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SECONDARY SEXUAL DIMORPHISM AND GEOGRAPHIC VARIATION IN ORD'S KANGAROO RAT, DIPODOMYS ORDII, ON THE LLANO ESTACADO AND IN ADJACENT AREAS OF TEXAS

ROBERT N. ROBERTSON, ROBERT R. HOLLANDER,
AND J. KNOX JONES, JR.

Ord's kangaroo rat, *Dipodomys ordii*, is widely distributed throughout much of western North America, from southernmost Canada to central México. Because of the broad range of these rats and their tendency to form semi-isolated populations, this species is an ideal subject for the study of geographic variation (Schmidly, 1971). Setzer (1949) examined intraspecific variation in *D. ordii*; he recognized 35 subspecies, which he grouped into six complexes. His Great Plains complex included seven races, two of which, *D. o. medius* and *D. o. richardsoni*, were recorded as occurring on the Llano Estacado of Texas and eastern New Mexico. Hall (1981) arbitrarily mapped the boundary between these two taxa (*D. o. richardsoni* to the north and *D. o. medius* to the south) through the middle of the Llano Estacado, although no obvious biogeographic barrier exists there.

The Llano Estacado is an extensive plateau encompassing approximately 35,000 square miles and is the southern extension of the Great Plains. It is located south of the Canadian River in western Texas and eastern New Mexico (Lotspeich and Coover, 1962), and is separated from adjacent areas by caprock breaks on the northern and eastern margins, and to a lesser extent on the western margin. To the south and southeast, the Llano merges with the Monahans Sandhills and the Edwards Plateau, respectively (Judd, 1970). The Llano Estacado is topographically uniform, with no geographic features that might present a barrier to gene flow in small mammals (with the possible exception of extensive cultivation in some areas, a relatively recent development). Jones *et al.* (1988) opined that the Canadian River and its breaks could provide an area where gene flow is discontinuous between populations of *Dipodomys ordii* distributed to the north and south. If this is the case, it is possible that the breaks on the eastern boundary of the Llano provide an area of discontinuous gene flow as well. The purpose of this study was to examine patterns of geographic variation in *D. ordii* on the Llano Estacado and in adjacent areas, using multivariate statistical techniques, and to relate those patterns to natural geographic features that might restrict gene flow, thus providing a taxonomic framework for future studies of this kangaroo rat.

METHODS

Specimens examined.—Specimens of *D. ordii* used in this study from the Llano Estacado and adjacent areas in Texas are housed in The Museum, Texas Tech University. Important details relative to examination and subsequent analyses of characters are discussed below.

Sex and age classes.—Individual specimens were separated according to sex and divided into age categories (prior to taking measurements) by the following methods described by Desha (1967): *subadult*—permanent dentition incomplete (p4 not fully erupted); *young adult*—permanent dentition complete, teeth showing slight to moderate wear with cusps and primary folds present, auditory bullae rough, opaque, and porous, and basioccipital-basisphenoid suture clearly evident; *adult*—substantial wear on teeth with cusps worn relatively smooth and each tooth with a peripheral band of enamel and a lake of dentine, auditory bullae smooth, shiny, nonporous, and showing at least some translucence, and the basioccipital-basisphenoid suture ankylosed. Only adult specimens were used in analysis of secondary sexual dimorphism and patterns of geographic variation.

Measurements.—Standard external measurements—total length, length of tail vertebrae, length of hind foot, and length of ear—were recorded from original specimen labels. Due to different measuring techniques of various collectors, these measurements were not used in multivariate and univariate statistical analyses for sexual dimorphism and geographic variation, although they are included in Table 1 for information. All cranial measurements were taken by Robertson using the same pair of Fowler digital calipers that were calibrated to the nearest 0.01 mm. Cranial measurements used in this study are the same as those used by various other investigators for study of geographic variation in *Dipodomys ordii* (Desha, 1967; Schmidly, 1971; Kennedy and Schnell, 1978; Kennedy *et al.*, 1980; Baumgardner and Schmidly, 1981). Those chosen for analysis were shown to be good indicators of variation between sexes and geographic localities in the previous studies. Cranial dimensions we used are as follows: greatest length of skull, mastoid breadth, postorbital constriction, maxillary breadth, rostral breadth, length of nasals, least supraoccipital breadth, bullar-premaxillary length, basal length, length of diastema, width of upper molar, length of maxillary toothrow, and depth of skull. These measurements have been described in detail by previous investigators (see citations above).

