

A NEW SUBSPECIES OF POCKET GOPHER (*GEOMYS*) FROM TEXAS (MAMMALIA: RODENTIA: GEOMYIDAE)

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Abstract.—Two isolated populations of pocket gophers were discovered far outside the previously known distribution of geomyids in southern Texas. These represent a new taxon, which is related to *Geomys texensis* in chromosome morphology and biochemical properties. The two share identical diploid number ($2N = 70$), fundamental number ($FN = 68$), and the presence of a distinctive large acrocentric X-chromosome. There are no fixed differences in any of the 18 loci analyzed with starch gel electrophoresis, when comparing the new taxon with *G. texensis*. However, both of these taxa share alleles at two loci that are present as fixed differences when compared to *G. bursarius major*. Analysis of cranial morphology indicates that the new taxon resembles *G. texensis*, but differs significantly in cranial dimensions of size and shape, related primarily to measurements of basal and palatal lengths and mastoid breadth. Because of the morphological distinctiveness and the extreme spatial separation (120 km) from populations of *G. texensis* confined to the central basin of the Edwards Plateau, we conclude that this new taxon is an isolated, relictual population of *G. texensis*, and is a distinctive subspecies.

During a recent survey of the pocket gophers in southern Texas, populations were discovered far outside the previously known distributional ranges of *Geomys*. *Geomys attwateri* and *G. personatus* are both broadly distributed species (Fig. 1) that occur over much of the eastern and central portions of an area herein referred to as South Texas and bounded by the Edwards Plateau, San Antonio River, Gulf of Mexico, and Rio Grande River (Davis 1940; Kennerly 1954, 1959; Williams & Genoways 1981). Their distributions are restricted to sandy and sandy-loam soils (Davis 1940, Honeycutt & Schmidly 1979) that are dispersed throughout this region. The northern and western parts of South Texas, however, consist almost entirely of hard indurate soils, with high clay content, and caliche. *Geomys* is occasionally found in isolated pockets of sandy or sandy-loam soils in this area.

Survey of these isolated patches of suitable habitats in the northwestern part of the

region detected previously unknown populations in Medina, Zavala and Uvalde counties. Karyotypic, morphometric and electrophoretic analyses identify these as relictual populations that are related to *Geomys texensis*, and they are described herein as representing a new subspecies.

Materials and Methods

Animals were live-trapped (Baker & Williams 1972) and returned to the laboratory. Metaphase spreads were prepared from bone marrow cells, using 0.075 M potassium chloride hypotonic and Carnoy's fixative (Baker et al. 1982). Fresh slides were prepared by dropping (1.5 m) the cells onto slides flooded with distilled water. Standard karyotypes were analyzed following staining with 2% giemsa stain in 0.01 M phosphate buffer. Diploid number ($2N$) was determined by counting at least 10 spreads, whereas fundamental number and chro-

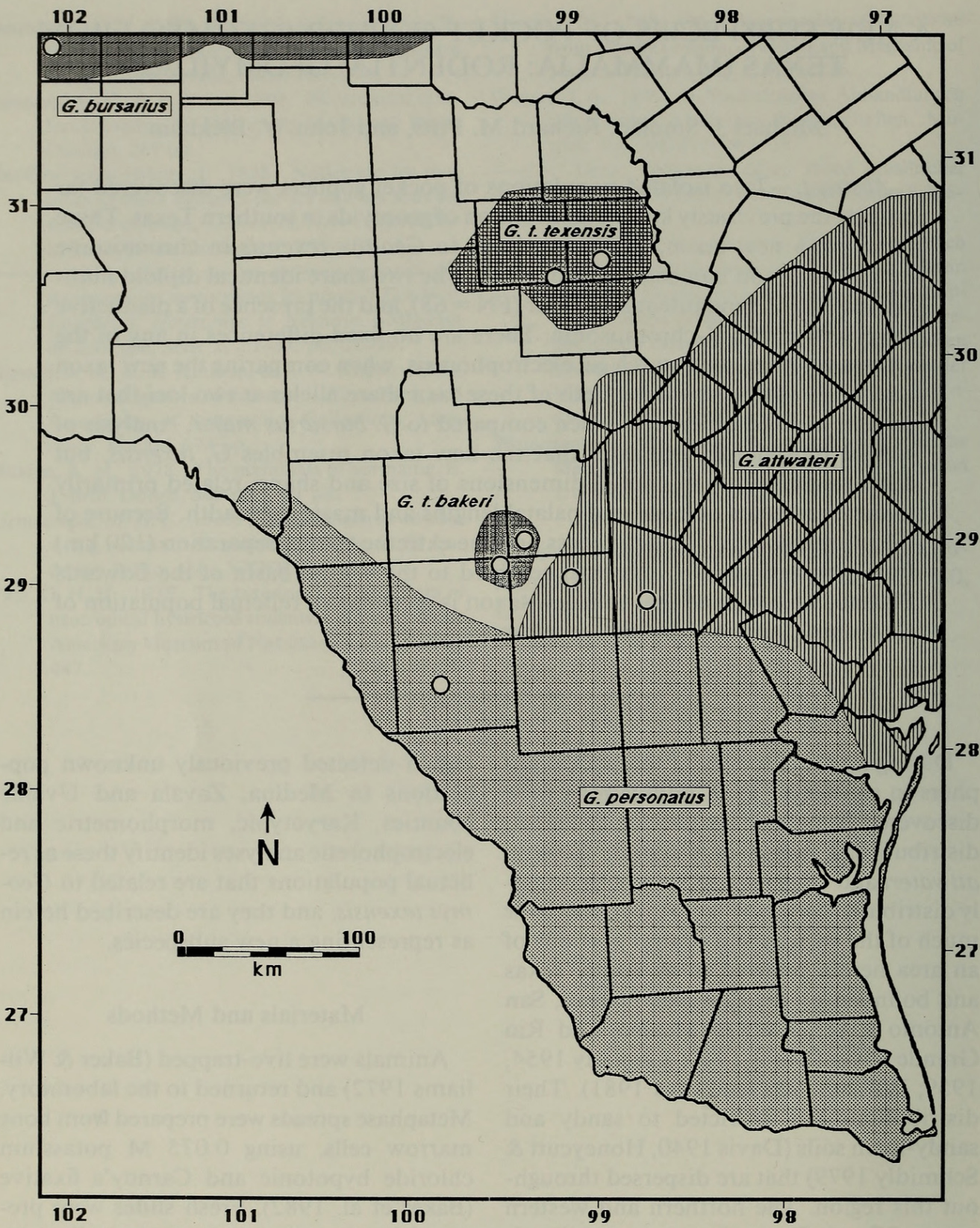


Fig. 1. Map of the distributions of pocket gophers in southern Texas. Open circles represent localities from which specimens were pooled to form samples.

mosome morphology were described from photographic prints of selected spreads.

Samples representing the unknown taxon ($n = 21$), *G. texensis* ($n = 13$), and *G. bursarius* ($n = 10$) were used to assay biochemical variation. Heart and kidney tissues were minced in a grinding solution (Tris/EDTA/NADP) and homogenized using a mechanical homogenizer (Tissue Tearor, Biospec Products). Samples were loaded into 12% starch gels (Starch Art). The techniques used for visualizing the allozymes were those described by Harris & Hopkinson (1976) and Honeycutt & Williams (1982). Proteins were examined on the following buffer systems: Poulik, continuous Tris-citrate II (pH 7.0 and 8.0), Tris-malate EDTA (pH 7.4), and Ridgway (pH 6.7). Eighteen presumptive loci and their respective Enzyme Commission numbers (Murphy et al. 1990) are as follows: glycerol-3-phosphate dehydrogenase (G3PDH; E.C. 1.1.1.8), malate dehydrogenase (MDH-1,2; E.C. 1.1.1.37), isocitrate dehydrogenase (IDH-1,2; E.C. 1.1.1.42), phosphogluconate dehydrogenase (6-PGDH; E.C. 1.1.1.44), superoxide dismutase (SOD-1,2; E.C. 1.15.1.1), purine-nucleoside phosphorylase (PNP; E.C. 2.4.2.1), aspartate aminotransferase (AAT-1,2; E.C. 2.6.1.1), creatine kinase (CK; E.C. 2.7.3.2), phosphoglucomutase (PGM-1; E.C. 5.4.2.2), esterase (EST-1,2; E.C. 3.1.1.-), peptidase (PEP-1 leucyl glycyl glycine, PEP-2 leucyl alanine; E.C. 3.4.-.-), aconitase hydratase (ACOH; E.C. 4.2.1.3), glucose-phosphate isomerase (GPI; E.C. 5.3.1.9). The allozyme data were scored in a side by side comparison of mobility where identical mobilities were recorded as individual alleles. Data were analyzed using BIOSYS-1 (Swofford & Selander 1981), which produced Rogers' genetic similarity and genetic distance values for the three taxa (Rogers 1972).

