GENETIC DIFFERENTIATION OF THE *GEOMYS* POCKET GOPHER COMPLEX OF TEXAS

THESIS

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By

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Genetic variation was analyzed for populations of seven taxa comprising four cytotypes of the Geomys bursarius chromosome complex, including G. b. major, G. b. knoxjonesi, and the Edwards Plateau taxa, G. b. llanensis and G. b. texensis. Genetic relationships of the Edwards Plateau gophers with other taxa and between themselves were examined. Genetic similarity, number of fixed allelic differences, and ectoparasite distribution indicate the Edwards Plateau gophers are a distinct gene pool. Isolation of the Edwards Plateau taxa precludes contact zone analysis. However, genetic differentiation is typical of that between other species of Geomys, and the Edwards Plateau taxa should be recognized as G. texensis. Distributions of allelic frequencies indicate little justification in retaining the subspecific status of the Edwards Plateau forms.

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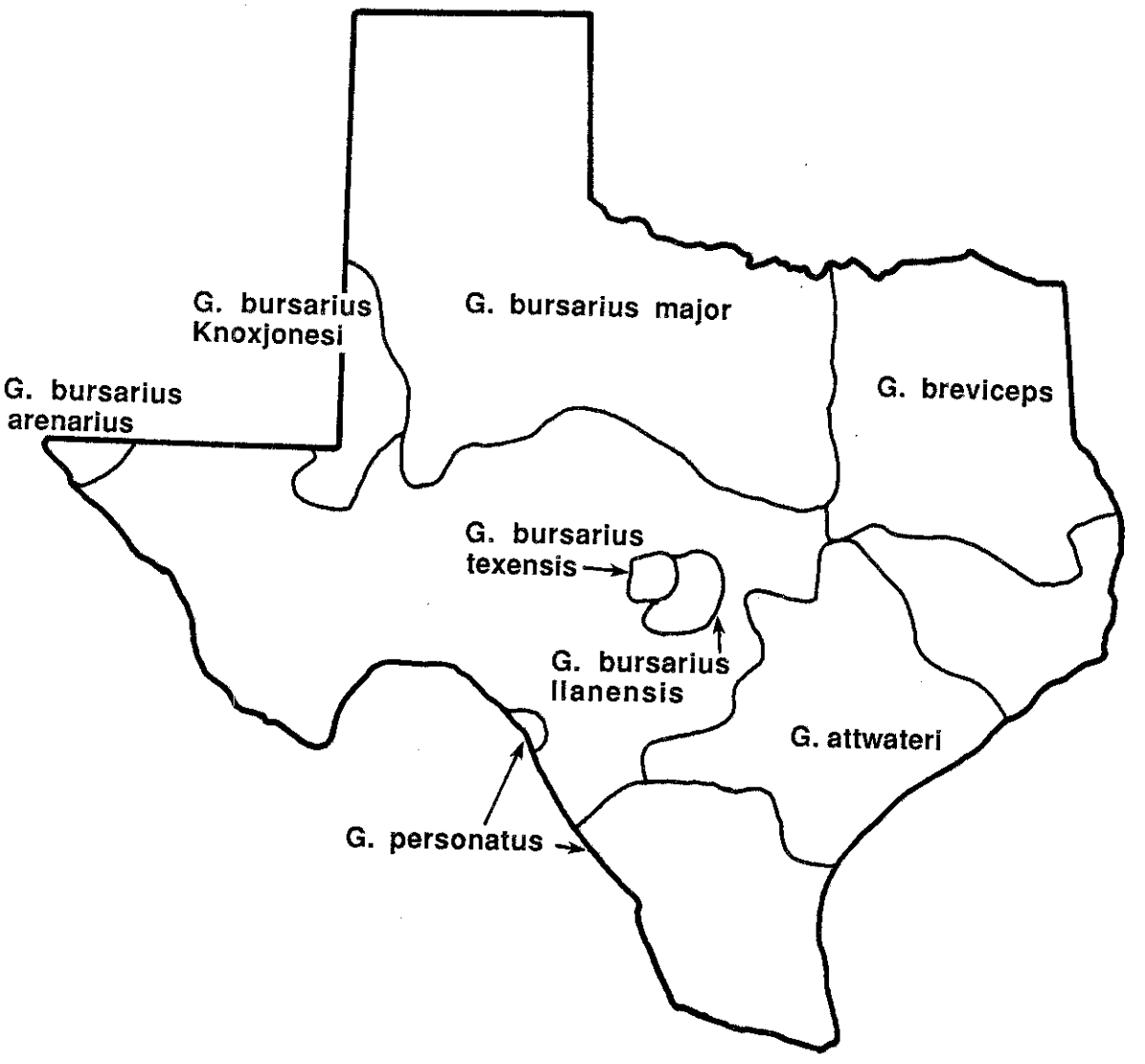
CHAPTER I

INTRODUCTION

There is a high degree of morphometric, chromosomal, and allozymic variation in the plains pocket gophers Geomys of Texas (Baker and Genoways,1975; Baker et al., 1973; Bohlin and Zimmerman, 1982; Cothran and Zimmerman, 1985; Honeycutt and Schmidly, 1979; Kim, 1972; Penney and Zimmerman, 1976; Pembleton and Baker,1978; Tucker and Schmidly, 1981). The large variation may be a result of several factors, including low vagility due to the fossorial nature of these rodents, restriction of suitable soil types, and small population sizes (Moulton et al., 1983). Small effective populations (Zimmerman and Gayden, 1981) along with the aforementioned processes may result in population subdivision leading to the high degree of interpopulation heterogeneity among pocket gophers. Currently five species of Geomys are recognized in Texas: G. arenarius, G. attwateri, G. breviceps, G. bursarius, and G. personates. Among the G. bursarius complex there are four subspecies and two chromosomal races (Figure 1).

Contact zones between chromosomal races or subspecies offer an opportunity to study chromosomal changes occurring with isolation (Pembleton and Baker, 1978). Genetic analyses of indivduals at contact zones between species can

Figure 1. Range of currently recognized taxa of Geomys in Texas.

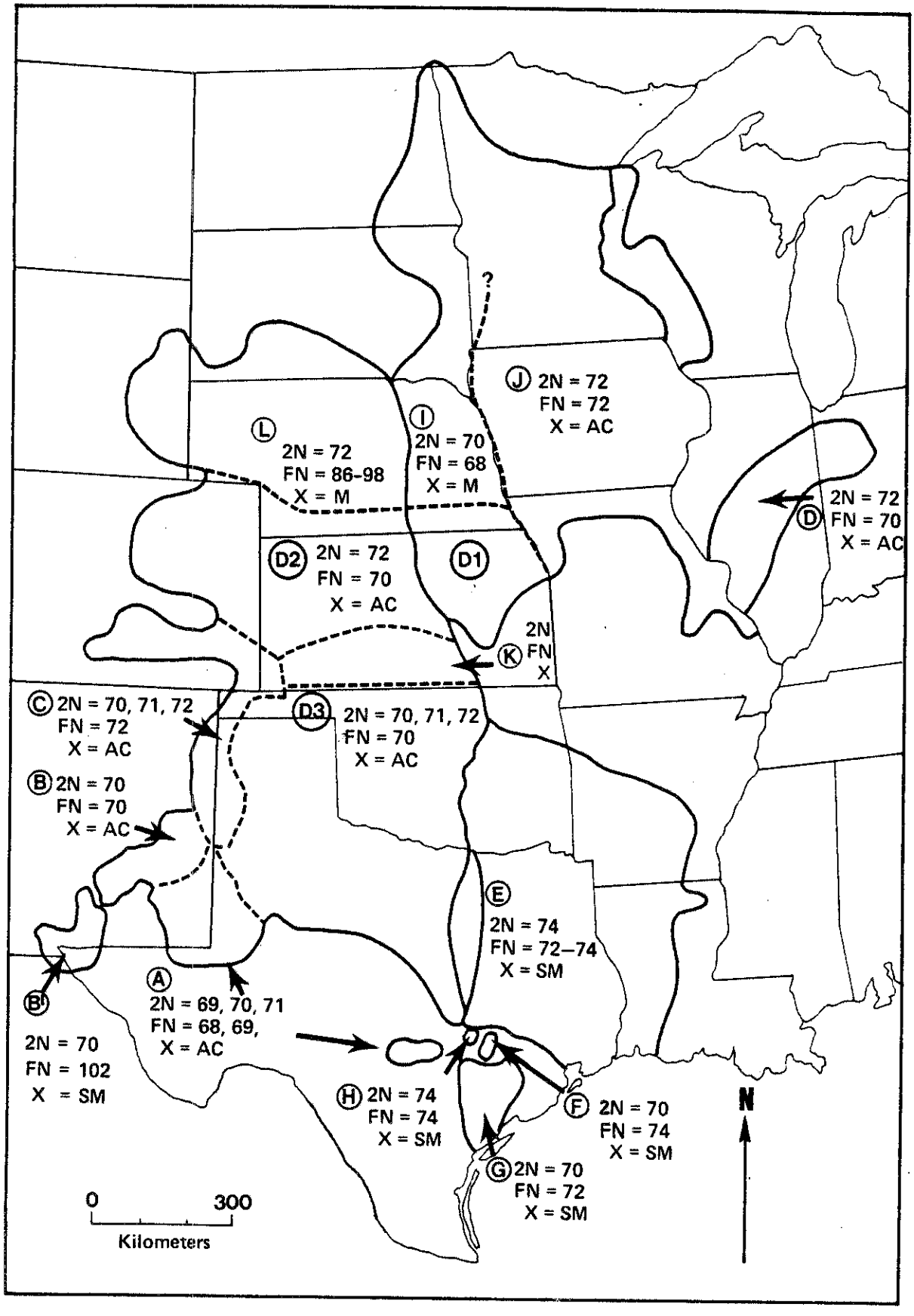

G. bursarius
Knoxjonesi
G. bursarius major
G. bursarius
arenarius
G. breviceps
G. bursarius
texensis
G. bursarius
llanensis
G. attwateri
G. personatus