Analysis.—Multivariate and univariate statistical techniques were utilized to examine cranial characters for adult specimens. All statistical tests used were from programs available in the SPSS/PC+ statistical package (SPSS Inc., 1988).

Specimens from immediately adjacent localities were pooled to form samples of sufficient size for statistical analysis (Fig. 1). All specimens that were not pooled were treated as unknown in the analyses. A general description of the groups will be given in the section on geographic variation.

In all statistical analyses, multivariate tests were used to detect group differences before any univariate tests were used. It has been demonstrated that the results of numerous univariate tests do not emulate the results of a multivariate test (Willig *et al*., 1986; Willig and Owen, 1987), and a multivariate question is asked when analyzing morphological variation in natural populations (Hollander, 1990). Specific statistical tests performed on the data will be discussed in detail in the following sections on secondary sexual dimorphism and geographic variation.

Accounts of subspecies follow the section on geographic variation and each terminates with a list of specimens examined. Localities from which specimens were examined also are plotted on Figure 1. Some localities from which kangaroo rats were studied are not plotted on the map because undue crowding of symbols would have resulted; for the same reason, a few symbols are slightly offset on the map. Also, a few localities from which specimens were available lie to the east or south of the map border. Those localities not mapped are in italic type. Localities are listed alphabetically by county; within a county, they are listed from north to south and, at the same latitude, from west to east.

Secondary Sexual Dimorphism

In his study of subspeciation in Ord's kangaroo rat, Setzer (1949), using small sample sizes, found sexual dimorphism to be nonsignificant. It has been found in more recent studies of *Dipodomys ordii* in western Texas, however, that sexual dimorphism was a significant factor; thus, authors analyzed sexes separately (Desha, 1967; Schmidly, 1971). Desha (1967) found significant sexual dimorphism in nine of 14 cranial characters in *D. o. medius*. He reported that sexes differed significantly in greatest length and depth of skull, basal, bullar-premaxillary, nasal, and diastemal lengths, and greatest cranial, maxillary, and least interorbital breadths.

Schmidly (1971) examined sexual dimorphism in four populations of *D. ordii* from western Texas and found significant sexual dimorphism in 14 of 26 characters in one population. He found that two of the remaining three populations were dimorphic in five characters and the fourth population dimorphic in 10. He noted that the degree of sexual dimorphism varied geographically. From these findings, he suggested that sexes should be considered separately in further taxonomic studies of *D. ordii*. However, Baumgardner and Schmidly (1981) did not find consistent sexual dimorphism in any characters that were analyzed from 13 separate localities in southern Texas and northern México. Schmidly and Hendricks (1976) also noted only limited sexual dimorphism in cranial and external measurements of *D. ordii* from southern Texas and México.

A multivariate analysis of variance (MANOVA) was performed on a single large sample of 119 individuals from the Muleshoe Sand Hills (Bailey, Lamb, and Hale counties—group 1 of Table 1) to determine the presence or absence of secondary sexual dimorphism. The results of the MANOVA ($P = 0.035$) indicated significant differences between sexes and as a result they were separated in subsequent analyses.

Schmidly (1971) reported no significant differences between males and females in external measurements for the four populations he investigated. Although no tests for significance were utilized on external characters in the present study, the means of external measurements of the samples were similar between males and females. Males were generally larger cranially than females in all but two groups. Females from group 2 were larger than males in all characters except length of nasals and length of maxillary toothrow, and females from group 5 were larger in all characters except maxillary breadth, length of nasals, and length of diastema (Table 1).