The new taxon was compared to *G. attwateri*, *G. personatus*, and *G. texensis* using univariate and multivariate statistical anal-

yses of morphological data. *Geomys attwateri* was represented by two populations from the western extent of its distribution and thus in relatively close proximity to the new taxon. *Geomys personatus streckeri* was selected as a representative of the *personatus* complex because its distribution also approaches that of the new gopher. Two populations of *G. texensis* represent the previously recognized subspecies, *G. bursarius texensis* and *G. bursarius llanensis*. They were recently elevated to specific ranking and synonymized as the monotypic *G. texensis* (Block & Zimmerman 1991) based on patterns of biochemical variation. Although neither *G. texensis* nor *G. bursarius* are closely distributed to the new taxon, they are included because they are karyotypically identical to it.

Geomyids show extensive variation in secondary sexual characteristics (Baker & Genoways 1975; Honeycutt & Schmidly 1979; Williams & Genoways 1977, 1978, 1980, 1981), which necessitated separate analysis of males and females. Three external measurements were recorded from specimen labels, and 11 cranial characters were measured using dial calipers. Skull measurements were taken as described by Williams & Genoways (1977). Measurements we evaluated are as follows: total length (TL), length of tail (T), length of hind foot (HF), condylobasal length (CBL), basal length (BL), palatal length (PL), prefrontal depth (PFD), length of nasals (LN), diastema (DIAS), zygomatic breadth (ZB), mastoid breadth (MB), squamosal breadth (SB), rostral breadth (RB), interorbital constriction (IOC), breadth across third molars (M3), length of maxillary toothrow (M1). Only adult animals were used and they were identified by the degree of ossification of the sutures of the skull, particularly the fusion of the basisphenoid and basioccipital bones (Williams & Genoways 1981). The adults were classified into two categories based on the degree of fusion and ossification. The

skulls of older adults continue to grow, causing shape of the skull to become more angular and massive (Russell 1968); this is particularly noticeable in rostral, zygomatic arches as well as other cranial measurements. The oldest adult age class consisted of animals with a total obliteration of the suture line separating the basisphenoid and basioccipital bones. The number of animals in this oldest age class varied among populations, with most being males. The largest sample sizes were in the younger of the adult age classes, and these were used in the morphological analysis.

Univariate analysis of cranial characters (mean, range, standard error, coefficient of variation) was carried out using the UNIVARIATE procedure of SAS (SAS Institute 1988a, 1988b) for each sex. The relationships among the taxa were assessed using multiple analysis of variance (GLM procedure), and Tukey's studentized range test (TUKEY's option of GLM) was used to identify maximally nonsignificant subsets. Principal component analysis (PRIN procedure) using a correlation matrix of characters was used to identify the source of variation among the characters. Mean eigenvectors were computed for each taxon and the first two components plotted. Canonical discriminant analysis (CANDISC procedure) was used to compute canonical variates for multivariate analysis of variation among taxa. The centroid for each taxon was plotted on the first two canonical variates and the 95% confidence ellipse was computed using the method described by Owen & Chmielewski (1985). Each individual was plotted by its first two canonical variates in order to visualize the dispersion of individuals in relationship to the centroids. The contribution of each cranial variable used in the canonical discriminant analysis was determined as a percentage, using the procedure described by Schmidly & Hendricks (1976).

Phenetic relationships were assessed using correlation and distance matrices

generated from the character data using NTSYS (Rohlf 1988, version 1.50), with clustering using UPGMA (unweighted pair group method using arithmetic averages). A minimum spanning tree also was computed and taxa plotted by the first three canonical vectors were connected.

Results

The diploid number of 16 specimens representing the new populations in Medina, Zavala, and Uvalde counties is $2N = 70$, and the fundamental number is 68. The X-chromosome is a large acrocentric and the Y-chromosome is medium-sized and acrocentric. The morphology of the chromosomes is indistinguishable from those previously reported for both *G. bursarius* and *G. texensis* (Baker et al. 1973, Hart 1978).

Four of the presumptive loci were monomorphic within and among all three taxa (Table 1). Two fixed differences were observed (PEP-1 and SOD-1) between *G. bursarius* and both *G. texensis* and the new taxon. No fixed differences were observed between *G. texensis* and the new population. The mean heterozygosities for the new taxon, *G. texensis*, and *G. bursarius* are low, 0.037, 0.041, and 0.017, respectively. The percentage of the loci that are polymorphic varied from a low in *G. texensis* of 27.8%, to 38.9% in the new taxon, and 44.4% in *G. bursarius*. Rogers' genetic similarities were high when comparing *G. texensis* to the new taxon (0.915), whereas the similarities of these two taxa to *G. bursarius* were much lower, 0.690 and 0.648, respectively. The genetic distance was low when comparing the newly discovered populations and *G. texensis* (0.085), whereas these two taxa were both more distantly related to *G. bursarius*, 0.352 and 0.310, respectively.

Coefficients of variation produced in the univariate analysis of the nongeographic variation showed exceedingly high variation in the external characters (TL, T, HF)

for both sexes, and were excluded from further morphometric analyses. The new taxon had the lowest measurements of the taxa used in this study in 22 of the 28 skull characters measured in the two sexes (Table 2). In the six incidences (female—BL, DIAS, IOC; male—CBL, DIAS, IOC) where this population did not have the smallest mean value, one of the populations of *G. texensis* was the smallest. Analysis of geographic variation in individual characters using a single classification *MANOVA* test showed significant differences in CBL, BL, PL, DIAS, ZB, MB, SB, RB, IOC, M3 and M1 among the populations of females; PFD and LN showed no significant differences in this analysis. Males had fewer characters displaying significant differences among the taxa, and these were limited to LN, MB, SB, RB, IOC, M3 and M1. Further analysis of these data using Tukey’s standardized range test identified much of these differences to be attributed to relationships between only two or three of the taxa, especially regarding *G. texensis*, relating it to *G. attwateri* and *G. personatus*. Six characters displayed significant differences that involved all taxa in both males and females (Table 3): MB, RB, SB, M3, M1 and IOC. The new taxon was not significantly different from the other *G. texensis* populations in MB, SB, M1 and IOC in either females or males. Rostral breadth (RB) deviates from this clustering pattern in both sexes in that the new taxon’s measurements are much smaller than those of *G. texensis*.

The first three principal components describe 76.7% and 85.3% of the variation observed in females and males, respectively. The eigenvectors of component I were all positive and range from 0.110 to 0.355. Skull length measurements (CBL, BL, PL) and mastoid breadth (MB) account for most of the variation observed. Zygomatic breadth (ZB) accounts for additional variation in males. Components II and III also are influenced by the variation in condylobasal length (CBL) and basal length (BL)

Table 1.—Alleles present in three taxa. Lowercase letters denote alleles appearing in frequencies less than 5%, while uppercase letters represent occurrences greater than 5%.

	<i>G. t. bakeri</i>	<i>G. texensis</i>	<i>G. bursarius</i>
Pep-1	A	A	B
SOD-1	A	A	B
EST-1	A	A	A, B
EST-2	A, b	A	A, B
GPI	A, B	A	A
G3PDH	A, B	A, b	A, B
PGM-1	A	A, B	A, B
6-PGD	A, B	A, B	A
MDH-1	A	A	A, B
MDH-2	A, b	A	A, B
SOD-2	A	A	A, B
AAT-1	A, b	A	A
IDH-1	A, C	B, C	B, C
IDH-2	A	A, B	A
Pep-2	A	A	A
ACOH	A	A	A
CK	A	A	A
PNP	A	A	A

in both sexes; however, squamosal breadth, mastoid breadth, and prefrontal depth are important characters in females. When plotted by the mean values for the first two principal components, the relationships of the taxa are identical to those seen for a similar analysis described below using the canonical variates, and thus are not presented.