indicate the degree of hybridization. Many studies have been conducted at contact zones of fossorial mammals (Pembleton and Baker, 1978; Patton et al., 1979; Patton et al., 1984). The width of a hybrid zone is influenced by the dispersal of the progeny and the degree of selection against the heterozygotes (Nevo, 1985). Thus, if the width of the hybrid zone and the dispersal rates are known, one can estimate the effects of selection against the hybrids. In accordance, as selection increases and dispersal decreases, the more narrow the hybrid zone becomes.

Until 1979, the Geomys bursarius complex was recognized as a highly variable species. Using morphometric and chromosomal analyses, Honeycutt and Schmidly (1979) determined there were six subspecies and seven chromosomal races of G. bursarius in Texas (Figure 2); G. bursarius (2N = 70-72, FN = 70) occupied the panhandle and the north-central regions, G. sagittalis (2N = 70-74, FN = 72,74) was found in East Texas, G. b. attwateri (2N = 70, FN = 72) was located in the coastal region, G. b. llanensis and G. b. texensis (2N = 69-71, FN = 68,69) were located in the Edwards Plateau area, and G. b. knoxjonesi (2N = 69-71, FN = 68,69) occupied the southern high plains region of Texas.

Other studies have utilized the groundwork laid by Honeycutt and Schmidly to discern the taxonomic status of G. bursarius in Texas. Tucker and Schmidly (1981) examined the contact zone of G. b. sagittalis and G. b. attwateri in

Figure 2. Distribution of chromosomal races of the Geomys bursarius complex in the central United States.


?
J 2N = 72
FN = 72
X = AC
L
2N = 72
FN = 86–98
X = M
I
2N = 70
FN = 68
X = M
D
2N = 72
FN = 70
X = AC
D2 2N = 72
FN = 70
X = AC
D1
2N
FN
X
K
C 2N = 70, 71, 72
FN = 72
X = AC
D3 2N = 70, 71, 72
FN = 70
X = AC
B 2N = 70
FN = 70
X = AC
E
2N = 74
FN = 72–74
X = SM
B'
2N = 70
FN = 102
X = SM
A
2N = 69, 70, 71
FN = 68, 69,
X = AC
H 2N = 74
FN = 74
X = SM
F 2N = 70
FN = 74
X = SM
G 2N = 70
FN = 72
X = SM
N
0
300
Kilometers

Burleson County, Texas. Morphometric analysis could not distinguish between these subspecies, and no ecological differences were found. Karyotypic analysis showed F_1 hybrids but no F_2 individuals. Hybrids were restricted to a narrow zone with no introgression between these forms. They concluded G. b. attwateri should be elevated to a species recognized as G. attwateri. Bohlin and Zimmerman (1982) studied the contact zone of G. b. major and G. b. sagittalis in Falls and McClennan Counties of Texas and in central Oklahoma. Using electrophoretic analysis they determined there was a high degree of genic differentiation between the two forms. The researchers concluded these two taxa were separate species because of the alternately fixed alleles for the ADH-1, MDH-2, LDH-1, and IDH-1 loci, the low interracial genic identity (I = 0.685), the different levels of heterozygosity, and only one F_1 hybrid was found. G. b. sagittalis was elevated to G. breviceps sagittalis.

Baker and Genoways (1975) studied Geomys in the southern high plains of Texas. Based on morphometric and karyologic analyses, they concluded there were two subspecies of G. bursarius located in that area, G. b. major in the northern part of the panhandle and G. b. knoxjonesi in southern plains and eastern New Mexico. They also remarked that G. b. knoxjonesi was more closely related to G. b. llanensis and G. b. texensis of central Texas than to G. b. major, even though these forms are geographically

separated. However, Honeycutt and Schmidly (1979) found G. b. major and G. b. knoxjonesi to be more similar than G. b. knoxjonesi and the Edwards Plateau forms. They concluded that this discrepancy could be due to the use of different morphometric characters and a small sample size of the west Texas form. No further research has been done to distinguish between these four forms.

Although morphometric and chromosomal techniques have done much to clarify the taxonomic status of Geomys in Texas, many of the studies have not explained geographic variation of these rodents, since convergent morphology in pocket gophers occurs in widely separated populations inhabiting similar soil types. Similarly, chromosomal evidence is often ineffective for discerning the degree of introgression between races whose karyotypes exhibit only minor differences. Thus, additional information using electrophoretic techniques is needed to discern the evolutionary status of certain chromosomal races. The purpose of this study is to ascertain the genetic relationships of Geomys from the Edwards Plateau region and the southern high plains region using electrophoretic techniques and comparing these pocket gophers with others in Texas. The Edwards Plateau taxa and G. b. knoxjonesi are chromosomally identical, thus allozyme analysis should indicate the same genetic similarity between these forms.

CHAPTER II

MATERIALS AND METHODS

Pocket gophers (n = 94) were collected from 17 localities in Texas as follows (sample size in parentheses): Geomys bursarius texensis - 1. 4.6 km NW Mason, Mason Co. (2); 2. 32.8 km S Mason, Mason Co. (5); Geomys bursarius llanensis - 3. 1 km N Fredricksberg, Gillespie Co. (3); 4. 8.5 km W Enchanted Rock State Park, Llano Co. (3); 5. 8 km E Fredricksberg, Gillespie Co. (2); Contact zone between G. b. texensis and G. b. llanensis - 6. 0.3-3.3 km W Castell, Llano Co. (5); 7. 0.5-7.2 km E Castell (9); Geomys bursarius major - 8. 1-13.8 km N Needmore, Bailey Co. (7); 9. 7.2 km NNW Rosston, Cooke Co. (10); Geomys bursarius knoxjonesi - 10. 8.8 km N Plains, Yoakum Co. (10); 11. 3.2 km S Kermit, Winkler Co. (8); Contact zone between G. b. major and G. b. knoxjonesi - 12. 6.4 km S Morton, Cochran Co. (8); Geomys breviceps - 13. 11.3 km E Quitman, Wood Co. (5); Geomys atwateri - 14. 3.2 km S Moore, Frio Co. (3); 15. 1.6-4.8 km S Ottin, Gonzales Co. (5); Geomys personatus - 16. 5.8 km SW Mathis, San Patricio Co. (3); 17. 20 km E Corpus Christi, Nueces Co. (3).

Pocket gophers were collected within the ranges and at the contact zones of the specific races. The contact zone between G. b. knoxjonesi and G. b. major was in central

Cochran County in the vicinity of Morton, Texas. On the Edwards Plateau, the contact zone between G. b.texensis and G. b. llanensis was along the Mason and Llano County border in and around Castell, Texas.

A transect was sampled starting away from the contact zone, continuing through the zone, and ending beyond the area of contact, to determine if there was an intergradation zone between certain subspecies. If there was a cline present, it would become apparent using the transect method. In west Texas, pocket gophers were collected at selected locations through out the ranges of the subspecies. The ranges of the subspecies on the Edwards Plateau were much smaller than those subspecies in west Texas, thus a more extensive examination of these taxa was made.

Samples of muscle and liver were extracted in the field and placed in liquid nitrogen for transport to the laboratory. Specimens were measured (standard measurements for mammals), sexed, and prepared as museum specimens. Tissues were ground in double-distilled water, centrifuged at 1,000 x g for 10 min. and stored at -80° C. Starch gels were prepared as 12% suspensions of hydrolyzed starch (1.25:1; Sigma Chemical Company, St. Louis, Missouri; Electrostarch Company, Madison, Wisconsin). Electrophoretic techniques followed Selander, et al. (1971), Ayala, et al. (1974), and Bohlin and Zimmerman (1982).