Geographic Variation

When Setzer (1949) studied variation in *D. ordii*, he used both quantitative and qualitative characteristics to differentiate among subspecies, but the statistical significance of population variability was not presented. In addition, some of the samples used by Setzer were small. For example, he assigned 129 specimens to *D. o. medius*, but the largest sample from any one locality was 10 and the average sample size was four (Desha, 1967).

Several authors have examined geographic variation in *D. ordii* from the High Plains of Texas, New Mexico, and western Oklahoma (Desha, 1967; Schmidly, 1971; Hartman, 1980; and Kennedy *et al.*, 1980). These studies were conducted using specimens from within the ranges of three subspecies, namely *D. o. medius*, *D. o. richardsoni*, and *D. o.*

TABLE 1.—*Summary statistics for each sex for pooled samples (see Fig. 1) of* Dipodomys ordii *from the Llano Estacado and adjacent areas in Texas. Statistics for each group are sample size (N), mean, standard deviation (SD), standard error (SE), and range (minimum-maximum). All measurements are given in millimeters.*

Group	N	Mean	SD	SE	Range
			Greatest length of skull		
			Males		
1	54	39.54	0.92	0.12	36.82-41.44
2	16	39.28	0.70	0.18	38.08-40.75
3	53	39.51	0.73	0.10	37.46-41.11
4	23	39.77	0.93	0.19	38.59-41.82
5	19	39.44	0.89	0.20	37.46-40.81
6	32	40.03	0.85	0.15	37.69-41.41
			Females		
1	63	39.40	1.01	0.13	36.35-41.42
2	17	39.52	1.09	0.26	37.46-41.38
3	34	39.29	0.87	0.15	37.71-41.40
4	14	39.43	0.81	0.22	38.34-41.20
5	13	39.76	1.13	0.31	37.76-41.50
6	30	40.02	0.85	0.16	38.48-41.57
			Mastoid breadth		
			Males		
1	56	24.57	0.60	0.08	22.97-25.92
2	16	24.55	0.41	0.10	23.54-25.37
3	53	24.64	0.60	0.08	23.30-26.41
4	23	24.64	0.57	0.12	23.69-25.90
5	20	24.69	0.79	0.18	23.23-25.80
6	32	24.43	0.62	0.11	22.93-25.90
			Females		
1	63	24.61	0.66	0.08	22.82-26.11
2	17	24.74	0.75	0.18	22.96-25.90
3	36	24.56	0.68	0.11	22.98-25.71
4	15	24.59	0.73	0.19	23.55-26.42
5	14	24.70	0.67	0.18	23.32-25.78
6	30	24.43	0.54	0.10	23.23-25.65
			Postorbital constriction		
			Males		
1	56	13.38	0.72	0.10	12.07-16.21
2	16	12.98	0.47	0.12	12.21-13.94
3	58	13.19	0.57	0.08	11.57-14.39
4	21	13.02	0.66	0.14	11.51-14.11
5	20	12.80	0.50	0.11	11.97-13.78
6	31	13.08	0.61	0.11	11.85-14.03
			Females		
1	61	13.17	0.46	0.06	12.26-14.32
2	17	13.14	0.47	0.11	12.06-13.95
3	36	13.13	0.51	0.08	12.09-14.14
4	15	13.14	0.64	0.16	12.06-14.04
5	14	13.04	0.43	0.12	12.50-13.90
6	30	13.02	0.33	0.06	12:13-13.50