There were significant differences (Hotelling-Lawley’s Trace: females $P < F < 0.0001$; males $P < F < 0.0001$) in morphology among the taxa in an analysis of geographic variation as detected by the *MANOVA* test. The first canonical variate accounts for 67% and 57% of the phenetic variation in females and males, respectively. The second and third variates account for 17% and 9%, respectively, in females; and 28% and 8% in males. Three clusters are evident in the two dimensional plots of the first two canonical variates of both sexes (Fig. 2). Females of both samples of *G. attwateri* cluster with the *G. personatus*. The two populations of *G. texensis* also cluster

Table 2.—External and cranial measurements (mean, range, *n*, *SE*, *CV*) of the six populations used in the morphometric analysis.

	TL	T	HF	CBL	BL	PL	PFD	LN	DIAS	ZB	MB	SB	RB	IOC	M3	M1
<i>Geomys texensis bakeri</i>																
Males																
Mean	231.0	71.8	29.0	40.2	37.5	26.0	15.5	13.8	14.1	25.5	22.0	16.9	9.2	6.0	6.9	8.5
Minimum	210.0	70.0	27.0	38.6	36.0	24.7	13.6	12.9	13.5	22.7	21.4	16.6	8.9	5.7	6.8	8.2
Maximum	246.0	78.0	32.0	42.8	40.6	27.8	17.1	14.8	15.0	26.3	22.3	17.4	9.5	6.4	7.1	8.8
<i>n</i>	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5
<i>SE</i>	6.00	1.56	0.84	0.57	0.66	0.41	0.46	0.25	0.26	0.49	0.15	0.12	0.10	0.11	0.04	0.10
<i>CV</i>	5.79	4.86	6.45	3.46	4.30	3.85	7.33	4.53	4.53	4.93	1.69	1.75	2.72	4.08	1.59	2.99
Females																
Mean	223.0	63.3	28.8	38.7	36.3	24.6	15.1	12.6	13.1	22.8	21.1	16.6	8.4	5.8	6.9	8.2
Minimum	203.0	56.0	27.0	37.9	35.4	24.4	14.7	12.5	12.8	21.7	20.5	16.3	8.0	5.5	6.5	7.8
Maximum	238.0	76.0	30.0	39.1	36.7	25.1	15.5	12.7	13.7	23.7	21.9	17.1	8.8	6.3	7.3	8.5
<i>n</i>	6	6	6	6	6	6	6	2	6	6	6	6	6	6	6	6
<i>SE</i>	6.07	3.53	0.40	0.18	0.18	0.14	0.11	0.07	0.13	0.27	0.19	0.13	0.12	0.11	0.13	0.10
<i>CV</i>	6.66	13.64	3.41	1.15	1.24	1.42	1.89	0.84	2.48	2.89	2.24	1.90	3.44	4.75	4.63	2.91
<i>Geomys texensis texensis</i> (<i>G. b. texensis</i>)																
Males																
Mean	246.1	68.7	31.6	42.1	39.6	27.4	16.3	15.6	14.5	26.4	23.6	17.9	10.2	5.9	7.7	9.1
Minimum	225.0	57.0	29.0	37.0	34.5	24.4	14.1	13.4	12.8	24.0	20.8	16.5	9.3	5.5	7.2	8.1
Maximum	272.0	80.0	35.0	46.8	43.8	30.3	18.3	17.9	16.1	29.3	25.3	18.9	11.2	6.4	8.1	10.2
<i>n</i>	8	8	8	15	15	15	15	14	15	15	15	15	15	15	15	15
<i>SE</i>	5.03	2.64	0.62	0.59	0.59	0.38	0.24	0.34	0.25	0.40	0.27	0.19	0.14	0.08	0.08	0.13
<i>CV</i>	5.78	10.88	5.59	5.43	5.73	5.33	5.61	8.19	6.07	5.80	4.49	4.17	5.30	5.17	3.88	5.76
Females																
Mean	215.5	60.9	28.4	38.7	36.3	24.9	15.3	13.3	12.9	23.7	21.5	17.0	9.2	5.8	7.4	8.6
Minimum	185.0	51.0	25.0	36.7	34.2	23.6	14.2	12.1	11.8	21.9	19.9	16.0	8.5	5.4	6.1	7.9
Maximum	258.0	70.0	31.0	41.3	38.9	26.8	16.1	14.7	14.5	25.3	22.8	17.9	9.8	6.3	7.8	9.3
<i>n</i>	13	13	13	19	19	19	19	19	19	19	19	19	19	19	19	19
<i>SE</i>	5.22	1.45	0.60	0.25	0.26	0.19	0.13	0.16	0.15	0.21	0.16	0.12	0.09	0.06	0.05	0.08
<i>CV</i>	8.74	8.59	7.68	2.86	3.13	3.26	3.76	5.21	5.07	3.92	3.27	3.14	4.22	4.64	2.86	4.08

Table 2.—Continued.

	TL	T	HF	CBL	BL	PL	PFD	LN	DIAS	ZB	MB	SB	RB	IOC	M3	M1
<i>Geomys texensis texensis</i> (<i>G. b. llanensis</i>)																
Males																
Mean	248.4	69.5	30.5	43.2	40.6	28.2	16.9	16.3	15.0	26.8	23.8	17.8	10.2	5.9	7.7	9.0
Minimum	225.0	63.0	26.0	40.1	37.7	26.2	16.2	14.8	13.5	24.6	21.9	16.9	9.2	5.5	7.3	8.6
Maximum	264.0	77.0	33.0	46.5	43.9	30.9	17.9	18.1	17.1	29.1	25.4	18.8	11.4	6.3	8.3	9.7
<i>n</i>	9	9	9	13	13	13	13	12	13	13	13	13	13	13	13	13
SE	4.41	1.57	0.73	0.59	0.59	0.42	0.14	0.32	0.26	0.39	0.29	0.13	0.18	0.06	0.08	0.11
CV	5.33	6.78	7.15	4.91	5.20	5.40	3.01	6.77	6.22	5.30	4.41	2.64	6.45	3.84	3.86	4.27
Females																
Mean	222.6	61.2	26.0	39.3	36.9	25.3	15.9	13.6	13.1	23.7	21.8	16.8	9.3	5.7	7.6	8.7
Minimum	199.0	54.0	15.0	37.1	35.3	23.7	14.8	12.2	12.3	24.7	20.5	16.1	8.6	5.5	7.0	8.1
Maximum	240.0	69.0	30.0	40.9	39.1	27.1	16.5	15.3	14.2	24.5	23.0	17.8	10.1	6.4	8.3	9.0
<i>n</i>	5	5	5	12	12	12	12	11	12	11	12	12	12	12	12	12
SE	6.28	2.52	2.84	0.27	0.28	0.25	0.11	0.29	0.14	0.22	0.20	0.11	0.09	0.04	0.10	0.08
CV	6.31	9.20	24.48	2.38	2.62	3.38	2.49	7.12	3.65	3.15	3.13	2.19	3.53	2.60	4.59	3.15
<i>Geomys personatus streckeri</i>																
Males																
Mean	244.9	75.9	30.0	42.1	39.6	27.4	16.1	15.4	14.8	25.9	24.3	18.9	9.5	6.2	7.9	9.4
Minimum	223.0	64.0	26.0	37.2	35.0	23.8	14.2	12.8	12.2	22.3	22.3	17.5	8.6	5.9	7.2	8.3
Maximum	282.0	88.0	34.4	47.8	45.4	32.3	18.3	18.1	18.0	30.2	28.1	21.3	10.7	6.6	8.9	11.1
<i>n</i>	22	22	22	24	24	24	24	21	24	24	23	23	24	23	24	24
SE	3.23	1.36	0.53	0.61	0.61	0.48	0.21	0.30	0.33	0.41	0.33	0.20	0.12	0.03	0.10	0.15
CV	6.19	8.40	8.25	7.07	7.56	8.53	6.41	9.05	10.95	7.82	6.50	5.10	6.16	2.75	6.14	7.76
Females																
Mean	228.0	70.6	28.4	38.8	36.4	24.9	15.4	13.6	13.2	23.8	22.8	18.2	8.8	6.1	7.7	9.0
Minimum	211.0	61.0	24.0	36.7	34.3	23.1	14.2	12.1	12.1	22.7	21.5	17.3	8.1	5.8	7.2	8.5
Maximum	258.0	87.0	31.0	41.4	38.8	26.9	16.4	15.2	15.0	24.8	24.1	19.0	9.5	6.6	8.3	9.8
<i>n</i>	25	25	25	27	27	27	27	24	27	27	27	27	27	27	27	27
SE	1.87	1.36	0.36	0.26	0.24	0.19	0.10	0.16	0.15	0.11	0.15	0.09	0.06	0.03	0.05	0.07
CV	4.10	9.67	6.41	3.43	3.54	3.99	3.35	5.91	5.92	2.46	3.50	2.69	3.72	3.01	3.74	4.01

Table 2.—Continued.

