.817*
Maxillary arch spread	8	21.67	21.51	1,252	0.902
Interorbital width	9	10.62	10.62	1,257	0.017
Nasal length	10	14.26	14.14	1,257	2.274
Intermaxillary width	11	7.60	7.59	1,259	0.089
Alveolar length	12	5.06	5.05	1,260	0.112
Lacrimal length	13	3.84	3.83	1,263	0.011
Maxillary arch spread	14	5.20	5.24	1,263	0.303
Basioccipital length	15	5.67	5.56	1,243	6.025*
Greatest depth	16	13.47	13.41	1,241	1.233
Greatest width	17	25.31	25.06	1,243	4.236*
Zygomatic width	18	19.44	19.29	1,256	1.279
Nasal width	19	3.72	3.66	1,258	3.799
Mandible length	20	16.58	16.49	1,263	0.684
Mandible depth	21	7.50	7.41	1,263	1.581
Postcranial skeleton					
Radius length	22	18.21	17.86	1,262	8.531**
Ulna length	23	22.03	21.63	1,263	7.172**
Humerus length	24	14.66	14.40	1,262	5.790*
Humerus distal width	25	4.53	4.48	1,262	1.533
Humerus proximal width	26	3.74	3.72	1,262	0.483
Clavicle length	27	9.12	8.95	1,262	3.665
Scapula width	28	8.22	8.07	1,220	2.764
Scapula length	29	16.90	16.71	1,232	1.414
Scapula depth	30	2.73	2.74	1,253	0.090
Tibia length	31	38.97	38.09	1,257	7.816**
Tibia distal width	32	4.26	4.19	1,262	3.173
Tibia proximal width	33	5.37	5.32	1,263	0.776
Femur length	34	28.83	28.33	1,262	3.992*
Femur distal width	35	5.08	4.99	1,263	3.190
Femur proximal width	36	3.17	3.12	1,261	1.636
Pelvis length	37	31.97	31.38	1,263	3.335
Pelvis depth	38	11.86	10.93	1,263	48.106**
Pelvic foramen length	39	9.61	9.85	1,263	4.958*
Pelvic foramen width	40	3.82	3.66	1,263	7.702**
Width fused vertebrae	41	9.76	9.45	1,257	6.845**
Number fused vertebrae	42	4.84	4.77	1,260	1.628

¹ Single-classification analysis of variance, sexes compared pairwise for each character.

² Minimally significant sexual dimorphism assumed where $P \leq 0.05$ (one asterisk); two asterisks indicate $P \leq 0.01$.

³ Dimensions in mm; G = number of localities; N = number of specimens.

primarily in lengths of the major structures of the body. Only two widths of structures, characters 17 (skull width) and 41 (width of fused vertebrae), show sexual dimorphism in size.

Significant interOTU character variation was found among 41 of the 42 characters in

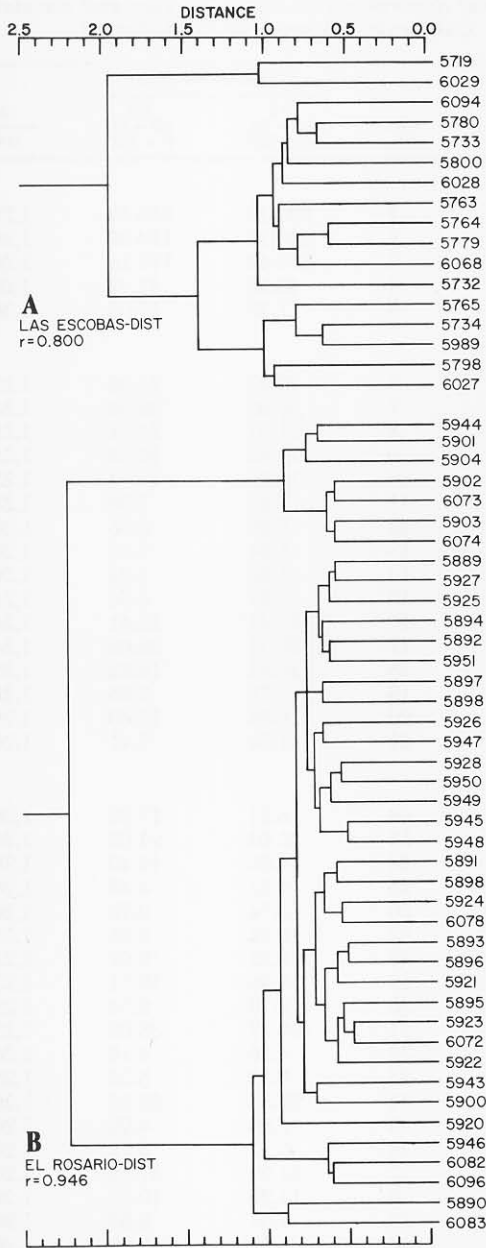


FIG. 2.—Phenograms constructed from distance matrices calculated from 42 skin and skeletal characters of Baja California kangaroo rats (*Dipodomys*). A. A single specimen from 2 mi E Colonia Guerrero and 16 from 8.5 mi N San Quintin. B. Forty-one specimens from 6 mi E El Rosario. Specimen numbers in the figures refer to my original field numbers. The cophenetic correlation coefficients (r) are given.

both sexes ($P \leq 0.05$). The only character not showing variation was character 42 (number of fused vertebrae). For a number of characters (for example, 3, 7, 31, and 34) the extent of interOTU variation was different for males and females as indicated by the F -ratios for each sex (see Table 3 of Best, 1976).