Alleles were designated alphabetically in order of

decreasing mobility. Proteins encoded by 25 loci were examined as follows: superoxide dismutase (SOD), two peptidases, glycyl-l-leucine (P-GLL) and l-valyl-l-leucine (P-VLL), aspartate aminotransferase (AAT-1 and AAT-2), malic enzyme (ME-2) hemoglobin (HBB-1 and HBB-2), esterase (EST-1, EST-2 EST-4), two peptidases, l-leucylglycyl-glycine (P-LGG) and l-leucyl-l-alanine (P-LLA), α-glycerophosphate dehydrogenase (α-GPD), alcohol dehydrogenase (ADH-1), xanthine dehydrogenase (XDH-1), lactate dehydrogenase (LDH-1 and LDH-2), phosphoglucomutase (PGM-1), 6-phosphogluconate dehydrogenase (6-PGD), isocitrate dehydrogenase (IDH-1 and IDH-2), malate dehydrogenase (MDH-1 and MDH-2), phosphoglucose isomerase (PGI-1). Pocket gophers collected from Cooke county were used as standards to compare electromorphs.

Calculations for genetic analyses were determined by BIOSYS-1 (Swofford and Selander, 1981) which computed allelic frequencies, genetic variation measures and F-statistics. Wright's F statistics (Wright, 1965) were calculated as follows:

$$F_{ST} = \frac{H_T - H_S}{H_T}$$

$$F_{IS} = \frac{H_S - H_I}{H_S}$$

$$F_{IT} = \frac{H_T - H_I}{H_T}$$

where H_T represents the heterozygosity in a panmitic total population, H_I represents the average observed heterozygosity, and H_S represents the heterozygosity of subpopulations. F_{ST} represents the relative measure of subdivision in a deme with a range of 0, no subdivision, to 1, complete subdivision. The inbreeding coeficient, F_{IS}, represents the reduction of heterozygotes due to inbreeding. F_{IT} reflects a measure of inbreeding and stochastic processes that may cause subdivision.

Roger's genetic similarity (1972) was calculated for paired combinations of all populations and was used to determine genetic relationships of Geomys. Genetic similarity was summarized in a dendrogram using the unweighted pair-group method (UPGMA) clustering procedure (Sneath and Sokal, 1973).

Phylogenetic analyses were summarized using the PAUP computer program (Swofford, 1984) which generates phylogenetic trees based on maximum parsimony using Farris' (1972) distance Wagner algorithm. The branch and bound option was used to produced the shortest possible trees. To combine equally parsimonious trees of different topology, a consensus tree was produced using the CONTREE option which calculates Adams and strict consensus trees. The electrophoretic data collected were considered to be

unordered, based on the assumption that any character state was potentially capable of altering to any other character state. Buth (1984) stated there is no generally accepted method of data transformation to character state when using electrophoretic data, and analyses followed those of Rogers and Engstrom (1988).

The cladistic analysis employed the loci as characters and the allozyme at each locus within each operational taxonomic unit (OTU) as a character state. When coding polymorphic character states within OTUs, using Pappogeomys castanops as the outgroup, either the autapomorphic (unique derived character) or symplesiomorphic (shared primitive character) alleles were deleted from the data matrix leaving a synapomorphic (shared derived character) character state (Appendix). If a single character state for an OTU was autapomorphic or there were three character states for an OTU, then the locus was excluded for that taxon (indicated by a question mark in the data matrix).

Multidimensional scaling (SAS) was used for analyzing geographic trends in allele frequencies for the Edwards Plateau pocket gophers. This algorithm, using alternating least squares scaling (Young, et al. 1980), develops a spatial configuration in two or more dimensions of the dissimilarities between the individuals. Nei's (1978) genetic identity values were log transformed to give dissimilarity coefficients used in the analysis.

CHAPTER III

RESULTS

Genetic analysis was performed for 17 populations representing seven taxa (species or subspecies) of pocket gophers from Texas to determine the genetic relationships of G. b. texensis and G. b. llanensis with other Geomys. Of the 25 loci examined, eight were found to be monomorphic for G. b. texensis/llanensis, as well as, the remaining taxa. These included SOD, P-GLL, P-VLL, AAT-1, AAT-2, ME-2, HBB-1, and HBB-2 (Table 1). The seventeen polymorphic loci were EST-1, EST-2, EST-4, P-LGG, P-LLA, α-GPD, ADH-1, XDH-1, LDH-1, LDH-2, PGM-1, 6-PGD, IDH-1, IDH-2, MDH-1, MDH-2, and PGI-1. Five loci showed low levels of polymorphism for shared alleles, while four loci were highly polymorphic among the taxa. The highly polymorphic loci were EST-1, EST-2, ADH-1, and EST-4, with the latter being the most variable.

Proportions of loci polymorphic per population (P) in the Edwards Plateau pocket gophers were not highly variable, 12% in G. b. llanensis to 16% in both G. b. texensis and contact zone populations between these subspecies (Table 2). These levels of polymorphism were quite different from that in G. b. major, 32%, however polymorphism in G. b. knoxjonesi was similar, 16%. G. b. major also had a higher proportion of loci heterozygous per individual (H), 0.059,

Table 1. Allelic frequencies at 17 loci for 17 populations of Geomys from Texas. Numbered localities are listed in Materials and Methods.

		POPULATION								
LOCI		1	2	3	4	5	6	7	8	9
EST-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.64
	B	1.00	1.00	0.83	1.00	1.00	0.90	0.79	0.00	0.21
	C	0.00	0.00	0.17	0.00	0.00	0.10	0.21	0.00	0.15
EST-2	A	0.00	0.30	0.83	0.50	1.00	1.00	0.89	0.29	0.44
	B	1.00	0.70	0.17	0.50	0.00	0.00	0.11	0.71	0.56
EST-4	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.43	0.81
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.50	0.13
	C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.06
P-LGG	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00
α-GPD	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00
ADH-1	A	0.75	0.80	1.00	0.75	1.00	0.60	0.89	1.00	1.00
	B	0.25	0.20	0.00	0.25	0.00	0.40	0.11	0.00	0.00
	C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
XDH-1	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LDH-1	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
LDH-2	A	0.50	0.00	1.00	1.00	1.00	0.20	1.00	0.14	0.00
	B	0.50	1.00	0.00	0.00	0.00	0.80	0.00	0.86	1.00
PGM-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.64	0.00
6-PGD	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 1 continued.

LOCI		POPULATION								
		1	2	3	4	5	6	7	8	9
IDH-1	A	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25
	B	0.75	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.75
IDH-2	A	0.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00
	B	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
MDH-1	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MDH-2	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
	C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PGI-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.00
P-LLA	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00

Table 1 continued.

LOCI		POPULATION							
		10	11	12	13	14	15	16	17
EST-1	A	0.75	0.00	0.81	0.00	0.00	0.00	0.00	0.00
	B	0.25	1.00	0.19	1.00	1.00	0.50	1.00	0.67
	C	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.33
EST-2	A	0.38	0.25	0.56	0.70	1.00	1.00	1.00	1.00
	B	0.62	0.75	0.44	0.30	0.00	0.00	0.00	0.00
EST-4	A	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.00
	B	1.00	1.00	0.94	0.20	1.00	1.00	1.00	1.00
	C	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
P-LGG	A	0.00	0.00	0.13	1.00	1.00	1.00	1.00	1.00
	B	1.00	1.00	0.87	0.00	0.00	0.00	0.00	0.00
α-GPD	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ADH-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	1.00	0.00	0.00	0.00	1.00	1.00
	C	0.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00
XDH-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LDH-1	A	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LDH-2	A	1.00	1.00	1.00	1.00	1.00	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00
PGM-1	A	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00
6-PGD	A	0.00	0.00	0.00	1.00	1.00	1.00	0.00	0.00
	B	1.00	1.00	1.00	0.00	0.00	0.00	1.00	1.00
IDH-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 1 continued.

LOCI		POPULATION							
		10	11	12	13	14	15	16	17
IDH-2	A	0.00	0.06	0.00	0.20	0.00	0.00	1.00	1.00
	B	1.00	0.94	1.00	0.80	1.00	1.00	0.00	0.00
MDH-1	A	1.00	0.94	1.00	1.00	1.00	1.00	1.00	1.00
	B	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00
MDH-2	A	0.00	0.00	0.00	0.00	0.00	1.00	1.00	1.00
	B	1.00	1.00	1.00	0.00	1.00	0.00	0.00	0.00
	C	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
PGI-1	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
P-LLA	A	1.00	0.06	1.00	0.00	0.00	0.00	0.00	0.00
	B	0.00	0.94	0.00	1.00	1.00	1.00	1.00	1.00

Table 2. Genetic variation of *Geomys* expressed as mean proportion of loci polymorphic (*P*) and proportion of loci heterozygous in the average individual (*H*).