	TL	T	HF	CBL	BL	PL	PFD	LN	DIAS	ZB	MB	SB	RB	IOC	M3	M1
<i>Geomys attwateri</i>																
Males																
Mean	237.4	68.8	28.7	42.7	40.4	28.5	16.4	15.3	15.4	27.5	25.0	18.7	9.8	6.5	7.8	9.6
Minimum	222.0	50.0	24.5	39.6	37.4	25.7	15.4	13.9	13.9	24.6	23.1	17.4	9.1	6.0	7.3	9.1
Maximum	262.0	81.0	33.0	47.8	45.4	32.2	18.8	17.9	17.9	31.5	27.6	20.7	10.9	6.8	8.4	10.3
n	20	19	20	20	20	20	20	18	20	20	20	20	20	19	20	20
SE	2.59	1.96	0.45	0.54	0.55	0.45	0.26	0.32	0.31	0.49	0.34	0.21	0.13	0.04	0.07	0.09
CV	4.87	12.75	7.09	5.66	6.05	7.05	7.10	9.03	9.09	7.99	6.06	5.02	5.87	3.07	3.82	4.01
Females																
Mean	225.9	69.5	27.8	40.2	37.7	26.2	15.2	13.9	14.0	24.8	23.4	18.0	8.9	6.2	7.6	9.1
Minimum	210.0	58.0	24.0	37.4	35.2	24.1	14.4	12.6	12.9	22.8	21.6	16.9	8.3	5.9	7.0	8.5
Maximum	240.0	76.0	31.0	41.6	39.3	27.4	16.3	14.9	15.1	26.3	24.8	19.1	9.7	6.7	8.2	9.7
n	23	23	23	23	23	23	23	19	23	23	23	23	23	23	23	23
SE	1.61	0.86	0.28	0.25	0.26	0.17	0.20	0.15	0.12	0.20	0.18	0.11	0.09	0.06	0.06	0.05
CV	3.42	5.93	4.89	2.95	3.28	3.15	6.40	4.75	4.24	3.89	3.71	3.02	4.76	4.39	3.83	2.91
<i>Geomys attwateri</i>																
Males																
Mean	246.3	72.8	30.5	43.7	41.4	29.0	16.3	15.6	16.0	28.2	25.0	19.3	10.2	6.5	7.9	9.5
Minimum	223.0	65.0	24.0	39.7	37.5	26.0	15.4	14.0	13.8	25.5	23.5	18.1	8.9	6.1	7.6	9.0
Maximum	257.0	80.0	33.0	46.8	43.9	30.9	17.2	17.1	17.3	30.9	26.7	21.1	11.2	6.9	8.5	10.2
n	11	11	11	11	11	11	11	10	11	11	11	11	11	11	11	11
SE	2.98	1.44	0.49	0.57	0.56	0.45	0.18	0.30	0.30	0.50	0.35	0.31	0.17	0.08	0.08	0.13
CV	4.02	6.58	5.29	4.30	4.47	5.19	3.68	6.16	6.32	5.93	4.63	5.38	5.67	4.12	3.19	4.47
Females																
Mean	229.0	61.7	28.2	40.1	37.9	26.2	15.3	13.9	13.7	25.3	23.5	18.0	9.6	6.6	7.5	9.2
Minimum	204.0	55.0	21.0	39.3	37.1	25.5	15.0	13.3	13.3	24.6	22.7	17.0	9.0	5.7	7.4	8.9
Maximum	241.0	65.0	32.0	41.2	39.1	26.8	16.0	14.5	14.9	26.0	24.1	18.3	10.1	6.9	7.6	9.5
n	4	4	4	4	4	4	4	4	3	4	4	4	4	4	4	4
SE	8.49	1.37	2.49	0.32	0.29	0.28	0.17	0.35	0.15	0.35	0.33	0.12	0.23	0.18	0.04	0.10
CV	7.42	4.46	17.67	1.60	1.54	2.16	2.25	4.38	2.14	2.78	2.77	1.32	4.83	5.49	1.27	2.20

together, with the centroid of each population well within the 95% confidence ellipse of the other. The centroid of the new taxon is well outside of the 95% confidence ellipses of all other taxa and its ellipse includes only the two centroids of *G. texensis* at the extremes of the confidence interval (Fig. 2). It should be noted here that the new taxon had the smallest sample size (Fig. 2), and that this is directly observed in the larger ellipse resulting from the high *F*-value component of the Owen & Chmielewski (1985) formulation of the 95% ellipse.

Males do not show as clear a demarcation among the clusters as do the females although an identical pattern is evident. The populations of *Geomys attwateri* cluster together and overlap *G. personatus*. The two populations of *G. texensis* form overlapping clusters with the centroid of the new taxon. The analysis of males is affected by smaller sample sizes and the increased variation associated with the continued growth of their skulls throughout adult life.

Those skull characters representing length (CBL, BL) and width (ZB, MB) account for most of the variation in canonical variate I of males (Table 4). Basal length (BL), palatal length (PL), and mastoid breadth (MB) provide most of the variation seen in the second variate. The third variate is also highly weighted to length and width variables. A similar pattern is seen in females, but this length and width variation is seen to be limited to condylobasal length (CBL) and mastoid breadth (MB) in the first variate. Overall skull length accounts for the variation seen in the second variate, whereas palatal length (PL) and squamosal breadth (SB) account for most of the variation seen in the third variate.

The phenograms constructed using the correlation matrices are identical between the sexes, and the cophenetic correlation values are 87% for females and 76% for males (Fig. 3). The phenograms based on distance matrices differ between both sexes and the phenograms derived from the cor-

relation matrices. The cophenetic correlation values are high for females (0.84) and males (0.87). The new taxon is quite distinct in both sexes, with the greatest distinction appearing in males. Although the clustering relationships vary among the analyses and sexes, the new taxon is always distinct when comparing the branch lengths to those of the other species. A similar relationship is seen in the branching pattern resulting from the minimum-spanning analysis (Fig. 3). Females of the new taxon join *G. texensis*, but *G. attwateri* joins *G. personatus*. Males also show a close relationship among the two populations of *G. texensis* and the new taxon.

Discussion

The newly discovered populations of pocket gophers at first were suspected to be only range extensions of taxa known to occur in the region. However, analysis of chromosomal morphology quickly identified them as being quite different from any taxon occurring in southern Texas, and more closely related to gophers in the *G. bursarius* complex to the north. They share a large and distinctive acrocentric X-chromosome and 68 acrocentric autosomes with *G. texensis* and race D of *G. bursarius major* (Baker et al. 1973, Hart 1978). They contrast with *Geomys personatus* and *G. attwateri*, both of which have a large, subtelocentric X-chromosome. Furthermore, *G. personatus* and *G. attwateri* are reported to share a diploid number of 70 in southern Texas and to possess a small metacentric autosome not seen in the new taxon.

In order to ascertain the relationship of the new taxon to *G. texensis* and *G. bursarius*, and to determine its taxonomic affiliation, we used starch gel electrophoresis to assay biochemical variation in 18 loci coding for structural proteins. Two fixed differences were observed between *G. bursarius* and both *G. texensis* and the new taxon. No fixed differences, however, were ob-

Table 3.—Six characters that separate taxa when analyzed in single classification *MANOVA*. Taxa are grouped in nonsignificant subsets (Tukey’s studentized range test) represented by the horizontal lines. Age class 4 males and females: characters by locality.