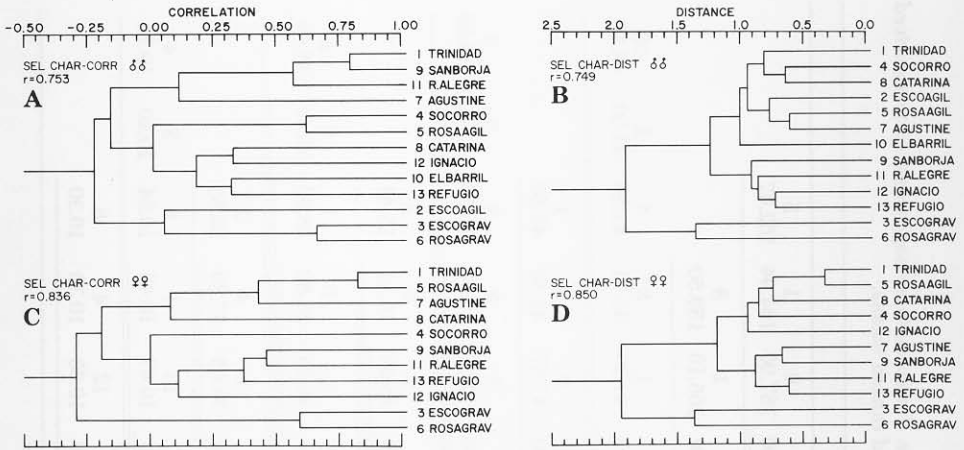


FIG. 3.—Phenograms constructed from correlation and distance matrices for male (A and B, respectively) and female (C and D, respectively) kangaroo rats from Baja California. Clusters were obtained using the UPGMA. Accuracy of the diagrams in depicting interpopulation relationships increases from left to right. Numerical identifications are the same as listed in Table 1.

The 42 characters showed considerable redundancy in both sexes. Using the criteria outlined above, I selected 16 female and 15 male characters. Only characters 7 (greatest length of skull), 23 (ulna length), 28 (scapula width), and 36 (femur proximal width) for females, and 15 (basioccipital length), 17 (greatest width of skull) and 38 (pelvis depth) for males, were not in common for both sexes. These characters for females were added to the selected set of characters for males and vice versa; thus a total of 19 characters (listed in Table 3) were chosen for further analyses.

The results of the SS-STP analysis for each of the 19 characters depicting the pattern of interOTU character variation is shown in Table 3. OTU 6 is the largest in all characters except the following cases: 3 (tail length) in males where it is second in size to OTU 13; 5 (ear length) in both sexes where it has, except for OTU 3, the shortest ears of all the OTUs; 12 (alveolar length) in males with OTU 3 being the only one greater; 42 (number of fused vertebrae) where it is fourth and second largest for males and females, respectively. In addition to OTU 6, OTUs 3, 11, and 13 are frequently among the largest OTUs. OTUs 1, 4, and 8 are generally smaller for most of the 19 characters.

Fig. 3 presents phenograms for both sexes constructed from correlation and distance matrices of the 19 selected characters. Each of the correlation phenograms (Figs. 3A and 3C) can be divided into two primary clusters. In males the lower cluster contains OTUs 2, 3, and 6 and the remaining OTUs comprise the second cluster; for females, OTUs 3 and 6 make up one cluster and the remaining OTUs make up the other group (there were no female specimens for OTUs 2 or 10).

The distance phenograms also show only two major clusters (Figs. 3B and 3D). For both males and females OTUs 3 and 6 comprise one cluster and the other OTUs are in a second cluster. Within the larger cluster in the female phenogram (Fig. 3D), OTUs do not appear to be grouped according to any taxonomic or geographic pattern. The large cluster of male OTUs exhibits subgroupings based upon geographical considerations, that is, OTUs 1, 2, 4, 5, 7, and 8 represent the northern forms, OTU 10 is the only east coast form, and OTUs 9, 11, 12, and 13 are the southern OTUs. The most highly correlated OTUs in the distance phenograms are OTUs 1 and 5 for females. All other OTUs in both phenograms (Figs. 3B and 3D) are joined at a phenetic distance of 0.5 or greater.

TABLE 3.—Variation in means of 19 skin and skeletal characters in Baja California kangaroo rats. Statistically homogeneous subsets derived from SS-STP analysis are shown by lines below the OTU numbers and ranked means.