Species	Number of Populations	*P*	*H*
G. b. llanensis	3	0.12	0.029
G. b. texensis	2	0.16	0.029
G. b. texensis / llanensis	2	0.16	0.014
G. b. major	2	0.32	0.059
G. b. knoxjonesi	3	0.16	0.028

than the other taxa. Both G. b. llanensis and G. b. texensis had heterozygous levels of 0.029, however at the contact zone, H was 0.014. G. b. knoxjonesi had levels of heterozygosity similar to the Edwards Plateau pocket gophers, 0.028. Due to small sample sizes which could not adequately represent the variation, heterozygous and polymorphic levels were not determined for G. breviceps, G. attwateri, and G. personatus.

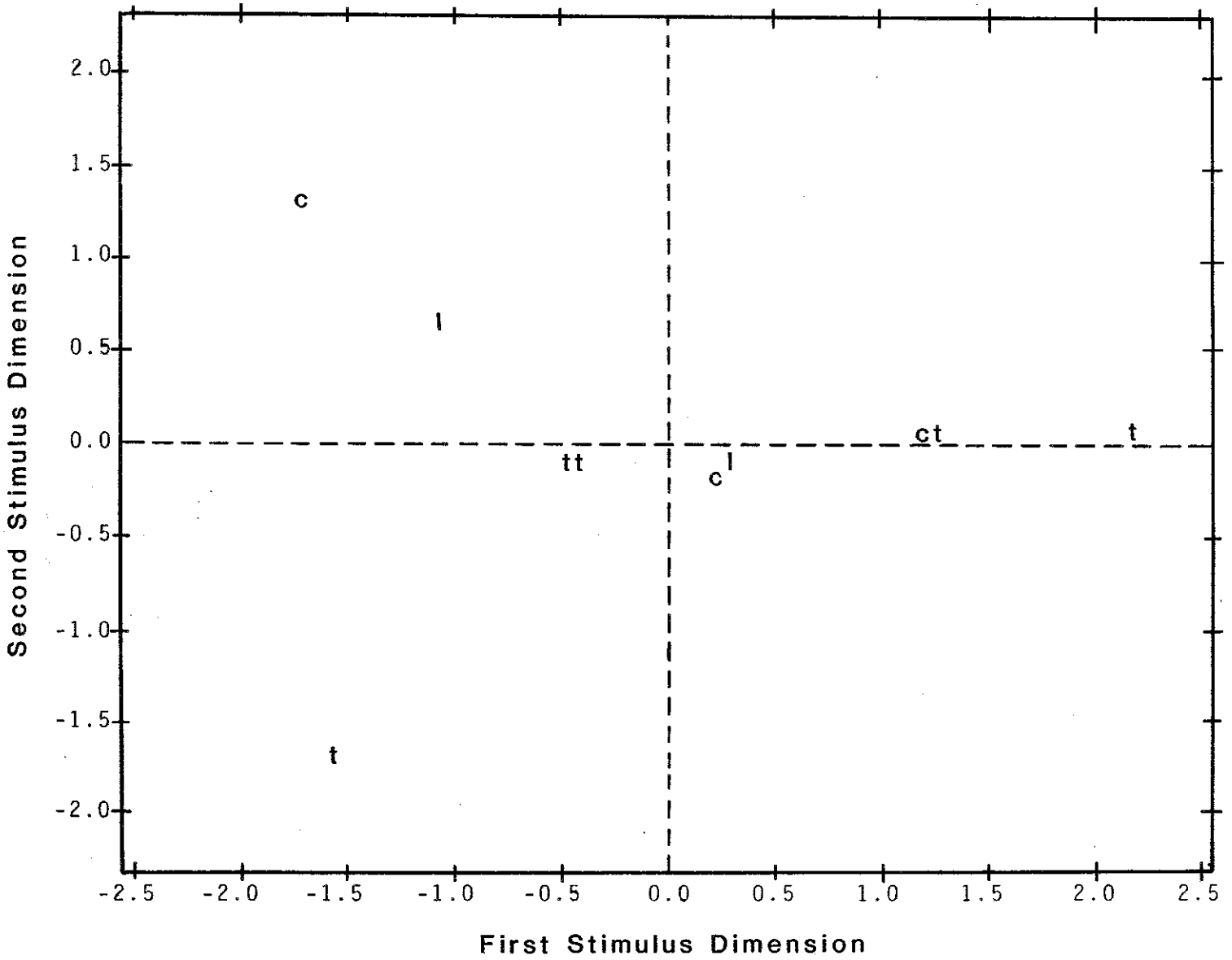
Among the Edwards Plateau pocket gophers, one locus, LDH-1 was polymorphic in G. b. texensis but not in G. b. llanensis. The $LDH\text{-}1^{A}$ allele was predominate in G. b. texensis and fixed in populations of G. b. llanensis. The remaining polymorphic loci had the same predominate allele, except for EST-2. In G. b. texensis, the $EST\text{-}2^{B}$ allele was predominate, while the $EST\text{-}2^{A}$ allele had a higher frequency in G. b. llanensis. There were no fixed allelic differences between these taxa.

Multidimensional scaling was employed using Nei's (1978) genic identities among paired combinations of variable individuals of the two subspecies and from the contact zone to characterize trends in geographic variation in allele frequencies among the Edwards Plateau pocket gophers. This analysis showed no apparent geographic trend in the location of individuals on the two dimensions (Figure 3). If, for instance, a trend were evident, G. b. texensis and G. b. llanensis would have been separated into different

areas on the graph, and contact zone animals would have fallen out between them. The multidimensional scaling analysis and the apparently low genetic differentiation between G. b. texensis and G. b. llanensis, only one of the 25 loci showed alternating predominate allelic frequencies, suggests that electrophoretically these taxa are a single genetic entity. Therefore, they will be considered as one when comparing them with the other taxa of Geomys.

Alleles at several loci were shared by the various races. These alleles included EST-1^{B}, EST-2^{A}, EST-4^{B}, IDH-1^{B}, and MDH-1^{A}. Certain alleles were present in some but not all taxa. The EST-1^{A} allele was found only in G. b. major and G. b. knoxjonesi, and the EST-1^{C} allele was found in all the taxa except G. b. knoxjonesi and G. breviceps. Two alleles occurred at the EST-2 locus in all species except G. attwateri and G. personatus, which did not possess the B allele. The EST-4^{B} allele was common to all taxa, while the A allele found only in G. b. major and G. breviceps. For the same protein, the C allele had a low frequency and was limited to G. b. major and G. b. knoxjonesi. ADH-1 showed variation across the taxa. The A allele for this locus was found in the Edwards Plateau gophers and G. b. major, the B allele was found in all taxa except G. breviceps, G. attwateri, and G. b. major, and the C allele was found exclusively in gophers occupying the eastern part of Texas, G. breviceps and G. attwateri.

Figure 3. Multidimensional scaling analysis for G. b. llanensis (l), G. b. texensis (t), and the contact zone (c) populations based on Nei's genetic identity.