	<i>n</i>	mean	min	max
Males				
MB				
<i>G. t. bakeri</i>	5	21.96	21.4	22.3
<i>G. texensis</i>	4	22.65	20.8	23.9
<i>G. texensis</i>	7	23.25	21.9	23.9
<i>G. personatus</i>	13	23.98	22.3	26.7
<i>G. attwateri</i>	11	24.06	22.6	25.7
<i>G. attwateri</i>	5	24.11	23.5	24.7
SB				
<i>G. t. bakeri</i>	5	16.94	16.6	17.4
<i>G. texensis</i>	7	17.52	16.9	18.0
<i>G. texensis</i>	4	17.63	16.8	18.5
<i>G. attwateri</i>	11	18.22	17.4	19.5
<i>G. attwateri</i>	5	18.63	18.1	19.5
<i>G. personatus</i>	13	18.69	17.5	19.8
RB				
<i>G. t. bakeri</i>	5	9.19	8.9	9.5
<i>G. personatus</i>	13	9.37	8.9	10.7
<i>G. attwateri</i>	11	9.43	9.1	9.9
<i>G. attwateri</i>	5	9.74	8.9	10.4
<i>G. texensis</i>	4	9.95	9.8	10.2
<i>G. texensis</i>	7	10.17	9.3	10.9
M3				
<i>G. t. bakeri</i>	5	6.90	6.8	7.1
<i>G. texensis</i>	4	7.48	7.2	7.8
<i>G. texensis</i>	7	7.61	7.3	8.0
<i>G. attwateri</i>	11	7.74	7.1	8.1
<i>G. personatus</i>	13	7.80	7.3	8.8
<i>G. attwateri</i>	5	7.92	7.6	8.5
M1				
<i>G. t. bakeri</i>	5	8.49	8.2	8.8
<i>G. texensis</i>	4	8.63	8.1	9.0
<i>G. texensis</i>	7	8.91	8.6	9.6
<i>G. attwateri</i>	11	9.36	9.1	9.8
<i>G. attwateri</i>	5	9.36	9.1	9.6
<i>G. personatus</i>	13	9.43	8.4	10.6
IOC				
<i>G. texensis</i>	4	5.87	5.5	6.3
<i>G. texensis</i>	7	5.88	5.6	6.2
<i>G. t. bakeri</i>	5	5.96	5.7	6.4
<i>G. personatus</i>	13	6.18	5.9	6.6
<i>G. attwateri</i>	11	6.40	6.0	6.7
<i>G. attwateri</i>	5	6.53	6.1	6.9

served between *G. texensis* and the new taxon. Block & Zimmerman (1991) identified fixed differences between *G. bursarius* and *G. texensis* in a study involving species of

geomyids from central Texas. Genetic similarities determined by them for *G. bursarius* and populations of *G. texensis* ranged from 0.607 to 0.648, whereas genetic sim-

Table 3.—Continued.

	<i>n</i>	mean	min	max
Females				
MB				
<i>G. t. bakeri</i>	6	21.14	20.5	21.9
<i>G. texensis</i>	15	21.36	19.9	22.8
<i>G. texensis</i>	9	21.77	20.8	23.0
<i>G. personatus</i>	13	22.93	21.7	24.0
<i>G. attwateri</i>	18	23.30	21.6	24.8
<i>G. attwateri</i>	3	23.30	22.8	24.1
SB				
<i>G. t. bakeri</i>	6	16.65	16.3	17.1
<i>G. texensis</i>	9	16.85	16.5	17.3
<i>G. texensis</i>	15	16.92	16.0	17.9
<i>G. attwateri</i>	18	17.97	16.9	18.7
<i>G. attwateri</i>	3	18.01	17.7	18.3
<i>G. personatus</i>	13	18.21	17.3	18.9
RB				
<i>G. t. bakeri</i>	6	8.40	8.0	8.8
<i>G. attwateri</i>	18	8.56	8.2	9.7
<i>G. personatus</i>	13	8.87	8.1	9.5
<i>G. texensis</i>	15	9.15	8.5	9.6
<i>G. texensis</i>	9	9.37	9.0	10.1
<i>G. attwateri</i>	3	9.60	9.0	10.1
M3				
<i>G. t. bakeri</i>	6	6.88	6.5	7.3
<i>G. texensis</i>	15	7.36	7.0	7.8
<i>G. attwateri</i>	3	7.50	7.4	7.6
<i>G. attwateri</i>	18	7.51	7.0	8.0
<i>G. texensis</i>	9	7.52	7.1	8.1
<i>G. personatus</i>	13	7.72	7.2	8.2
M1				
<i>G. t. bakeri</i>	6	8.25	7.8	8.5
<i>G. texensis</i>	15	8.51	7.9	9.3
<i>G. texensis</i>	9	8.66	8.1	9.0
<i>G. attwateri</i>	18	8.99	8.5	9.4
<i>G. personatus</i>	13	9.08	8.5	9.5
<i>G. attwateri</i>	3	9.21	9.0	9.5
IOC				
<i>G. texensis</i>	9	5.76	5.5	5.9
<i>G. t. bakeri</i>	6	5.83	5.5	6.3
<i>G. texensis</i>	15	5.86	5.4	6.3
<i>G. personatus</i>	13	6.07	5.8	6.6
<i>G. attwateri</i>	18	6.28	5.6	6.7
<i>G. attwateri</i>	3	6.49	6.2	6.9

ilarities produced from intraspecific comparisons involving *G. texensis* were high (from 0.931 to 0.937). The new taxon has a high genetic similarity when compared to *G. texensis* (0.915). Similar comparison to

G. bursarius yields a much lower value (0.648). Similarity values of 0.9 are comparable to previous studies of geomyids when making intraspecific comparisons of populations, and the lower genetic similar-