Character	No.	Sex	Results of SS-STP analysis												
Tail length	3	♂♂	13	6	10	12	11	3	7	8	9	1	5		
			181.14	179.94	179.50	176.00	174.00	173.71	168.23	167.00	167.00	164.94	162.67		
		♀♀	6	13	9	3	11	12	7	5	1	8			
			180.42	179.86	173.80	172.40	170.11	167.50	167.08	165.50	165.10	159.50			
Hind foot length	4	♂♂	6	3	12	13	11	9	5	7	1	8	4	2	10
			45.47	44.50	44.36	44.17	43.17	43.13	43.00	42.63	41.90	41.71	41.50	41.50	41.00
		♀♀	6	3	12	13	7	9	11	4	8	5	1		
			44.65	43.57	43.44	43.26	42.62	42.40	42.18	42.00	41.67	41.50	41.50		
Ear length	5	♂♂	11	12	10	13	9	7	1	4	5	8	2	6	3
			18.83	18.36	18.00	17.88	17.50	17.05	17.05	17.00	17.00	16.86	16.50	15.82	15.50
		♀♀	11	9	12	13	7	5	4	8	1	6	3		
			18.47	18.20	17.67	17.63	17.31	17.25	17.00	17.00	16.96	16.12	15.43		
Greatest length skull	7	♂♂	6	11	13	12	9	3	5	7	2	10	1	8	4
			42.51	40.85	40.16	39.97	39.89	39.53	39.47	39.39	39.25	38.80	38.80	38.40	38.00
		♀♀	6	11	13	9	7	5	12	8	1	4	3		
			41.75	40.06	40.02	39.52	39.27	39.22	39.10	38.40	38.05	37.80	36.63		
Interorbital width	9	♂♂	6	11	2	12	3	9	10	7	13	1	8	5	4
			11.01	10.92	10.90	10.76	10.67	10.65	10.55	10.53	10.47	10.43	10.24	10.20	10.15
		♀♀	6	11	7	9	3	5	13	1	12	4	8		
			11.10	10.79	10.73	10.68	10.67	10.60	10.47	10.39	10.33	10.30	10.30		

TABLE 3.—Continued.

Character	No. Sex	Results of SS-STP analysis													
		6	12	9	11	13	3	7	2	5	8	1	10	4	
Nasal length	10 ♂♂	6 15.19	12 14.44	9 14.41	11 14.41	13 14.37	3 14.06	7 14.05	2 13.90	5 13.87	8 13.80	1 13.70	10 13.55	4 13.50	
	♀♀	6 14.85	9 14.22	13 14.21	12 14.17	3 14.10	7 14.08	11 14.08	1 13.82	5 13.80	4 13.65	8 13.60			
Intermaxillary width	11 ♂♂	6 8.00	11 7.88	3 7.85	10 7.65	9 7.65	13 7.61	12 7.48	7 7.46	1 7.37	2 7.35	5 7.23	8 7.23	4 7.10	
	♀♀	6 8.02	3 7.82	11 7.65	7 7.62	9 7.62	13 7.58	5 7.45	12 7.44	8 7.40	1 7.36	4 7.20			
Alveolar length	12 ♂♂	3 5.41	6 5.41	7 5.15	11 5.11	13 5.10	2 5.05	5 4.90	4 4.90	12 4.87	10 4.85	9 4.81	1 4.80	8 4.77	
	♀♀	6 5.35	7 5.29	3 5.28	13 5.02	5 5.00	11 4.98	9 4.96	1 4.93	8 4.87	4 4.85	12 4.64			
Basioccipital length	15 ♂♂	6 6.35	3 5.91	2 5.80	11 5.73	13 5.64	9 5.56	8 5.53	7 5.50	1 5.48	12 5.47	5 5.47	10 5.30	4 5.10	
	♀♀	6 6.20	3 5.84	13 5.64	9 5.56	8 5.53	11 5.48	7 5.46	5 5.45	1 5.32	12 5.26	4 5.25			
Greatest depth skull	16 ♂♂	6 14.02	13 13.73	11 13.72	9 13.56	12 13.39	5 13.37	2 13.35	3 13.32	10 13.30	7 13.29	1 13.15	4 13.05	8 12.86	
	♀♀	6 13.96	13 13.64	11 13.58	7 13.47	3 13.44	8 13.17	12 13.16	5 13.12	9 13.12	1 13.08	4 12.75			

TABLE 3.—Continued.