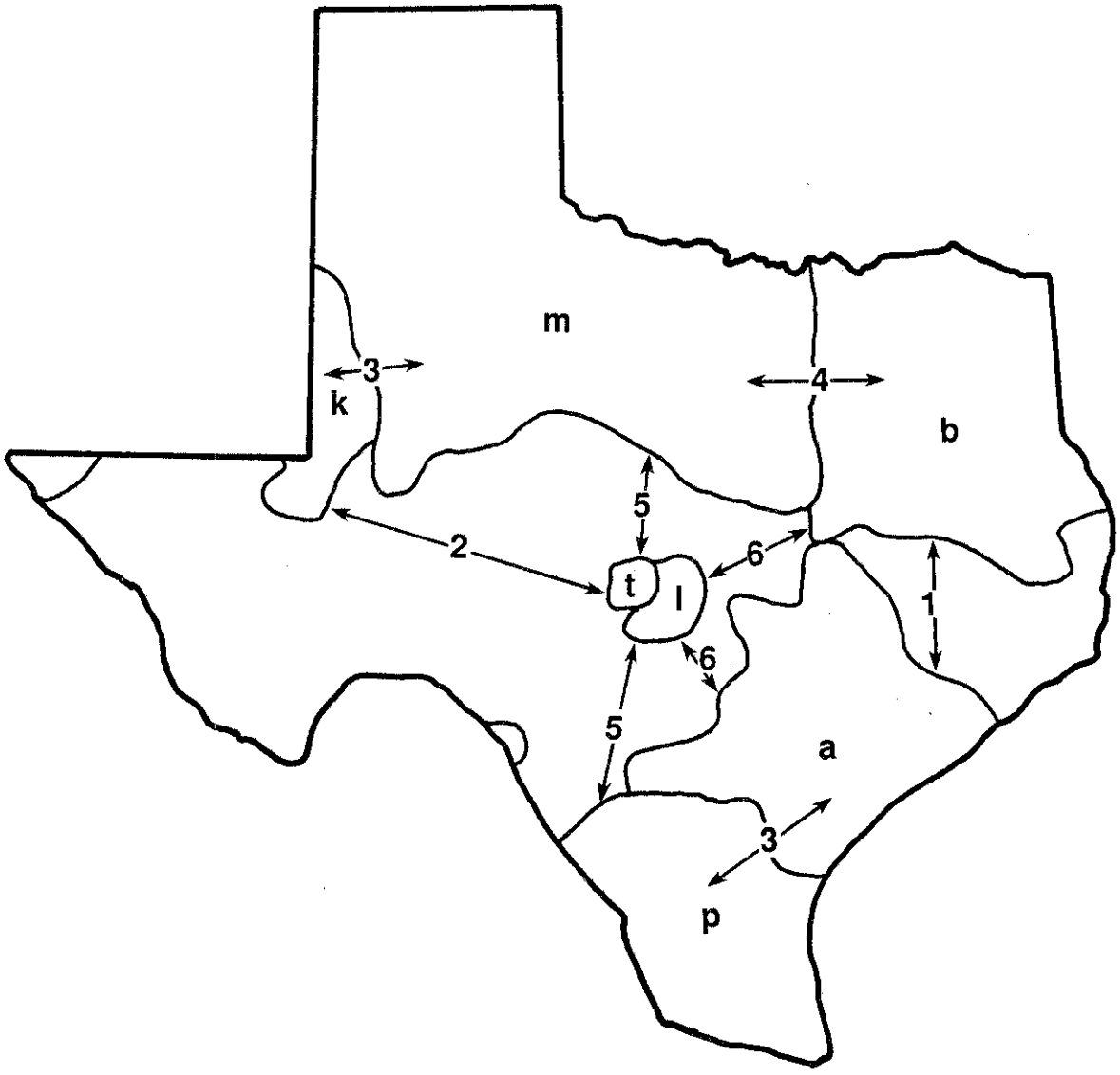

Second Stimulus Dimension
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-2.0
c
l
tt
c
l
ct
t
t
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
2.5
First Stimulus Dimension

Several diagnostic loci exhibited alternately fixed alleles among the taxa. The number of fixed allelic differences between the Edwards Plateau gophers and the remaining forms ranged from two to six, with a mode of five (Figure 4). Furthermore, the α-GPD^{B} allele occurred only in G. b. texensis/llanensis.

Such fixed differences were typical of the remaining taxa, as well. There were three fixed differences between the eastern and the western forms of G. b. major. Additionally, the LDH-1^{B} allele was unique to G. b. major. Four loci, LDH-1, ADH-1, XDH-1, and PGI-1, demonstrated fixed allelic differences between the parapatric forms, G. b. major and G. b. knoxjonesi. The LDH-2^{A} allele was fixed in G. b. knoxjonesi, while the B allele was predominate in G. b. major. For the P-LGG locus, the A allele was fixed in G. b. major, and the B allele was fixed in G. b. knoxjonesi. At the contact zone between these two subspecies, both alleles were found at the P-LGG locus, although the B allele was predominant, suggesting past interbreeding between these forms.

Calculations of genetic similarity for paired combinations of populations within and between the taxa provided an estimate of the genetic differentiation which has occurred during their evolution. Rogers' (1972) genetic similarity (S) among populations of a taxon ranged from means of 0.860 in G. b. major to 0.987 in G. personatus

Figure 4. Number of fixed allelic differences between taxa. Taxa are designated by letters: G. attwateri (a), G. breviceps (b), G. b. knoxjonesi (k), G. b. llanensis (l), G. b. major (t), G. personatus (p), and G. b. texensis (t). There were no fixed allelic differences between G. b. texensis and G. b. llanensis.


m
3
k
4
b
5
2
6
t
l
1
6
5
a
3
p

Similarity for all populations of Geomys populations collected from the Edwards Plateau was 0.947, while S for the two taxa considered as separate entities was somewhat lower, 0.931 (Table 3). Pocket gophers collected from the contact zone between the two were most similar to G. b. llanensis (S = 0.973) than to G. b. texensis (S = 0.939).

Mean genetic similarity between G. b.texensis/llanensis populations and other the other taxa ranged from 0.629 with G. breviceps to 0.779 with G. b. knoxjonesi. Similarly, those taxa whose ranges are in close proximity to the Edwards Plateau pocket gophers are G. b. major to the north and G. attwateri to the east. Genetic similarities between G. b. texensis/llanensis and these two species ranged from 0.621 with G. b. major to 0.648 with G. attwateri.

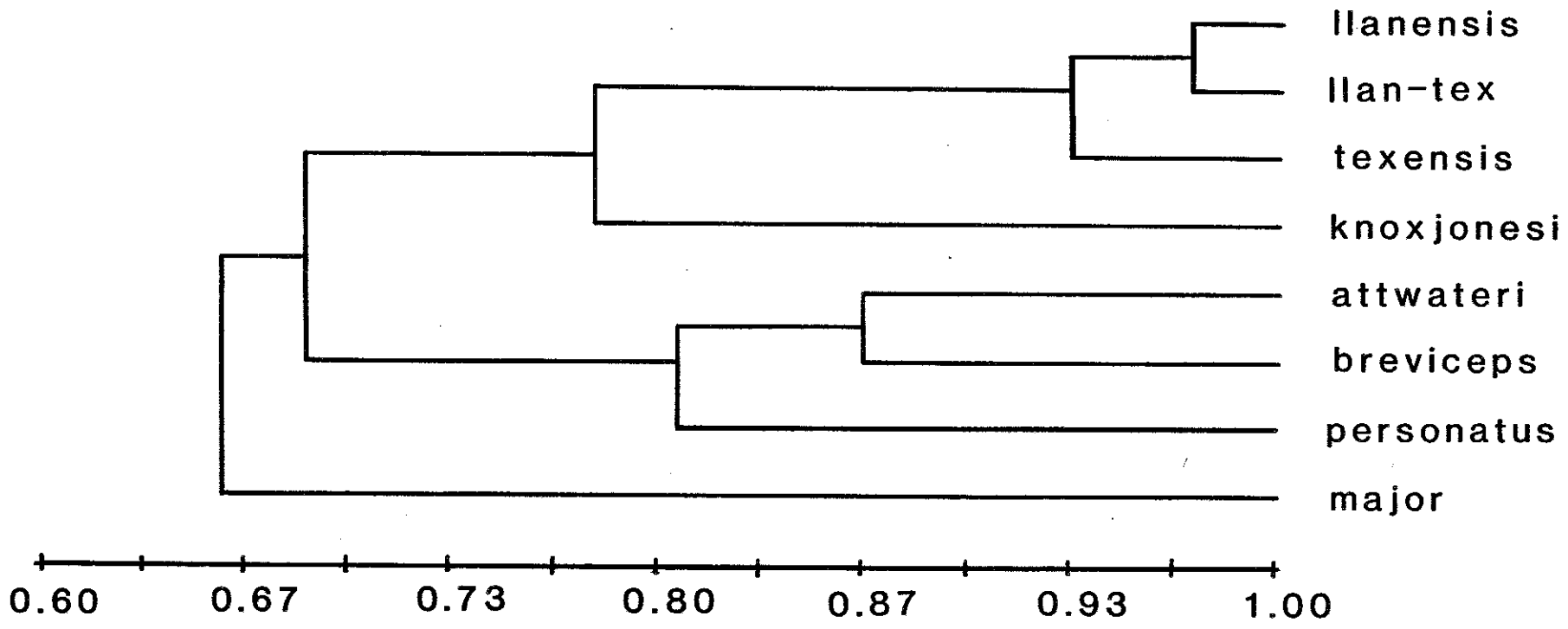
Cluster analysis of Rogers' genetic similarities (1972) for the taxa showed three distinct clusters (Figure 5). G. b. llanensis, G. b. texensis, and populations of their contact zone formed a tight cluster, and, in turn, these were clustered most closely with G. b. knoxjonesi. A second cluster included species occurring in eastern and southeastern Texas, G. breviceps, G. personatus, and G. attwateri. G. b. major was the sole member of a final cluster.

A cladistic analysis was utilized to develop a plausible phylogenetic tree for Texas Geomys. Five trees of equal parsimony but of different topologies were generated

Table 3. Mean genetic similarity (S) for paired combinations of taxa of the genus *Geomys*.