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Maxillary breadth			
		Males			
1	56	21.46	0.57	0.08	19.60-22.56
2	16	21.27	0.62	0.16	20.19-22.44
3	57	21.29	0.70	0.09	19.73-22.39
4	23	21.29	0.69	0.14	20.06-22.62
5	19	21.72	0.72	0.17	20.08-23.07
6	29	21.74	0.71	0.13	20.29-23.50
		Females			
1	62	21.58	0.67	0.09	19.81-22.97
2	17	21.33	0.76	0.19	19.95-22.46
3	35	21.04	0.63	0.11	19.83-22.22
4	14	21.20	0.81	0.22	20.20-23.51
5	14	21.67	0.61	0.16	20.58-22.43
6	29	21.72	0.61	0.11	20.66-23.14
		Rostral breadth			
		Males			
1	56	3.88	0.25	0.03	2.90-4.46
2	16	3.59	0.22	0.05	3.59-4.28
3	51	3.91	0.23	0.03	3.35-4.42
4	23	3.72	0.24	0.05	3.26-4.15
5	20	4.03	0.27	0.06	3.59-4.45
6	31	4.11	0.20	0.04	3.73-4.55
		Females			
1	63	3.91	0.23	0.03	3.34-4.43
2	17	3.96	0.18	0.04	3.57-4.28
3	35	3.98	0.23	0.04	3.52-4.68
4	15	3.78	0.17	0.04	3.39-3.96
5	14	4.12	0.25	0.07	3.79-4.67
6	30	4.01	0.16	0.03	3.76-4.43
		Length of nasals			
		Males			
1	54	14.48	0.68	0.09	11.68-15.45
2	16	14.56	0.58	0.14	13.86-15.71
3	53	14.49	0.47	0.06	13.62-15.96
4	23	14.43	0.58	0.12	13.56-15.94
5	20	14.52	0.48	0.11	13.85-15.51
6	32	14.49	0.46	0.08	14.13-15.88
		Females			
1	63	14.53	0.57	0.07	13.24-16.16
2	17	14.54	0.44	0.11	13.73-15.29
3	34	14.34	0.60	0.10	13.11-15.80
4	14	14.20	0.53	0.14	13.13-14.94
5	13	14.44	0.83	0.23	12.73-15.52
6	30	14.82	0.52	0.10	14.10-16.11

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Least supraoccipital breadth			
		Males			
1	56	2.63	0.41	0.05	1.78-3.63
2	16	2.65	0.49	0.12	1.80-3.58
3	60	2.50	0.38	0.05	1.44-3.54
4	23	2.44	0.35	0.07	1.79-3.31
5	20	2.78	0.32	0.07	2.20-3.40
6	31	2.88	0.39	0.07	1.79-3.68
		Females			
1	63	2.56	0.41	0.05	1.58-3.44
2	17	2.76	0.45	0.11	2.20-3.78
3	35	2.53	0.32	0.05	1.87-3.37
4	15	2.50	0.45	0.12	1.79-3.25
5	14	2.87	0.47	0.13	2.03-3.67
6	30	3.01	0.37	0.07	2.23-3.62
		Bullar-premaxillary length			
		Males			
1	56	36.52	0.83	0.11	34.37-38.47
2	16	36.27	0.69	0.17	35.07-37.49
3	55	36.54	0.65	0.09	35.30-38.33
4	23	36.63	0.84	0.18	35.55-38.28
5	19	36.54	0.85	0.20	34.84-38.15
6	27	37.16	0.70	0.14	35.78-38.30
		Females			
1	62	36.48	1.08	0.14	33.49-39.28
2	16	36.47	0.95	0.24	34.85-38.24
3	35	36.22	0.85	0.14	34.80-38.41
4	15	36.38	0.67	0.17	35.04-37.34
5	14	36.73	1.04	0.28	35.15-38.53
6	26	36.92	0.76	0.15	35.24-38.02
		Basal length			
		Males			
1	55	28.95	0.61	0.08	27.73-30.22
2	14	28.64	0.44	0.12	27.80-29.38
3	50	28.97	0.74	0.10	26.14-30.64
4	23	28.89	0.80	0.17	27.48-30.47
5	19	29.09	0.57	0.13	28.05-30.22
6	25	29.67	0.63	0.13	28.21-30.62
		Females			
1	59	29.04	0.85	0.11	27.08-32.22
2	16	28.84	0.91	0.23	27.11-30.48
3	31	28.59	0.78	0.14	27.43-30.76
4	15	28.81	0.64	0.17	27.43-30.08
5	13	29.22	0.89	0.25	27.77-30.91
6	25	29.56	0.73	0.15	28.00-31.02