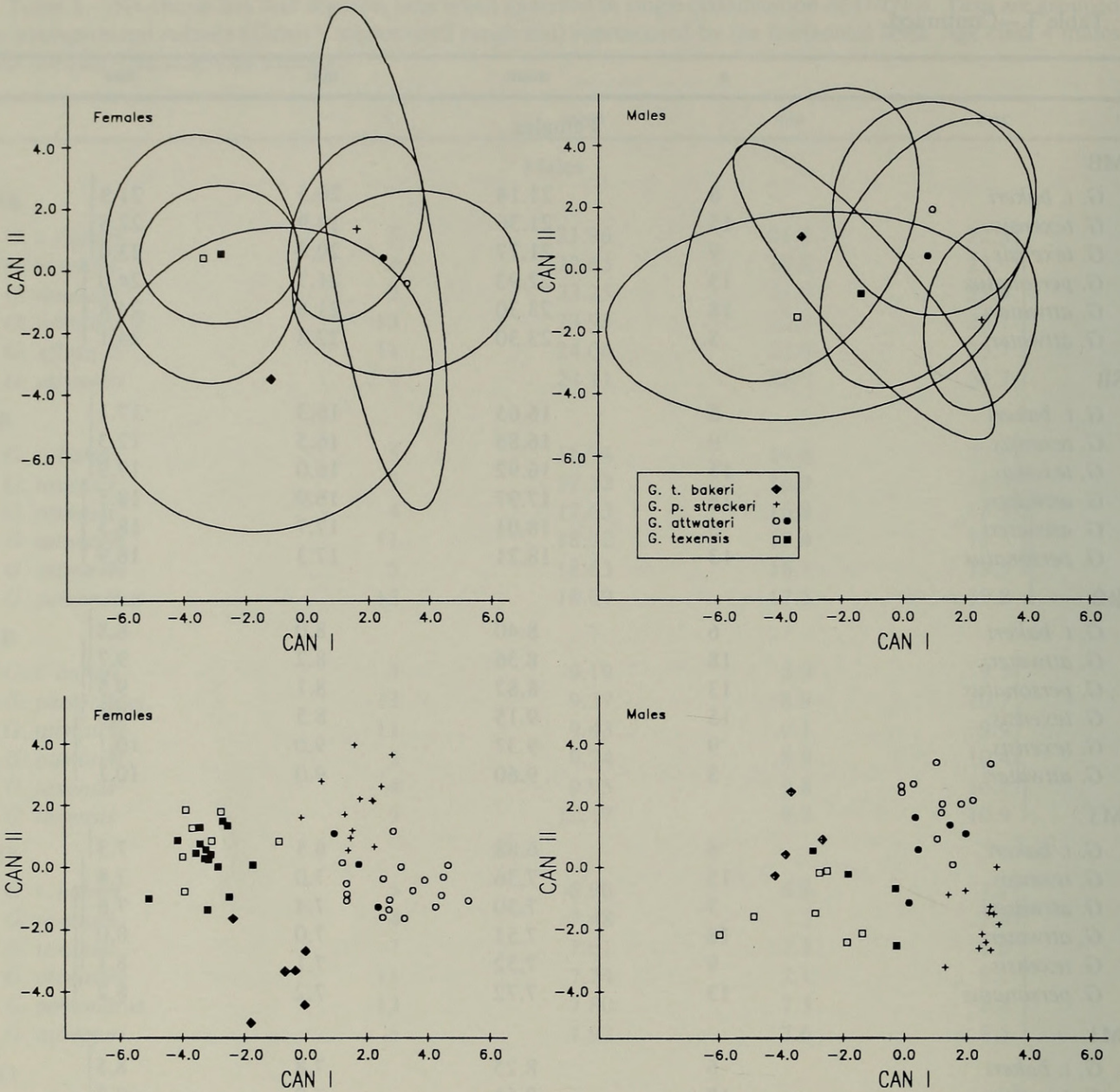


Fig. 2. Plots of the centroids of taxa along the first two canonical variates. Top plots include the 95% confidence ellipse for each taxon around its centroid. Bottom plots include the dispersion of the mean canonical scores for each individual in the populations.

ity values, seen when comparing the new taxon to *G. bursarius*, are within the range associated with interspecific comparisons (Block & Zimmerman 1991, Dowler 1982). Relationship between *G. texensis* and the new taxon is supported further by the morphometric analysis. In an analysis of the cranial characters that appear to separate *G. personatus* and *G. attwateri* from *G. texensis*, the new taxon was associated with *G. texensis* in mastoid breadth, squamosal breadth, interorbital constriction, and length

of molar toothrow. A relationship to *G. texensis* also is seen in the two phenetic clustering results. The phenograms based on the correlation matrices describe the new taxon as similar to the two *G. texensis* populations. Minimum-spanning analysis yields similar relationships with a population of *G. texensis* serving as the branching neighbor to the new taxon. These data support a proposal that the new taxon is closely related to *G. texensis*. The question then arises, do these new pop-

Table 4.—Coefficients for canonical variates and the percent influence of each variable for the variates.

Character	Canonical Variate I		Canonical Variate II		Canonical Variate III	
	Variable coeff.	%	Variable coeff.	%	Variable coeff.	%
Males						
CBL	−1.8433	28.51	−0.3363	3.36	−4.3026	41.24
BL	0.6980	10.14	−4.5368	42.57	1.8989	17.09
PL	−0.6005	6.09	2.1302	13.95	2.7239	17.11
PFD	−0.9800	5.87	−0.6656	2.58	0.9685	3.60
DIAS	1.1349	6.15	2.1888	7.67	−0.5400	1.81
ZB	−1.1519	11.26	0.6130	3.87	0.5727	3.47
MB	2.0305	17.87	2.2454	12.77	−2.0193	11.01
SB	0.8427	5.67	−1.8478	8.03	0.3642	1.52
RB	−0.5925	2.10	0.0785	0.18	−0.1217	0.27
IOC	−0.6612	1.52	0.8264	1.23	0.6400	0.91
M3	0.8382	2.38	−1.2829	2.35	0.6570	1.16
M1	0.7154	2.44	0.6592	1.45	0.3881	0.82
Females						
CBL	−1.9191	35.85	0.7594	15.53	−0.0083	0.28
BL	0.4529	7.94	−1.7802	34.17	−0.2815	8.76
PL	0.5315	6.44	0.9833	13.05	1.3095	28.18
PFD	−0.4949	3.63	0.1148	0.92	−0.3503	4.56
DIAS	0.6719	4.25	−1.1497	7.96	−0.7237	8.13
ZB	0.1029	1.18	0.3581	4.49	0.5166	10.49
MB	2.4876	26.45	−0.5207	6.06	0.5198	9.81
SB	−0.3687	3.06	0.9749	8.87	−1.3019	19.20
RB	−1.0596	4.56	0.7393	3.48	0.6176	4.71
IOC	0.7276	2.09	−0.2932	0.92	0.7603	3.87
M3	−0.4172	1.50	0.9869	3.88	−0.0849	0.54
M1	0.7203	3.05	0.1459	0.68	−0.1930	1.45

ulations, isolated and 120 km distant from the previously known distribution of *G. texensis*, constitute a new subspecies? An analysis of cranial morphology identifies the new populations as being quite distinct from *G. texensis*. They are smaller in 22 of 28 comparisons involving both sexes. Canonical discriminant analysis identifies measurements reflecting the length of the skull (BL, PL) and mastoid breadth accounting for much of the variation separating the taxa. The centroids produced from plotting these taxa along the first two canonical variates are widely separated, although the ellipses are overlapping. Separation is more clearly seen in analysis of females, where the two populations of *G. texensis* are closely associated with each other, and each is well

within the ellipse of the other. The new taxon has a centroid separated from these two primarily along the axis of the second canonical variate. The centroid is well outside the range of the ellipses of the *G. texensis* populations although the two centroids of *G. texensis* occur within the 95% ellipses of the new taxon. This distinction is less clear in males where the ellipses of both taxa include the centroids of the other. The new taxon is also seen to be quite distinct from the two populations of *G. texensis* in the phenogram produced from the clustering of the correlation matrices.

The populations of *G. texensis* represent two previously recognized subspecies, *G. b. texensis* and *G. b. llanensis*. Honeycutt & Schmidly (1979) identified primarily size-