Character	No.	Sex	Results of SS-STP analysis												
Greatest width skull	17	♂♂	6	11	10	13	9	12	3	5	7	1	2	8	4
			26.66	26.09	25.80	25.77	25.63	25.22	25.09	24.80	24.77	24.51	24.45	23.86	23.80
		♀♀	6	13	11	3	9	7	12	5	1	8	4		
			26.13	25.55	25.44	25.13	25.10	24.86	24.60	24.52	24.33	24.27	23.90		
Nasal width	19	♂♂	6	11	9	3	5	13	7	4	12	1	10	2	8
			3.99	3.93	3.91	3.79	3.70	3.66	3.65	3.60	3.60	3.60	3.50	3.45	3.37
		♀♀	6	11	3	13	4	5	7	1	9	12	8		
			3.93	3.78	3.73	3.67	3.65	3.62	3.59	3.58	3.57	3.36	3.33		
Ulna length	23	♂♂	6	3	11	13	9	5	4	7	12	2	8	1	10
			24.36	23.34	22.25	22.07	21.87	21.57	21.45	21.45	21.37	21.35	21.01	20.95	20.65
		♀♀	6	3	13	11	4	5	8	9	7	1	12		
			23.72	23.33	21.62	21.61	21.40	21.35	21.20	21.10	21.07	20.76	20.51		
Scapula width	28	♂♂	6	3	11	13	4	7	5	9	12	2	1	8	
			9.35	8.92	8.64	8.43	8.00	7.91	7.90	7.86	7.84	7.80	7.59	7.57	
		♀♀	6	3	11	13	4	8	9	1	7	5	12		
			8.88	8.73	8.28	8.26	8.00	7.80	7.75	7.71	7.67	7.50	7.31		
Scapula depth	30	♂♂	6	3	11	13	5	9	2	12	4	7	1	8	
			3.13	3.01	2.78	2.76	2.73	2.69	2.65	2.65	2.60	2.60	2.54	2.41	
		♀♀	6	3	13	11	4	5	12	9	7	1	8		
			3.10	3.00	2.77	2.76	2.70	2.65	2.64	2.62	2.60	2.57	2.35		

TABLE 3.—Continued.

Character	No.	Sex	Results of SS-STP analysis												
			6	11	3	13	5	10	9	7	2	12	4	8	1
Femur proximal width	36	♂♂	6 3.47	11 3.35	3 3.29	13 3.25	5 3.13	10 3.10	9 3.07	7 3.06	2 3.05	12 3.03	4 2.95	8 2.93	1 2.92
		♀♀	6 3.36	3 3.27	13 3.21	11 3.19	9 3.12	7 3.08	4 3.05	12 3.03	8 3.00	5 2.95	1 2.94		
Pelvis depth	38	♂♂	6 13.85	11 12.56	13 12.25	3 12.16	5 11.63	12 11.56	9 11.56	10 11.55	2 11.20	7 11.14	8 10.67	1 10.60	4 10.25
		♀♀	6 12.58	3 12.03	11 11.22	13 11.05	7 10.49	5 10.42	9 10.38	12 10.34	8 10.33	4 10.30	1 10.07		
Pelvic foramen width	40	♂♂	6 4.54	3 4.37	2 3.95	11 3.83	13 3.82	12 3.75	10 3.70	9 3.70	5 3.63	7 3.62	8 3.44	1 3.42	4 3.40
		♀♀	6 4.37	3 4.21	13 3.73	11 3.72	12 3.70	9 3.50	7 3.42	8 3.40	1 3.29	4 3.25	5 3.12		
Number fused vertebrae	42	♂♂	2 5.00	4 5.00	5 5.00	6 4.94	13 4.92	12 4.91	11 4.89	3 4.88	8 4.86	7 4.83	9 4.63	1 4.58	
		♀♀	5 5.00	6 4.94	1 4.86	3 4.86	7 4.85	12 4.78	8 4.67	11 4.65	9 4.60	13 4.58	4 4.50		