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Length of diastema			
		Males			
1	56	8.83	0.32	0.04	8.16-9.49
2	16	8.81	0.31	0.08	8.12-9.42
3	60	8.94	0.29	0.04	8.33-9.64
4	23	8.97	0.36	0.08	8.42-9.78
5	20	9.02	0.32	0.07	8.45-9.76
6	32	9.26	0.25	0.04	8.84-9.77
		Females			
1	62	8.83	0.41	0.05	7.77-9.69
2	17	8.90	0.39	0.10	8.09-9.89
3	36	8.76	0.33	0.06	8.08-9.40
4	15	8.83	0.24	0.06	8.23-9.34
5	14	8.90	0.46	0.12	7.89-9.62
6	30	9.16	0.25	0.05	8.62-9.60
		Width of upper molars			
		Males			
1	56	7.39	0.23	0.03	6.94-7.90
2	16	7.34	0.26	0.06	6.83-7.83
3	60	7.41	0.32	0.04	6.81-9.06
4	21	7.41	0.24	0.05	6.88-7.85
5	20	7.42	0.31	0.07	6.80-7.96
6	32	7.50	0.23	0.04	6.99-7.98
		Females			
1	63	7.31	0.34	0.04	5.04-7.84
2	17	7.35	0.30	0.07	6.67-8.09
3	35	7.35	0.23	0.04	6.81-7.90
4	13	7.40	0.18	0.05	7.12-7.77
5	14	7.44	0.22	0.06	7.11-7.78
6	30	7.42	0.23	0.04	7.01-7.93
		Length of maxillary toothrow			
		Males			
1	56	5.33	0.29	0.04	4.69-5.92
2	16	5.13	0.19	0.05	4.82-5.43
3	60	5.14	0.24	0.03	4.54-5.74
4	20	5.13	0.26	0.06	4.63-5.54
5	20	5.15	0.31	0.07	4.71-5.66
6	32	5.34	0.32	0.06	4.51-5.89
		Females			
1	63	5.18	0.29	0.04	4.68-5.69
2	17	5.12	0.33	0.08	4.65-5.57
3	36	5.13	0.30	0.05	4.56-5.78
4	14	5.09	0.28	0.07	4.74-5.69
5	14	5.40	0.46	0.12	4.59-6.17
6	30	5.40	0.32	0.06	4.69-5.90

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Depth of skull			
		Males			
1	56	14.10	0.31	0.04	13.32-15.01
2	16	14.00	0.27	0.07	13.55-14.54
3	59	13.99	0.32	0.04	13.10-14.88
4	23	14.10	0.30	0.06	13.59-14.81
5	19	14.01	0.34	0.08	13.28-14.96
6	28	14.12	0.37	0.07	13.20-14.65
		Females			
1	63	14.04	0.35	0.04	12.92-14.79
2	17	14.14	0.34	0.08	13.43-14.64
3	33	13.99	0.33	0.06	13.34-14.81
4	14	13.97	0.37	0.10	13.48-14.84
5	14	14.16	0.47	0.13	13.53-15.15
6	30	14.13	0.33	0.06	13.27-14.66
		Total length			
		Males			
1	43	243.67	10.33	1.53	225-276
2	15	245.33	7.50	1.94	227-259
3	57	236.93	14.57	1.93	199-271
4	22	242.05	14.75	3.14	207-280
5	4	248.75	8.54	4.27	240-260
6	31	244.58	13.71	2.46	200-266
		Females			
1	41	244.71	13.63	2.13	215-278
2	15	243.40	13.55	3.50	217-260
3	36	238.94	13.26	2.21	214-270
4	14	234.79	16.92	4.52	187-257
5	5	253.20	11.34	5.07	239-270
6	25	244.36	11.53	2.31	218-265
		Length of tail vertebrate			
		Males			
1	43	130.70	8.21	1.25	118-156
2	15	129.53	7.00	1.81	118-145
3	56	127.64	11.72	1.57	85-152
4	22	127.27	9.24	1.97	98-142
5	4	132.00	9.09	4.55	120-140
6	31	132.97	9.43	1.69	109-154
		Females			
1	41	129.93	11.94	1.86	99-160
2	15	128.67	11.63	3.00	105-150
3	36	130.11	9.10	1.52	103-143
4	14	126.21	16.06	4.29	83-146
5	5	138.40	10.01	4.48	130-155
6	25	131.64	5.89	1.18	120-140