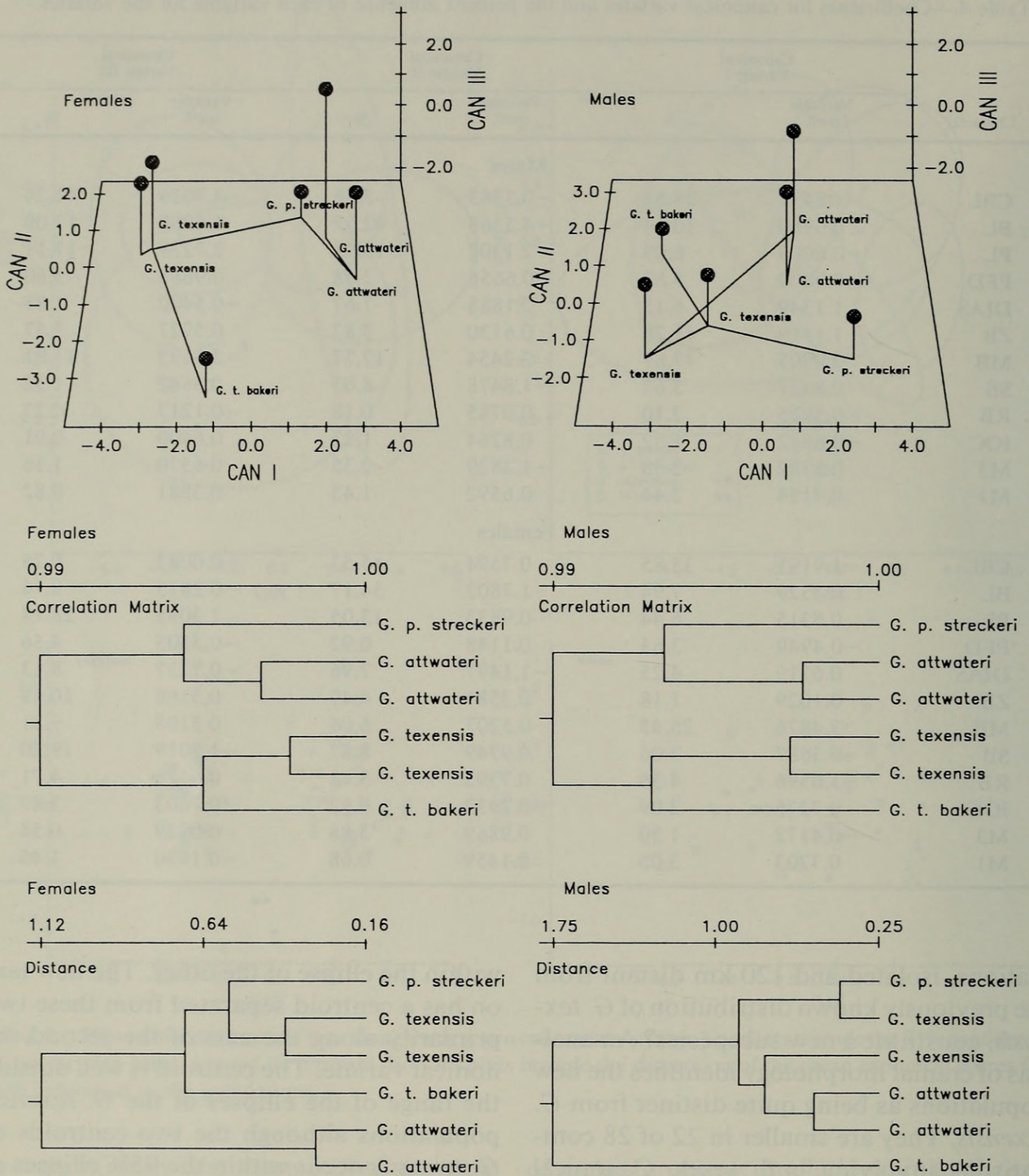


Fig. 3. Plot of the centroids of taxa along their first three canonical variates. The centroids are connected by the branching order of the minimum-spanning analysis produced from the variance-covariance matrices of measurements of cranial characters. UPGMA phenograms produced from correlation and distance matrices of the cranial measurements.

related differences between these taxa. When compared to these populations of *G. texensis*, the new populations seem to have differences in cranial features that have resulted in alteration of both skull size and shape. Cranial morphology has been pro-

posed to be greatly influenced by both soil composition and texture (Hendricksen 1972, Smith & Patton 1988, Wilkins & Swearingen 1990). Wilkins & Swearingen (1990) noted an increase in the mean values of all cranial characters in populations of *G.*

personatus in sandy soils when compared to other soil types. This difference also extended into a multivariate analysis which effectively separated populations inhabiting fine sandy loams, loamy fine sand, and fine sand, with an increase in size from smaller to larger along that axis. *Geomys texensis* occurs in sandy-loam soils in the central basin region of the Edwards Plateau. These are porous, well drained soils. The new taxon from South Texas inhabits a loam sand, Atco soil that is denser and less friable. Gophers in the heavier and denser soil are smaller and have cranial changes which alter the skull shape, and conform to the models described by Smith & Patton (1988) and Wilkins & Swearingen (1990).

Geomys texensis was previously known only from the central basin of the Edwards Plateau, and isolated there by barriers of stony to gravelly clay, clay, and shallow loamy soils (Godfrey et al. 1973). Block & Zimmerman (1991) described a scenario involving a late Wisconsin to Holocene environmental change that isolated *G. texensis* as the warmer and drier conditions approximately 9000 B.P. accelerated erosion. The presence of *G. texensis* along the southern edge of the Edwards Plateau is plausible within the framework of this hypothesis. The distribution of *G. texensis* once could have been more widespread in south-central Texas, and probably extended further into southern Texas. A cooler climate and deeper soils would have allowed *G. texensis* in the central basin to contact populations south of the Edwards Plateau across the upper reaches of the Llano River drainages. Subsequent xeric conditions merely separated these populations, isolating those to the south and ultimately restricting them to the smaller pockets of suitable soils south of the newly created indurate soils of the plateau. Fossil remains of geomyids from cave deposits on the Edwards Plateau (Dalquest & Kilpatrick 1973) provide evidence for a wider distribution, with geomyids ranging over at least the eastern por-

tions of the plateau from 10,000 to 4000 B.P.

The new subspecies described below demonstrates close affinities to *G. texensis* in cranial and chromosome morphologies, and in biochemical variation. Analyses of cranial morphology indicate that these populations resemble *G. texensis*, but appear to differ significantly in having size- and shape-related changes. These cranial differences alone could indicate a species distinction but the presence of a low level of genetic differentiation leads us to be more conservative. We conclude that, based on the observed variation and the extreme spatial separation, this new taxon is related to *G. texensis* and is an isolated, relictual population of this species, forming a distinctive subspecies.

Geomys texensis bakeri, new subspecies

Holotype.—Adult male, skin, skull, and body skeleton, no. 52310, Texas Cooperative Wildlife Collections (TCWC); from 1 mi E D'Hanis, Medina Co., Texas; obtained on 3 Jan 1987 by R. M. Pitts, original no. 1998.

Distribution.—Two isolated populations have been found along separated drainages of the Frio River. One population occurs along the Sabinal and Frio rivers in Uvalde and Zavala counties. A second population in Medina County is restricted to soils along Seco and Parker creeks, tributaries of the Frio River. Both populations are associated with nearly level Atco soil (Stevens & Richmond 1976, Dittmar et al. 1977), which has a patchy distribution in this region. The soil is well drained and consists of sandy surface layers with loam extending to as deep as 2 m. This soil is associated with stream terraces formed by the drainage systems in each locality. These two populations are widely separated (40 km); however, there may be additional populations along Seco and Parker creeks as they flow southward to join the Frio River. The nearest geomyids are

G. attwateri (Medina County), *G. personatus streckeri* (Dimmit County), and *G. t. texensis* (Kimble County).

Description.—Small size which is especially evident in the measurements of body length, skull length (CBL, BL), nasal length (LN), and skull breadth (ZB, MB, SB). Pelage coloration is russet brown on the dorsum, and grades to a paler color along the sides. The basal portions of the hairs are gray. A dark dorsal stripe extends from the head to the rump. The ventral surface is white with gray coloration on basal parts of the hairs. The tail is sparsely haired and consists of a mixture of brown and white hairs. The feet are white haired. Subadult pelage is a tawny brown, whereas adult pelage is a darker, richer brown, and appears glossy and more reflective.

Pelage color appears paler in gophers collected in the more sandy surface soil along the Frio River in Uvalde and Zavala counties than in those from Medina County. This difference in pelage coloration correlates with the much paler color of the substrate at this locality than the darker color of the loamy soil at the Medina locality.

Karyotypic features.—The diploid number is 70 and the fundamental number is 68. The X-chromosome is a large acrocentric and the Y-chromosome is a medium-sized acrocentric.

Measurements.—Measurements (in millimeters), as described in Williams & Genoways (1977), from 12 adult individuals from the two populations are listed in Table 4. Measurements of the holotype (TCWC 52310) are: total length, 227; length of tail, 66; length of hind foot, 27; length of ear, 6; greatest length of skull, 40.8; condylobasal length, 40.4; basal length, 38.3; palatal length, 26.3; prefrontal depth, 15.5; length of nasals, 13.3; length of diastema, 14.3; zygomatic breadth, 25.6; mastoid breadth, 22.4; squamosal breadth, 16.9; rostral breadth, 9.4; interorbital constriction, 6.3; breadth across third molars, 7.1; length of maxillary toothrow, 8.5.

Comparisons.—Cranial measurements of individuals of *G. t. bakeri* are smaller in size than those of *G. attwateri*, *G. p. streckeri* and *G. bursarius major* (Baker & Genoways 1975). This is especially evident in the measurements reflecting the length (CBL, BL) and breadth (ZB, MB, SB) of the skull. *Geomys b. major* is a larger gopher in all comparative external and cranial measurements as seen when comparing the measurements herein to those given by Baker & Genoways (1975). *Geomys attwateri* is the taxon nearest geographically to *G. t. bakeri*. It has external measurements comparable to those of *G. t. bakeri*, but the skull is longer (CBL, BL) and wider. Significant differences are detectable in mastoid breadth, squamosal breadth, and interorbital constriction (*G. t. bakeri* males MB = 21.9, SB = 16.9, IOC = 5.9; females MB = 21.1, SB = 16.6, IOC = 5.8; *G. attwateri* males MB = 24.0, SB = 18.6, IOC = 6.4; females MB = 23.3, SB = 18.0, IOC = 6.3). *Geomys attwateri* has a paler pelage that is a buffy tan in color, and the pelage has a uniform, nonglossy appearance. Other populations of *G. attwateri* in the eastern part of southern Texas have pelage colors that are similar to that of *G. t. bakeri*.