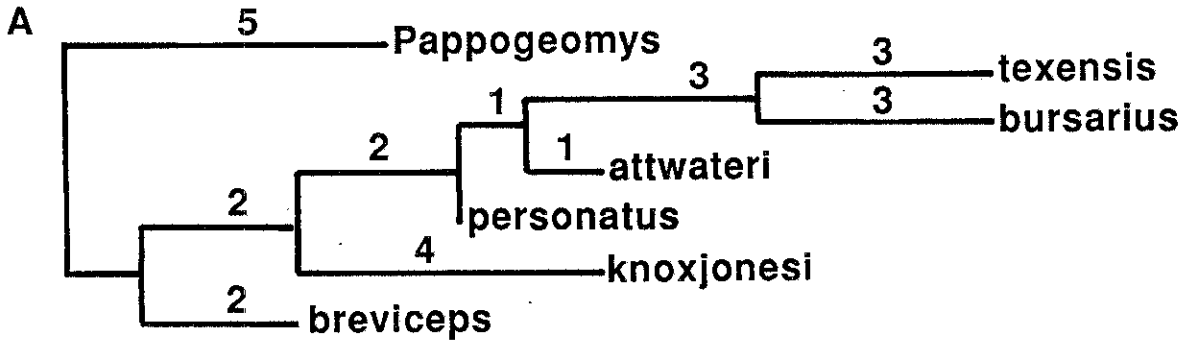
Population	1.	2.	3.	4.	5.	6.	7.	8.
1. *llanensis*	-----	0.931	0.973	0.607	0.791	0.641	0.710	0.651
2. *texensis*		-----	0.939	0.648	0.766	0.640	0.722	0.603
3. *llan-tex*			-----	0.609	0.780	0.664	0.737	0.632
4. *major*				-----	0.702	0.694	0.686	0.657
5. *knoxjonesi*					-----	0.752	0.774	0.745
6. *attwateri*						-----	0.852	0.867
7. *personatus*							-----	0.757
8. *breviceps*								-----

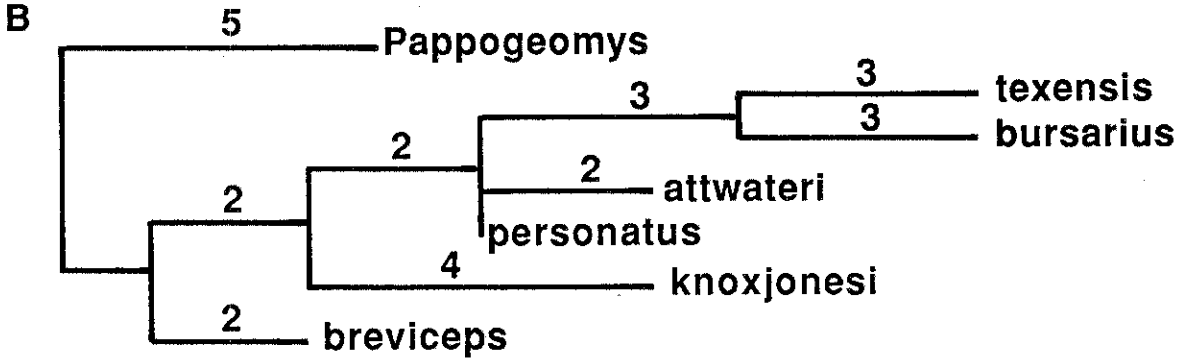
Figure 5. Phenogram for seven taxa of *Geomys* based on Roger's genetic similarity (*S*).


llanensis
llan-tex
texensis
knoxjonesi
attwateri
breviceps
personatus
major
0.60
0.67
0.73
0.80
0.87
0.93
1.00

(Figure 6). G. texensis and G. bursarius formed a single clade in all the trees. A difference in branching sequence of G. personatus and G. attwateri occured, with minor changes in respective positions. The consensus tree (consensus fork index [normalized] = 0.600 and Rohlf's consistency index = 0.600) summarized these trees. Four clades were generated by this method. G. texensis and G. bursarius comprised one clade, G. attwateri and G. personatus another, and G. knoxjonesi and G. breviceps grouped separately.

Figure 6. Three Wagner trees produced from electrophoresis data. All trees are of equal length. Branch lengths are included for all trees.


A
5
Pappogeomys
3
texensis
3
3
bursarius
1
2
1
attwateri
2
personatus
4
knoxjonesi
2
breviceps


B
5
Pappogeomys
3
3
texensis
3
bursarius
2
2
attwateri
2
personatus
4
knoxjonesi
2
breviceps

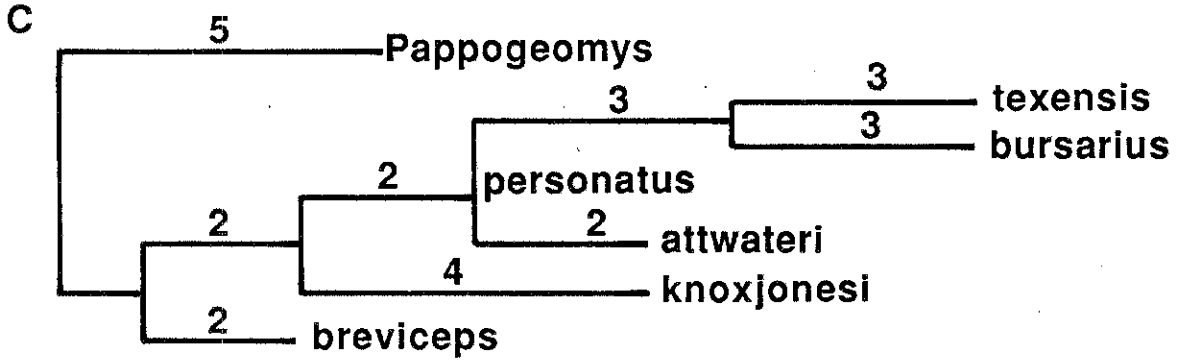
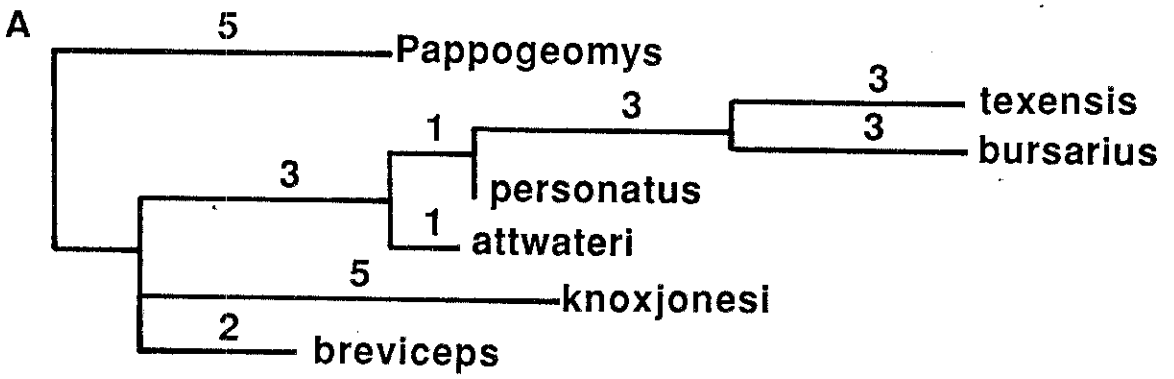
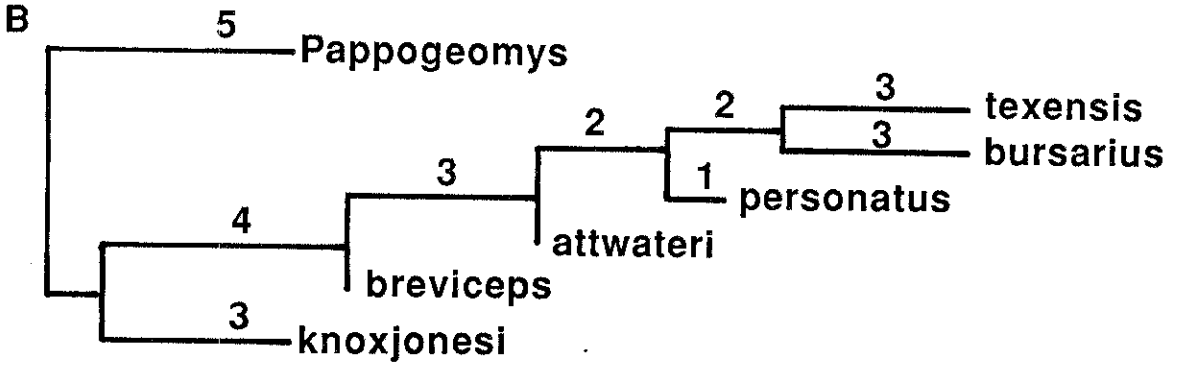
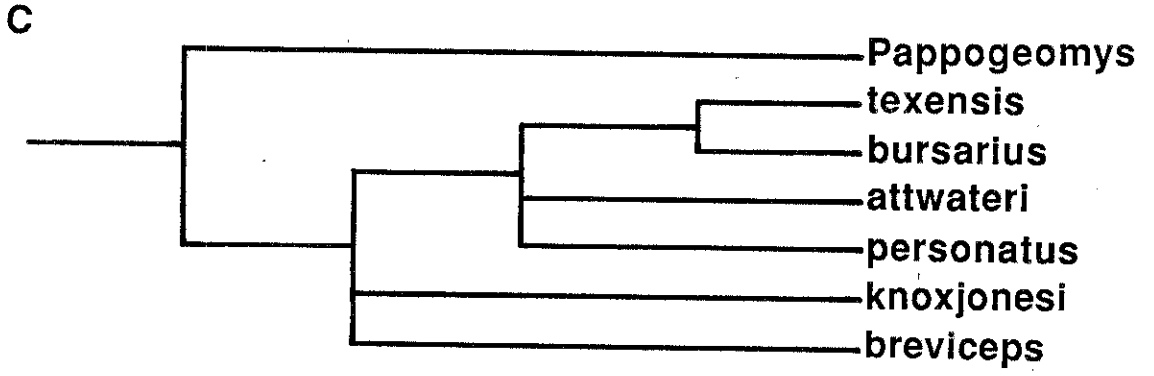

C
5
Pappogeomys
3
3
texensis
3
bursarius
2
personatus
2
2
attwateri
4
knoxjonesi
2
breviceps

Figure 7. Two Wagner trees produced from electrophoretic data. Strict consensus tree developed from the five Wagner trees.