TABLE 1.—*Continued.*

Group	N	Mean	SD	SE	Range
		Length of hind foot			
		Males			
1	38	38.63	1.62	0.26	35-41
2	15	38.13	2.17	0.56	34-41
3	57	37.75	2.19	0.29	41-57
4	22	38.55	1.60	0.34	36-43
5	4	38.75	2.63	1.31	35-41
6	31	40.52	2.16	0.39	35-49
		Females			
1	36	39.25	2.41	0.40	35-49
2	15	37.80	2.18	0.56	34-42
3	36	37.14	2.11	0.35	33-40
4	14	37.79	1.37	0.37	35-40
5	5	38.00	2.74	1.22	34-41
6	25	40.00	2.60	0.52	35-50
		Length of ear			
		Males			
1	43	13.37	1.35	0.21	10-18
2	15	12.40	0.91	0.24	11-14
3	57	12.25	1.87	0.25	08-16
4	22	13.59	1.47	0.31	08-15
5	4	13.25	2.36	1.18	10-15
6	31	13.84	1.92	0.34	08-16
		Females			
1	41	13.22	1.71	0.27	09-20
2	15	13.53	2.07	0.53	11-19
3	36	12.33	1.87	1.31	07-16
4	14	14.00	1.11	0.30	12-15
5	5	13.80	3.11	1.39	11-19
6	24	13.88	1.83	0.37	08-16

oklahomae, the first two of which are of immediate concern as the focus of this investigation.

Four populations of *D. ordii* from the High Plains of Texas that encompass the ranges of *D. o. medius* and *D. o. richardsoni* (as described by Hall and Kelson, 1959) were examined by Schmidly (1971). Schmidly did not assign subspecific status to these populations, but he did find that one from north of the Canadian River varied significantly when compared to those to the south of the river in 11 of the 14 characters examined. The two most southerly populations varied little from each other, whereas the fourth (Needmore, Bailey County) seemed to lie in a zone of intergradation between the two southernmost populations and the one to the north of the Canadian. Several factors may contribute to reduction of gene flow between northern and southern populations of Ord's kangaroo rat on the High Plains of Texas and adjacent New Mexico.

First, because the four populations studied by Schmidly were arranged essentially in a north-south direction, spatial separation alone may account for much of the isolation between them. Second, the northern edge of the Llano Estacado (Canadian River breaks) may serve as a barrier to gene flow, and finally the agricultural activity on the Llano may be partially involved in producing divergence among semi-isolated populations (Schmidly, 1971). Schmidly's findings agreed with those of Desha (1967) in suggesting that patterns of variation in *D. ordii* are more complex than previously thought by Setzer (1949), and that there was a need to re-evaluate geographic variation in this species using statistical techniques.

For analysis of geographic variation, specimens from adjacent localities were pooled to form six groups (Fig. 1) of sufficient sample size for statistical analyses. Care was taken not to cross any potential biogeographic barrier in selecting pooled samples. We decided a sample size of 20 individuals (10 males and 10 females) from immediately adjacent localities would be the minimum number necessary before individuals could be pooled. Six pooled groups were formed using that criterion. Three of these groups were from atop the Llano Estacado and three were from adjacent areas. Also, three of the groups were within the presumed range of *D. o. richardsoni* and the remaining three were within the presumed range of *D. o. medius* (as mapped by Hall, 1981). Specimens from adjacent localities that were not in sufficient number to pool were left ungrouped and treated as unknown in subsequent analyses. General location of the six groups follows (see Table 1 for sample sizes).