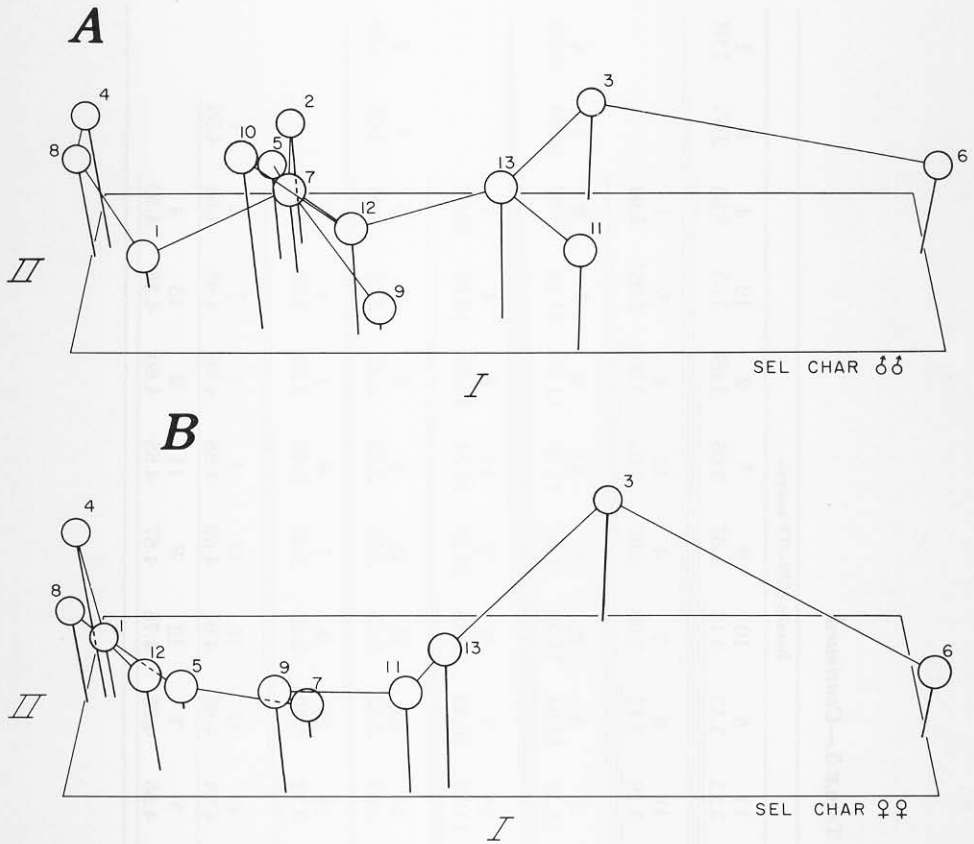


FIG. 4.—Three-dimensional projection of OTUs onto the first three principal component axes of variation in the matrix of correlations of 19 skin and skeletal characters of male (A) and female (B) *Dipodomys* from Baja California. The shortest simply-connected network, derived from the matrix of distance coefficients for the same characters, is superimposed on the principal component space to indicate where possible distortion may be present. The numbers correspond to the OTUs listed in Table 1.

The loadings of characters on the first three component axes are presented in Table 4 and three-dimensional projections are depicted in Fig. 4. The character correlations with principal component I for both males and females are high for all characters except 5 (ear length) and 42 (number of fused vertebrae). Following the reasoning of Johnston and Selander (1971), Niles (1973), and Kennedy and Schnell (1978), this component may be taken to represent overall size in both sexes, because it accounts for most of the covariation among characters.

On principal component II, character 5 (ear length) has the highest loading for both sexes (Table 4). Other characters have only weak associations with this component.

The third principal component for males has highest loadings for characters 3 (tail length) and 42 (number of fused vertebrae). The females have high negative loadings for character 42 (number of fused vertebrae) and much lower loadings for all other characters. As noted previously, character 42 is the only one examined that did not exhibit interOTU variation.

The three components explain almost 90% of the total character variation for each sex (see bottom of Table 4). Thus, distortion of the phenetic distances between OTUs is very small when the character space is reduced to three dimensions.

TABLE 4.—Character loadings¹ of the first three principal components of interOTU phenetic variation among 19 selected characters.

Char. no. ²	Sex	Principal components		
		I	II	III
3	♂♂	.629	-.294	.604
	♀♀	.827	-.354	.311
4	♂♂	.837	.033	-.176
	♀♀	.833	-.062	.158
5	♂♂	-.212	-.923	.158
	♀♀	-.426	-.852	.003
7	♂♂	.931	-.203	-.132
	♀♀	.496	-.728	-.291
9	♂♂	.743	-.207	-.035
	♀♀	.847	-.152	-.366
10	♂♂	.869	-.196	-.238
	♀♀	.870	-.348	-.097
11	♂♂	.894	-.207	-.026
	♀♀	.948	-.045	-.178
12	♂♂	.823	.426	.123
	♀♀	.768	.287	-.300
15	♂♂	.861	.267	-.168
	♀♀	.925	.130	-.073
16	♂♂	.890	-.325	-.033
	♀♀	.876	-.240	-.176
17	♂♂	.844	-.472	.058
	♀♀	.910	-.376	-.041
19	♂♂	.791	-.140	-.380
	♀♀	.802	.029	.034
23	♂♂	.915	.330	-.114
	♀♀	.891	.390	.099
28	♂♂	.941	.166	.199
	♀♀	.858	.250	.328
30	♂♂	.932	.253	.007
	♀♀	.892	.157	.161
36	♂♂	.951	-.010	.142
	♀♀	.940	-.060	.288
38	♂♂	.970	-.114	.076
	♀♀	.962	.177	.078
40	♂♂	.908	.303	.097
	♀♀	.900	.087	.191
42	♂♂	.134	.205	.887
	♀♀	.300	.373	-.826
Total ³	♂♂	68.105	10.805	8.221
	♀♀	67.900	11.847	7.695

¹ Correlations of locality mean values ($n \text{ ♂♂} = 13; n \text{ ♀♀} = 11$) of individual characters with the component axes.² Character numbers correspond to the list of characters in Table 2.³ Percent of total phenetic variance explained.

Principal component I, which accounts for about two-thirds of the phenetic variation, separates populations according to size (see Fig. 4). Among males OTUs 3, 6, 11, and 13 are the largest and 1, 8, and 4 are the smallest. The same is true for females, except OTUs 11 and 13 are more closely allied with smaller OTUs. Except for OTUs

3 and 6, female OTUs form a chain grading in size from OTU 8 (the smallest) to OTU 13 (the largest). For both sexes, OTU 6 has a much higher loading for component I than any of the other OTUs.