A
5
Pappogeomys
3
3
texensis
1
3
3
bursarius
personatus
3
1
attwateri
5
knoxjonesi
2
breviceps


B
5
Pappogeomys
3
2
2
texensis
3
bursarius
1
personatus
3
attwateri
4
breviceps
3
knoxjonesi


C
Pappogeomys
texensis
bursarius
attwateri
personatus
knoxjonesi
breviceps

CHAPTER IV

DISCUSSION

In view of the biochemical variation found in Geomys of Texas, two questions arise concerning the systematics of the Edwards Plateau pocket gophers. First, what is the relationship of these pocket gophers to other Geomys in Texas? Second, what is the relationship of these two forms to each other?

It is apparent that the Edwards Plateau taxa, G. b. llanensis and G. b. texensis, are genetically similar, but they are as distinct from the remaining taxa as are reproductively isolated forms formerly recognized as subspecies of G. bursarius. For instance, interracial genic identity between G. b. major and G. breviceps was 0.685, and four loci had alternately fixed alleles delineating the species at a contact zone near Norman, Oklahoma (Bohlin and Zimmerman, 1982). A single F_1 hybrid was found in an area where both species occurred sympatrically. Genic similarity between G. breviceps and G. attwateri in southeast Texas was 0.74, with five fixed alternate alleles between the species (Dowler, 1982). More extensive hybridization was found, but hybrids occurred in a narrow contact zone. Comparing the Edwards Plateau pocket gophers with the most similar taxon in Texas, G. b. knoxjonesi, indicated a similarity of 0.779

with two fixed alternate alleles and two predominate allelic differences. Similarly, G. b. texensis/llanensis have fixed alternate allelic differences ranging from 5 to 7 loci with the other taxa examined.

There was other evidence which suggested the distinctiveness of the Edwards Plateau taxa. The distribution of ectoparasites can aid in distinguishing between species of hosts. For host specific parasites, speciation is often dependent on the host's distribution and population dynamics. Patton et al. (1984) found two species of chewing lice, Geomydoecus shastensis and Geomydoecus idahoensis, occurring on Thomomys bottae saxatilis and T. townsendii relictus, respectively. At the contact zone of the smooth-toothed pocket gophers, no evidence was found to indicate that these parasites occurred on either of the opposite gopher species. In another study, two species of lice, Geomydoecus geomydis and Geomydoecus nebrathkensis, were found on Geomys bursarius and Geomys lutescens, respectively (Heaney and Timm, 1985). No evidence of hybridization between the lice was found. Hybrid pocket gophers rarely had lice, although when they did, Geomydoecus nebrathkensis was found. Bohlin and Zimmerman (1982) also found evidence of host specificity of Geomydoecus spp. on G. b. major and G. breviceps. The Edwards Plateau taxa are parasitized by a louse species which does not occur on other Geomys species (Timm and Price, 1980). This unique species,

described by Timm and Price (1980) as Geomydoecus heaneyi, was similar to another found on G. b. knoxjonesi and G. b. major but not on the other Geomys species in Texas.

Morphometrically the Edwards Plateau taxa also appear to be less distinct from other taxa in Texas. Baker and Genoways (1975) found G. b. texensis/llanensis to be similar to G. b. knoxjonesi based on cranial and external measurements, although Honeycutt and Schmidly (1979) found G. b. texensis/llanensis to be most similar to certain G. b. major based on cranial measurements. However, morphology cannot adequately distinguish between certain congeneric species of pocket gophers. Morphology of pocket gophers has been correlated with substrates (Hendrickson, 1972), with a high degree of convergence in forms inhabiting similar soil types (Sudman et al., 1987).

Baker and Genoways (1975) and Honeycutt and Schmidly (1979) also found G. b. texensis/llanensis and G. b. knoxjonesi to have similar karyotypes. Chromosomal analysis was used to distinguish between taxa by comparing fundamental numbers of G. b. major (FN = 70 or 72) with G. b. knoxjonesi (FN = 68 in Texas and 70 in New Mexico). The taxa with FN = 70 were distinguished by a pair of small biarmed elements occurring only in G. b. knoxjonesi. The karyotypes of G. b. knoxjonesi and G. b. texensis/llanensis were found to be indistinguishable.

Based on evidence presented here, the number of

alternately fixed alleles and low genetic similarity, coupled with other features, unique ectoparasites, and karyotype, it is obvious that the Edwards Plateau taxa represent a separate gene pool and should be recognized as a distinct species. These pocket gophers are geographically isolated, but at this point it is not known if they are reproductively isolated. However, other forms which show this degree of differentiation have been shown to be acting as separate species. The decision to elevate this taxon is warranted based on the genetic data presented in this study. The valid name should be G. texensis, since it was described first by Merriam (1895). The type locality is in Mason, Mason County, Texas.

G. texensis showed polymorphism at the ADH-1, EST-1, EST-2, LDH-2, and IDH-1 loci. An examination of the variability of the five loci was used to determine the relationship of the two recognized subspecies comprising G. texensis. No apparent pattern of allelic frequencies of the Edwards Plateau taxa was found using the multidimensional scaling analysis. The MDS configuration showed a random distribution of the taxa instead of a grouping of each taxon with the contact zone placed between them. Also, only one predominant allelic frequency difference was found between the taxa. These results suggest that total introgression occurs across the range of the Edwards Plateau Geomys, and there is little justification in retaining the subspecific

status of G. t. llanensis.

G. texensis occurs in an isolated area on the Edwards Plateau referred to as the Central Basin, which includes parts of Kimble, McCulloch, Mason, San Saba, Llano, Gillespie, and Blanco Counties. The northern limit of the range of G. texensis appears to be along a line from the San Saba River in McCulloch County to Cherokee, San Saba County. The southern limit extends to south of Fredericksburg, Gillespie County, while the western and eastern limits are near London, Kimble County, and the Colorado River in Llano County, respectively.

The Central Basin is characterized by soil types of the Castell, Pedernales, and Pontotoc series (Godfree et al., 1973). These soils are generally a brown loamy sand or gravelly sandy loam surface, 33 cm deep. The Central Basin is isolated by surrounding indurate soils, characterized as shallow to moderately deep clayey and loamy with areas of shallow stony to gravelly clayey soils. G. texensis is geographically isolated by these shallow soils which represent unsuitable habitat to pocket gophers and are responsible for separating G. texensis from G. attwateri to the east, G. personatus to south, and G. b. major to the north.

The Edwards Plateau pocket gophers have the most restricted range of Texas Geomys and appear to be less heterozygous than the other taxa. Isolated populations of

mammals generally have lower genetic variation than those with widespread distributions (Tolliver et al., 1984 and Nygren, 1980). The geographic isolation of G. texensis is reflected by the low genetic variation, with P and H being 15% and 2.4%, respectively. The more widespread forms such as G. b. major and G. breviceps have higher levels of variation with P = 32%, H = 5.9% and P = 38%, H = 3.9%, respectively. The F_{ST} for G. texensis (F_{ST} = 0.474) indicates high population subdivision, typical for most pocket gophers. This also suggests that genetic drift, and associated low genetic variability, could be important in shaping the genome.

Electrophoretic data from this study are in agreement with the conclusions from karyotypic analyses which indicated G. b. knoxjonesi and G. texensis were more similar to each other than to other Geomys species (Baker and Genoways, 1975; Honeycutt and Schmidly, 1979). It is interesting to note the similarity, because G. b. knoxjonesi and G. texensis are separated by approximately 3000 km, and three other taxa, G. b. major, G. attwateri, and G. personatus, are geographically closer. The degree of similarity between G. texensis and G. b. knoxjonesi suggests the taxa were more widely distributed and conspecific or had a common ancestor in the past.