Group 1—Muleshoe Sand Hills—Bailey, Lamb, and Hale counties
Group 2—Cochran and Yoakum counties
Group 3—Winkler County
Group 4—Lynn County
Group 5—Dickens County
Group 6—Hemphill County

These were tested for the presence of significant geographic variation among groups with a MANOVA. For both males and females, highly significant ($P < 0.001$) differences were obtained, indicating that at least some of the groups were different. The groups then were subjected to one-way ANOVAs on each cranial character with the

TABLE 2.—*Results of the Student-Newman-Kuels multiple range test (MRT) on cranial characters that showed significant differences with one-way ANOVAs (similar results were obtained with Duncan and Scheffes). Asterisks (*) in a column indicate homogenous subsets of the groups.*

Males					Females				
Group	Means	MRT			Group	Means	MRT		
				Greatest length of skull					
2	39.27	*			3	39.29	*		
5	39.43	*			1	39.39	*		
3	39.50	*			4	39.42	*	*	
1	39.54	*			2	39.51	*	*	
4	39.76	*	*		5	39.76	*	*	
6	40.03		*		6	40.01		*	
				Postorbtial constriction					
5	12.80	*							
2	12.98	*	*						
4	13.02	*	*			NS			
6	13.08	*	*						
3	13.19	*	*						
1	13.37		*						
				Maxillary breadth					
2	21.27	*			3	21.04	*		
4	21.28	*			4	21.19	*	*	
3	21.28	*			2	21.33	*	*	
1	21.46	*	*		1	21.58		*	
5	21.72		*		5	21.67		*	
6	21.74		*		6	21.72		*	
				Rostral breadth					
4	3.72	*			4	3.77	*		
1	3.87	*			1	3.90		*	
3	3.90		*		2	3.96		*	*
2	3.95		*	*	3	3.97		*	*
5	4.02		*	*	6	4.01		*	*
6	4.11			*	5	4.11			*
				Length of nasals					
4	14.03	*			4	14.20	*		
1	14.47	*			3	14.33	*		
3	14.48	*			5	14.43	*	*	
5	14.52	*	*		1	14.52	*	*	
2	14.56	*	*		2	14.54	*	*	
6	14.89		*		6	14.81		*	
				Least supraoccipital breadth					
4	2.44	*			4	2.50	*		
3	2.49	*			3	2.53	*		
1	2.62	*	*		1	2.56	*		
2	2.77	*	*	*	2	2.75	*	*	
5	2.77		*	*	5	2.86		*	
6	2.87			*	6	3.00		*	

TABLE 2.— *Continued.*

Males				Females			
Group	Means	MRT		Group	Means	MRT	
			Bullar-premaxillary length				
2	36.27	*					
1	36.51	*					
5	36.54	*			NS		
3	36.54	*					
4	36.62	*					
6	37.15		*				
			Basal length				
2	28.64	*		3	28.58	*	
4	28.89	*		4	28.81	*	
1	28.94	*		2	28.87	*	
3	28.96	*		1	29.04	*	
5	29.08	*		5	29.21	*	*
6	29.67		*	6	29.55		*
			Length of diastema				
2	8.81	*		3	8.76	*	
1	8.82	*		1	8.82	*	
3	8.93	*		4	8.82	*	
4	8.96	*		5	8.90	*	
5	9.01	*		2	8.90	*	
6	9.25		*	6	9.16		*
			Length of maxillary toothrow				
2	5.12	*		4	5.08	*	
4	5.12	*		2	5.11	*	
3	5.14	*		3	5.13	*	
5	5.15	*		1	5.18	*	
1	5.32		*	6	5.39		*
6	5.34		*	5	5.40		*

pooled geographic localities as the main effect and, if significant differences were present, to *a posteriori* multiple range tests. Finally, a discriminant function analysis (DFA-program DISCRIMINENT) was utilized to ascertain how well the geographic groupings were discriminated from each other as well as to determine to which group the individuals treated as unknown were most closely associated.

Eight of the 13 characters were significant ($P = 0.05$) for both males and females. Additionally, males exhibited significance in postorbital constriction and bullar-premaxillary length ($P = 0.05$), whereas females did not ($P = 0.05$) (see Table 2). Characters found to be significant were then subjected to three multiple range tests (Duncans, Student-Newman-Keuls, and Scheffes) to identify which of the groups formed maximally nonsignificant subsets.