The second principal component separates the shorter-eared OTU 3, which is located toward the back of the models, and places the longer-eared OTUs 9, 10, 11, 12, and 13 near the front. Thus, longer ear lengths are found in the more southern forms, as indicated in Table 3.

Principal component III is represented by the lengths of the vertical lines in the three-dimensional models (Fig. 4). The two male OTUs (1 and 9) near the base of the diagram have the smallest number of fused vertebrae and also have (except OTU 5) the shortest tail length (see Table 3). These forms are separated from the other OTUs by component III. For females, there is not as distinct a break in terms of this component. However, OTUs 5 and 7, which are placed near the base, are among the shortest-tailed forms.

DISCUSSION

My results indicate that the only localities with two taxa present are from 8.5 mi N San Quintin-2 mi E Colonia Guerrero and from 6 mi E El Rosario (see Table 1). Only one of the other nine localities has been indicated as having sympatric forms. Huey (1951) listed six specimens of *D. peninsularis pedionomus* from San Borjas Mission, but later did not include these specimens in those listed for *D. antiquarius* (Huey, 1962, 1964). He described *D. antiquarius* (Huey, 1962) as being known only from eight specimens collected at San Juan Mine, Sierra San Borja, alt. 4,000 ft, 28°41'N, 113°37'W. These localities are within 2 km of each other. I have examined all of these specimens and cannot distinguish between them. I attempted to collect specimens along the slopes at the San Juan Mine but failed. Along the canyon floor at the base of San Juan Mine (a few hundred m away), I was successful in obtaining 13 adult specimens. As mentioned previously, the cluster analysis for these specimens did not reveal any distinctive groupings. This could have been because my sample included only one of the species present. However, the sample was taken from the only suitable habitat in the area, that is, it was not rocky and shallow soiled, and there were several *Dipodomys* burrows observed in the area.

Sexual dimorphism has been described previously in *D. ordii* (Desha, 1967; Schmidly, 1971; Kennedy and Schnell, 1978; Schmidly and Hendricks, 1976), and in *D. merriami* (Lidicker, 1960). Sexual dimorphism in the Baja California populations is particularly noteworthy because of the degree and numbers of characters involved as compared to *D. ordii* and *D. merriami*. Kennedy and Schnell (1978) found significant sexual dimorphism in 11 of 16 skull characters in *D. ordii*, and Lidicker (1960) noted at least some sexual dimorphism in 11 or 13 characters in *D. merriami*. Only three of the skull characteristics I studied (greatest length of skull, basioccipital length, and greatest width of skull) showed significant sexual dimorphism. None of these appear to be related to food habit separation of the sexes as has been suggested in birds (Selander, 1966). Size in post-cranial skeletal elements, except for clavicle, scapula, and pelvic lengths, is strongly dimorphic.

InterOTU character variation was shown in all except character 42 (number of fused vertebrae in the pelvic girdle). It is not surprising that a character of this type (the only non-metric one taken) does not vary significantly among OTUs or between the sexes. The support given by the fusion of these vertebrae in the pelvic girdle probably is closely associated with the saltatorial mode of locomotion of kangaroo rats.

Phenograms resulting from cluster analyses of correlation and distance matrices for both sexes (Fig. 3) indicate that there are two primary clusters of OTUs. Except for the male correlation phenograms where OTU 2 joins them, OTUs 3 and 6 consistently

group separately from the remaining OTUs (Fig. 3A). A portion of Huey's (1925) original description characterizes *D. gravipes* (OTUs 3 and 6) as, "A large-sized, heavy-bodied, small-eared animal, with thick tail of medium length, belonging to the *heermanni* group. Tip of tail dark and five toes on hind foot, which is extremely large-boned." This characterization is adequate to separate specimens of *D. gravipes* from the remaining OTUs.

Further subdivisions of the non-*D. gravipes* cluster in each of the female phenograms (Figs. 3C and 3D) and the male correlation phenogram (Fig. 3A) does not seem warranted, particularly on taxonomic or geographic bases. The male distance phenogram can be divided into three subclusters at a phenetic distance of about 1.05. The upper subcluster represents the northern forms (OTUs 1, 2, 4, 5, 7, and 8), the center single-member subcluster (OTU 10) represents the east coast form, and the lower subcluster (OTUs 9, 11, 12, and 13) represents the remaining southern forms. Correlations between environmental variables and morphologic variation of the non-*D. gravipes* OTUs are presented elsewhere (Best, manuscript submitted for publication).