The karyotypes of *Geomys attwateri* and *G. personatus* differ from that of *G. t. bakeri* in that they have a large, submetacentric X-chromosome and a small, metacentric autosome (Davis et al. 1971, Honeycutt & Schmidly 1979, Tucker & Schmidly 1981). *Geomys texensis* (Honeycutt & Schmidly 1979) and races of *Geomys bursarius* (Baker et al. 1973) have an identical diploid and fundamental number, and appear identical when standard karyotypes are compared.

Etymology.—The subspecific name is a patronym and is selected to honor Dr. Robert J. Baker for his many contributions to mammalogy, particularly to the systematics and evolution of *Geomys*, as well as his overall research program, activity in professional societies, and involvement in graduate education.

Acknowledgments

We very much appreciate the help of many individuals. E. Abbott, J. Berry, J. Fell, J. Raney, K. Raney, J. Scharninghausen, E. Uptagrafft assisted in doing field work. R. Lopez, J. Lopez, and J. Lopez assisted in the preparation of specimens. Mr. DeWitt of Zavala County graciously allowed us to collect on his ranch. We thank S. Anderson (American Museum of Natural History), F. Stangel (Midwestern University), D. Wilson (National Museum of Natural History), H. Garner (Tarleton State University), G. Baumgardner (Texas Cooperative Wildlife Collections), R. Martin (Texas Natural History Collection), R. Owen (The Museum, Texas Tech University), and their respective staff, who provided specimens through loan or making them available to us during our visit to their museum collections. Dr. D. Schmidly, Dr. J. McEachran and Dr. S. Johnston were involved in valuable discussions that helped direct the development of this study. We greatly appreciate the many valuable suggestions concerning the final manuscript that were made by Dr. J. Knox Jones, Dr. R. C. Dowler, and M. Carleton. Financial support for the field work and laboratory materials was received from the Texas Agricultural Experiment Station Expanded Research Area funds and Program Development funds. This is contribution number 6 of the Center of BioSystematics and BioDiversity.

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Appendix

Specimens examined.—Two hundred ninety seven specimens were used from the following collections: American Museum of Natural History (AMNH), Midwestern University (MSU), Tarleton State University (TSU), Texas Cooperative Wildlife Collections (TCWC), Texas Natural History Collection (TNHC), Texas Tech University (TTU), National Museum of Natural History (USNM).

Geomys attwateri.—(85). Texas: Atascosa Co.: 6 mi W Campbellton, 1(TNHC); 2 mi NW Campbellton, 3(TCWC); 1 mi E Lytle, 16(TCWC); 7 mi E Lytle, 16(TNHC); 2.4 mi SE Lytle, 3(TCWC); 7 mi SE Lytle, 8(TCWC). Bexar Co.: 15 mi SE San Antonio, 1 (TSU). Frio Co.: 1 mi N Moore, 3(TCWC); Pearsall city limits, 2(TCWC); 2.25 mi S, 1 mi E Pearsall, 1(TCWC); McCoy, 1(TNHC); 0.3 mi E McCoy, 1(TNHC); 2 mi N Pleasanton, 7(TNHC). Medina Co.: 5 mi W Devine, 4(TCWC); 7.2 mi E Yancy, 1(TCWC), 1(TSU). Wilson Co.: 11 mi NW Floresville on HWY 181, 6(TCWC); 4 mi W Floresville, 1(TNHC); 1 mi W Floresville, 2(TCWC); ¾ mi S, 2½ mi E Floresville, 4(TCWC); 3.2 mi NW Poth, 1(TNHC); 3.6 mi SSE Poth, 1(TNHC); 5.4 mi W San Antonio River, between Floresville and Pleasanton, 1(TNHC).

Geomys personatus streckeri.—(68). Texas: Dimmit Co.: 13 mi N Carrizo Springs on HWY 277, 3(TTU); 13 mi NE Carrizo Springs, 3(TTU); 13 mi NE Carrizo Springs on US HWY 277, 5(TTU); 4 mi N, 9 mi W Carrizo Springs, 1(TCWC); 1 mi S Carrizo Springs, 700 ft, 2(TCWC); 15 mi S, 11 mi W Carrizo Springs,

5(TCWC); 1½ mi E Carrizo Springs, 6(TCWC); E Carrizo Springs, 3(TTU); Carrizo Springs, 30(TNHC), 11(TCWC); near Carrizo Springs on HWY 277, 5(TTU); 1.0 mi SW Carrizo Springs, HWY 186, 4(TCWC); 2 mi S Carrizo Springs, low water crossing Dentonio Rd, 1(TCWC).

Geomys texensis bakeri. —(35). Texas: Medina Co.: 1 mi E D'Hanis, 5(TCWC); D'Hanis, 5(TCWC); 5½ mi W Hondo, 6(TCWC); 6.2 mi W Hondo, 4(TCWC). Uvalde Co.: 16 mi S Sabinal on FM 187, 6(TCWC); 17 mi S Sabinal on FM 187, 4(TCWC). Zavala Co.: 18 mi S Sabinal on FM 187, 1(TCWC); ¾ mi S Uvalde County line, 4(TCWC).

Geomys texensis texensis. —(108). Texas: Gillespie Co.: 13 mi N Fredericksburg, 1(TSU); 1 mi N Fredericksburg, 2(TCWC); 0.5 mi N Fredericksburg, 1(TCWC); 9 mi W Fredericksburg, 1(TNHC). Kimble Co.: Junction, 3(TCWC). Llano Co.: 2.6 mi N, 1.8 mi E Castell, 5(TTU); 6.4 mi E Castell, 1(TCWC); Castell, 1(TTU); 6.4 mi E Castell 1(TCWC); 1 mi E Castell 1(TCWC); 1.2 mi W Castell on FM 152, 1(TCWC); 8 mi S, 0.9 mi W Kingsland, 4(TTU); 9.2 mi S, 1.1 mi E Kingsland, 1(TTU); 10 mi S, 1.8 mi E Kingsland,

2(TTU); 2.9 mi NW Llano on HWY 71, 2(TTU); 0.2 mi N, 8.7 mi W Llano, 3(TTU); Drier Cr at Lone Grove, 7 mi W Llano, 10(TCWC); 4 mi W Llano 1(TCWC), Llano, 1(TCWC); 0.2 mi E Llano, 1(TCWC); 1 mi E Llano, 2(TCWC); 2 mi E Llano, 4(TCWC); 7.2 mi E Llano, 1(TCWC); Oatman Cr, 3 mi S Llano, 6(TCWC); 51.6 mi W Austin on HWY 71, 2(TTU); 3 mi S Jct FM 268 and HWY 29 on 29, 2(TTU); 9.3 mi N Jct Texas 29, Texas 16 on Texas 16, 1(TTU). Mason Co.: 3.1 mi E Art, 1(TCWC); Art city limits, 3(TCWC); 12 mi N Mason, 6(MWU); 3.6 mi N, 1.5 mi W Mason, 1(TTU); 1 mi N, 1.1 mi W Mason, 4(TTU); 12 mi W Mason, 2(MWU); 9.4 mi W Mason on US 377, 3(TTU); Mason, 1(TCWC); 1 mi E Mason, 6(TCWC); 6.5 mi E Mason on Texas 29, 1(TTU); 2.0 mi S, 2.7 mi W Castell, 1(TTU); 5 mi S Mason, 1(MWU). in Mason Co.: 3½ mi W Castell, 3(TCWC); 0.3 mi S, 1.5 mi W Castell, 3(TTU); 0.3 mi S, 0.9 mi W Castell, 1(TTU); 0.3 mi S, 0.8 mi W Castell, 1(TTU); 2.6 mi S, 3.0 mi W Castell, 1(TTU); 0.7 mi S, 2.1 mi W Castell, 2(TTU); 1.0 mi S, 2.3 mi W Castell, 2(TTU); 11 mi NE London, HWY 377, 2(TCWC); 13 mi NE London, HWY 377, 2(TCWC).



Smolen, M J, Pitts, R M, and Bickham, John W. 1993. "A new subspecies of pocket gopher (*Geomys*) from Texas (Mammalia: Rodentia: Geomyidae)." *Proceedings of the Biological Society of Washington* 106, 5–23.

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