By examining late Wisconsinan and Holocene environments, a possible explanation for the disjunct

distribution of the taxa can be given. Pollen analysis of Wisconsinan-age sediments (ca. 15,000 yr. B.P.) indicated pine forests occurred in west Texas at this time (Wells, 1970). Woodrat (Neotoma) middens with plant macrofossils from the Guadalupe Mountains (Van Devender et al., 1974) and from the Chisos Mountains (Wells, 1966) in west Texas support the pollen evidence. Wells (1974) has suggested that in the northern Chihuahuan Desert, pinyon pine, juniper, and scrub oak were the dominant species, thus indicating a much cooler and wetter environment than exits today. Baker and Penteado-Orellana (1977) reported the existence of mixed forest and grassland in north-central Texas before 9000 yr. B.P., based on fauna and pollen evidence. During the early Holocene prior to 7000 yr. B.P., there was a rapid decrease in vegetation in north-central Texas due to an extreme drought (Knox, 1983). This change to warmer, drier conditions, about 8000 yr. B.P., caused accelerated erosion concomitant to the decrease in mesic vegetation. At the peak of the drier climate, erosion lessened but increased again with subsequent wetter and cooler conditions. Knox (1983) concluded most erosion during the Holocene occurred during the periods 6000 to 4500 and 3400 to 2000 yr. B.P. and more recently since 700 yr. B.P.

The change of climates during the Holocene not only altered vegetation but also modified faunal distribution

(Harris, 1985). An example of such a change in vertebrate distribution is that of the short-tailed shrew, Blarina carolinensis, which has a present day range restricted to eastern Texas and the southeastern U. S. This burrowing insectivore can be found in grassy areas, wooded floodplains, and pine-oak uplands (Schmidly, 1983). Graham (1976) found evidence of this shrew in Friesenhahn Cave on the Edwards Plateau in Bexar County, Texas. B. carolinensis no longer occurs on the Edwards Plateau because of high temperatures, thin soils, and a xeric climate. Graham suggested the alteration in range (7000 to 9000 yr. B.P.) was attributed to the periods of erosion resulting from decreased vegetation accompanying the drier climate.

Thus, a possible explanation for the disjunct G. texensis distribution could be due to fluctuating climates of the Holocene. The pluvial climate of early Holocene suggests more suitable soils for pocket gophers in central and west Texas. Geomys sp. was found in cave deposits dating back to 10,000 years in Edwards and Kerr Counties (Dalquest and Kilpatrick, 1973) which are both outside of the present range for the genus. The ensuing xeric conditions, causing increased erosion and exposing indurate soils, isolated the Central Basin pocket gophers, thereby giving rise to the current distributions of G. texensis and G. b. knoxjonesi.

The contact zone between G. b. knoxjonesi and G. b.

major was also investigated, and electrophoretic data indicated distinctiveness between the taxa. Three fixed alternate alleles, ADH-1, LDH-1, and PGI-1, a low genetic similarity, 0.702, and the phenogram which showed G. b. major as a separate cluster all contributed to the genetic distinctiveness. These results are in agreement with those of Baker et al. (1988). Their analysis included mtDNA, electrophoretic, and karyotypic data, and they concluded that G. b. knoxjonesi should be recognized as a separate species.

Phylogenetic trees and a consensus tree were generated to develop an evolutionary history of Texas Geomys. However, the branching sequence does not agree with the electrophoretic data presented in this study, karyotypic and morphometric data (Honeycutt and Schmidly, 1979), or rDNA data (Davis, 1986). The east Texas species, G. breviceps, G. attwateri, and G. personatus, generally have a higher diploid numbers and/or higher fundamental numbers than the remaining species, G. bursarius, G. knoxjonesi, and G. texensis. Pocket gophers in west Texas are generally larger than those in east Texas, as well. Davis (1986) used rDNA sequences to develop a phylogenetic tree of Geomys using Pappogeomys castanops as an outgroup. Four major linkages were found, G. pinetus, from Florida; G. breviceps; a group comprising G. arenarius from west Texas, G. bursarius from Colorado and Texas, G. knoxjonesi, and G. lutescens from the

Central Plains; and a final group comprised of G. attwateri, G. personatus, and G. tropicalis from Mexico. Davis (1986) determined G. texensis was most closely related to certain G. bursarius and G. lutescens (occurring in western Nebraska and South Dakota). From these varying data sets, one would expect G. texensis, G. knoxjonesi, and G. bursarius to form a common clade on an allozymic phylogenetic tree, and pocket gophers of east Texas (G. attwateri and G. personatus) to comprise a second clade. In fact, this is a representation of the cladogram constructed from the allozymic data. A major difference between Davis' (1986) tree and that presented in this study is that G. knoxjonesi in the rDNA generated tree is grouped with G. bursarius, whereas allozymic data suggest it is remotely removed from the remaining species. Also G. breviceps is not as distinct in the rDNA tree as it is in the electrophoretic tree.

The discrepancies in the trees generated may be attributed to parallel changes in electromorphs, lack of inclusion of enough species, or different evolutionary rates of the genomic markers used. Felsenstein (1978) indicated that phylogenetic inferences may be misleading if parallel changes are more likely than single changes. Using a relatively small number of OTUs along with using an organism which generally has inherently low genetic variation, may not adequately separate the species for a cladistic analysis.

The assumption of constant evolutionary rates is often not realized for electrophoretic data, and three studies were cited by Baverstock et al. (1979) to illustrate different evolutionary rates. A study by Farris (1974) compared phenetic and cladistic relationships of Drosophila using electrophoretic data. The results revealed different relationships among the species due to differing evolutionary rates. Mickevich and Johnson (1976), studying evolutionary rates of the fish genus Menidia, compared trees of morphometric and electrophoretic data using phenetic analysis and by the Wagner method. The analyses indicated differing rates of electrophoretic and morphometric evolution. Baverstock et al. (1979) compared trees using karyotypes and electrophoretic data of the rodent genus Melomys. They concluded one species' electrophoretic evolutionary rate increased since its divergence from its parental species. Being aware of the above evolutionary processes, further research should explain the discrepancy between the relationships of the species generated phenetically and cladistically.

CHAPTER V

CONCLUSION

The Edwards Plateau pocket gophers have a high intraracial genetic similarity, but are distinct from other Texas Geomys. Based on allelic differences, along with ectoparasite distribution occurring on Geomys, it is evident that the Edwards Plateau taxa are a separate gene pool and warrant the recognition as a distinct species, G. texensis.

An examination of the genetic variability across the G. texensis subspecies and in the contact zone showed no discernable pattern to allelic distributions that would distinguish between the taxa. Therefore, no evidence was found supporting the subspecific status of G. t. llanensis.

G. texensis occurs in an isolated area known as the Central Basin. Indurate soils surround this area preventing contact with other Geomys species. It is suggested that the isolation began during the early and middle Holocene. Cycles of moist, cooler climate followed by xeric, warmer climates caused the loss of mesic vegetation thus increasing erosion when cooler, wetter conditions returned. Erosion of suitable soils exposing indurate soils could have led to the isolation of G. texensis.

The contact zone between G. knoxjonesi and G. b. major was also examined. Three fixed alternate alleles and a low

genetic similarity was found. These findings corroborate the taxonomic conclusions of Baker et al. (1988) that recognized G. knoxjonesi as a separate species.

A phylogenetic analysis was used to reconstruct the evolutionary history of Texas Geomys, however, the results are inconclusive at this time. The branching sequences are different than those expected from phenetic relationships based on electrophoretic, karyotypic, or rDNA data. The discrepancy may be attributed to a variety of factors such as parallel changes in electromorphs, not enough species, or differing evolutionary rates of species.

APPENDIX

Coding of 17 alleles as character states used in the cladistic analysis for six Geomys species and Pappogeomys as the outgroup.

	tex	bur	knox	attw	per	bre	Papp
EST-1	2	?	1	2	2	0	0
EST-2	1	1	1	1	1	1	0
EST-4	1	2	2	1	1	1	0
P-LGG	1	0	1	0	0	0	0
α-GPD	2	1	1	1	1	1	?
ADH-1	1	1	0	2	0	2	0
XDH-1	1	1	0	0	0	0	0
LDH-1	0	1	0	0	0	0	0
LDH-2	1	1	0	1	1	0	0
PGM-1	1	1	1	1	1	1	0
6-PGD	1	1	1	0	1	0	0
SOD-1	1	1	1	1	1	1	0
IDH-1	1	1	2	2	2	2	0
MDH-1	0	0	?	0	0	0	0
MDH-2	0	1	0	1	1	2	0
PGI-1	2	1	2	2	2	2	?
P-LLA	1	2	2	1	1	1	?

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