Two obvious taxonomic conclusions can be drawn from the data presented previously and herein. First, *D. gravipes* is separable from *D. agilis* on the basis of karyotypes (Stock, 1974), bacular measurements (Best and Schnell, 1974; Best, manuscript submitted for publication), and the set of morphologic characters analyzed herein. Second, *D. agilis*, *D. peninsularis*, *D. paralius*, and *D. antiquarius* are not distinct on the basis of these analyses. These findings support a contention that only two species of kangaroo rats (*D. agilis* and *D. gravipes*) of the *heermanni* group occur in Baja California, Mexico.

Huey (1951) separated *D. peninsularis* from *D. agilis* on the basis of the former's ". . . extremely inflated bullae, brightly colored and heavily boned tail and average dorsal color tones . . ." Stock (1974) in his "own examination of many specimens of this series" of Baja California populations believed that they all may be subspecies of *D. agilis* (including *D. paralius* and *D. antiquarius*). Stock (1974) based his conclusions primarily upon Lackey's (1967) cranial measurements and his own findings of identical karyotypes for *D. peninsularis pedionomus* and *D. agilis plectilis*. The evidence presented by Lackey (1967) and Stock (1974) as well as bacular analyses (Best and Schnell, 1974; Best, manuscript submitted for publication) seems to argue against Huey's (1951) justification for separating *D. peninsularis* from *D. agilis*. Therefore, I suggest that *D. peninsularis* and *D. agilis* are conspecific.

Huey (1951) described *D. paralius* on the basis of 28 specimens from three localities near Santa Catarina. I compared the specimens comprising OTU 8 with Huey's original series of *D. paralius* and found them to be indistinguishable. He characterized the species as follows: ". . . similar in color to *Dipodomys peninsularis pedionomus*, but it is smaller and has smaller ears. Cranially, it is widely divergent, with smaller, proportionally flatter, more inflated bullae and with slightly more angular and more widely spreading maxillary arches. This latter character is prominent and places this species very near to the broad-faced group of kangaroo rats. Compared with *Dipodomys agilis plectilis*, *D. paralius* is lighter in dorsal coloration and smaller in size, and further differs in the cranial characters mentioned above. The general outline of the skull is more nearly that of an equilateral triangle than that of an acute triangle, such as characterizes *D. a. simulans*, *D. a. plectilis* and other members of the *agilis* group. However, *paralius* is nearer to the *D. a. simulans-plectilis* chain than it is to the *D. peninsularis* group and it is best left under the *agilis* series." Stock (1974) did not examine this species karyotypically, but could not distinguish between specimens of *D. paralius* and *D. agilis* by visual inspection (nor can I). My analyses group *D. paralius* (OTU 8) consistently with the OTUs representing *D. agilis*, and particularly close to OTUs 4 (*D. agilis simulans*) and 5 (*D. agilis plectilis*). Bacular measurements (Best, manuscript submitted for publication) also indicate a close phenetic affinity with

nearby populations. Thus, I suggest that *D. paralius* is synonymous with *D. agilis plectilis*.

Dipodomys antiquarius was described as "very closely related" to *D. stephensi* (Huey, 1962). Lackey (1967) examined specimens of *D. antiquarius* and postulated that the species is more reasonably placed in the narrow-faced group than the broad-faced group. He considered *D. antiquarius* closer to *D. peninsularis* than *D. stephensi* and pointed out that his samples of *D. antiquarius* and four subspecies of *D. peninsularis* showed no important differences in the 10 characters he studied (see Table 3 of Lackey, 1967). He also noted that *D. antiquarius* differed more from *D. agilis* in inflation of auditory bullae than from *D. peninsularis*. Stock (1974) theorized that *D. antiquarius* was a subspecies of *D. agilis*. I have examined all the specimens of *D. antiquarius* and can not distinguish them from *D. agilis pedionomus* or *D. a. peninsularis* from nearby localities, nor from my 13 specimens comprising OTU 9. In addition, none of the analyses presented herein significantly differentiates *D. antiquarius* (OTU 9) from the other non-*D. gravipes* OTUs. Thus, I suggest that *D. antiquarius* is synonymous with *D. agilis pedionomus*.

According to my findings, the correct names for the taxa of the *heermanni* group of kangaroo rats in Baja California (with synonyms indented) are as follows:

***Dipodomys agilis plectilis* Huey 1951**

Dipodomys paralius Huey 1951

***Dipodomys agilis australis* Huey 1951**

Dipodomys peninsularis australis Huey 1951

***Dipodomys agilis eremoecus* Huey 1951**

Dipodomys peninsularis eremoecus Huey 1951

***Dipodomys agilis pedionomus* Huey 1951**

Dipodomys peninsularis pedionomus Huey 1951

Dipodomys antiquarius Huey 1962

***Dipodomys agilis peninsularis* (Merriam 1907)**

Dipodomys peninsularis peninsularis (Merriam 1907)

ACKNOWLEDGMENTS

This study was partially supported by a Doctoral Dissertation Improvement Grant from the National Science Foundation (GB-33062), a Grant-in-Aid of Research award from The Society of the Sigma Xi, and a National Science Foundation Grant (GB-30814) to G. D. Schnell. I am grateful to A. F. Best, W. W. Like, and J. W. Pepper for making available a field vehicle, a trailer, and other equipment that made the field work possible. J. R. Jehl (San Diego Natural History Museum), W. Z. Lidicker, Jr., and J. R. Patton (Museum of Vertebrate Zoology, University of California at Berkeley) generously made specimens available for my comparative studies. H. A. Smith and S. Erkenbeck gave valuable assistance in collecting the field data. B. Villa R., Director General de la Fauna Silvestre, Mexico, D. F., provided the necessary permits to collect specimens in Mexico. G. Davidson assisted in the preparation of Figs. 1 and 4. G. D. Schnell, C. E. Hopla, A. A. Echelle, and J. R. Estes provided assistance in the form of encouragement and guidance during the study and in critically evaluating the manuscript. Finally, very special thanks go to many friends and fellow graduate students for their encouragement, confidence, and discussions of the various aspects of this study, most especially these include B. Hoditschek, H. A. Smith, J. J. Hellack, and M. L. Kennedy.

LITERATURE CITED

- ALVAREZ, T. 1960. Sinopsis de las especies Mexicanas del genero *Dipodomys*. Rev. Soc. Mex. Hist. Nat., 21:391-424.
- BEST, T. L. 1976. Morphologic variation in kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Unpublished Ph.D. dissertation, Univ. Oklahoma, Norman, 90 pp.

- BEST, T. L., AND G. D. SCHNELL. 1974. Bacular variation in kangaroo rats (genus *Dipodomys*). *Amer. Midland Nat.*, 91:257-270.
- DESHA, P. G. 1967. Variation in a population of kangaroo rats, *Dipodomys ordii medius* (Rodentia: Heteromyidae) from the high plains of Texas. *Southwestern Nat.*, 12:275-289.
- GABRIEL, K. R., AND R. R. SOKAL. 1969. A new statistical approach to geographic variation analysis. *Syst. Zool.*, 18:259-278.
- HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. The Ronald Press, New York, 1:xxx + 1-546 + 79 pp.
- HUEY, L. M. 1925. Two new kangaroo rats of the genus *Dipodomys* from Lower California. *Proc. Biol. Soc. Washington*, 38:83-85.
- . 1927. A discussion of the zonal status of the Sierra San Pedro Martir, Lower California, Mexico, with descriptions of a new kangaroo rat and a new woodpecker from that region. *Trans. San Diego Soc. Nat. Hist.*, 5:3-10.
- . 1951. The kangaroo rats (*Dipodomys*) of Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.*, 11:205-256.
- . 1962. Two new species of broad-faced, five-toed kangaroo rats (genus *Dipodomys*). *Trans. San Diego Soc. Nat. Hist.*, 12:477-480.
- . 1964. The mammals of Baja California, Mexico. *Trans. San Diego Soc. Nat. Hist.*, 13:85-168.
- JOHNSTON, R. F., AND R. K. SELANDER. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution*, 25:1-28.
- KENNEDY, M. L., AND G. D. SCHNELL. 1978. Geographic variation and sexual dimorphism in Ord's kangaroo rat, *Dipodomys ordii*. *J. Mamm.*, 59:45-59.
- LACKEY, J. A. 1967. Biosystematics of *heermanni* group kangaroo rats in southern California. *Trans. San Diego Soc. Nat. Hist.*, 14:313-344.
- LIDICKER, W. Z., JR. 1960. An analysis of intraspecific variation in the kangaroo rat *Dipodomys merriami*. *Univ. California Publ. Zool.*, 67:125-218.
- NILES, D. M. 1973. Adaptive variation in body size and skeletal proportions of horned larks of the southwestern United States. *Evolution*, 27:405-426.
- ROHLF, F. J., J. KISHPAUGH, AND S. KIRK. 1972. Numerical taxonomy and multivariate statistical programs (NT-SYS). Version of October, 1972; State Univ. New York, Stony Brook.
- SCHMIDLY, D. J. 1971. Population variation in *Dipodomys ordii* from western Texas. *J. Mamm.*, 52:108-120.
- SCHMIDLY, D. J., AND F. S. HENDRICKS. 1976. Systematics of the southern races of Ord's kangaroo rat, *Dipodomys ordii*. *Bull. Southern California Acad. Sci.*, 75:225-237.
- SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor*, 68:113-151.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy: the principles and practice of numerical classification. W. H. Freeman and Co., San Francisco, 573 pp.
- STOCK, A. D. 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. *J. Mamm.*, 55:505-526.
- VILLA R., B. 1941. Nota acerca de algunas especies de roedores de los generos *Dipodomys*, *Perognathus* y *Peromyscus*. *Ann. Inst. Biol.*, Mexico, 12:335-399.

Department of Zoology and Stovall Museum of Science and History, The University of Oklahoma, Norman 73019 (present address: Natural Sciences Research Institute, Natural History Museum, Eastern New Mexico University, Portales, New Mexico 88130). Submitted 15 October 1976. Accepted 2 June 1977.