The results of the multiple range tests demonstrated kangaroo rats in group 6 (see Fig. 1) to be significantly different from those in the three groups (1, 2, and 4) from the Llano and group 3 from south of the Llano. Group 5 appeared to be an intermediate group. Groups 1 through 4 formed subsets for seven of 10 characters for males and six of eight characters for females. Rats in group 6 were consistently the largest for most characters (nine of 10 characters for males and six of eight in females), and it was isolated as a subset for three characters (bullar- premaxillary length, basal length, and length of diastema) in males and one in females (diastema). Group 6 was a member of two subsets for only one character in males (postorbital constriction) and females (rostral breadth). *D. ordii* in group 5 constituted the second largest specimens for most of the characters, being identified in overlapping subsets with six and the other groups for four characters in males, and five characters in females, suggesting it is an intermediate group in that it shows some characteristics of both group 6 and the other groups to the south and west. Interestingly, group 4 was the nearest geographically to group 5 but contained the smallest specimens for most mensural characters. Results of Student-Newman-Keuls *a posteriori* multiple range test are presented in Table 2.

The fact that group 6 did not overlap in the majority of the subsets indicates that this group is significantly different from the others. The difference can be attributed partly to the geographic distance from the other groups and also to the fact that 6 is isolated north of the Canadian River and its breaks. Group one, recognized as representing *D. o. richardsoni* by Hall (1981), clearly showed a greater similarity to groups to the south that currently are regarded as *medius*.

The DFA classified males correctly 55 percent of the time or better in all groups except group 3, in which only 26 percent of the individuals were classified correctly. Males and females from group 3 were dispersed relatively evenly among the other groups, suggesting that group 3 represents an heterogenous population. The groups with the highest correct classification were groups 5 and 6, in which 70 and 74 percent were correctly classified, respectively. Females were more heterogenous than males; there were only two groups in which more than 50 percent of the individuals were correctly classified (groups 4 and 6). The results of DFA are presented in Table 3.

Locations of specimens treated as unknown in relation to the pooled groups are shown in Figure 1. Sixty-five percent of all individuals

TABLE 3.—*Results of discriminant function classification using the six sample groups. Columns are the groups into which selected individuals were classified and rows are the groups to which the same individuals belong.*

Group	1	2	3	4	5	6
			Males			
1	29	5	4	8	3	4
2	2	8	1	2	1	0
3	6	7	10	6	6	4
4	2	0	2	12	2	1
5	1	0	0	2	12	2
6	1	1	0	0	4	17
			Females			
1	23	8	3	15	4	5
2	2	2	5	3	1	3
3	3	6	10	5	2	2
4	2	2	1	6	1	0
5	1	1	1	1	5	3
6	2	4	0	0	4	15

from north of the Canadian River were classified with group 6, with an additional 19 percent assigned to group 5; only four individuals were assigned to groups on the Llano. Individuals obtained from the Llano were classified with groups on the Llano or with group 3 from south of the Llano 55 percent of the time. Specimens from along the eastern margin of the Llano Estacado, on and off the caprock, were divided between groups on the Llano and groups 5 and 6. For example, Garza County samples from on and off the caprock were divided between groups 1 and 3 and 5 and 6. There was no particular pattern in assignment of individuals in that kangaroo rats from both on the caprock and east of it were assigned to groups centered on and off the Llano. However, those individuals from locations farthest east of the Llano were classified primarily with groups 5 and 6. For example, a sample of 13 individuals from Wichita and Wilbarger counties, which are located on the eastern margin of the currently recognized distribution of *D. o. richardsoni*, had only one individual (a female) that was not classified as belonging to group 5 or group 6. Also, individuals from Childress and Collingsworth counties were classified with group 6 almost exclusively. Unknown animals from south of the Llano Estacado were classified with all groups at about the same frequency, probably due the heterogenous nature of these populations as exemplified by group 3.

The results of these data indicate that there is a significant difference between populations of *D. ordii* on the Llano south of the Canadian

River and those to the north, and that these are not members of the same subspecies. Furthermore, populations from south of the Canadian River on the Llano currently recognized as *D. o. richardsoni* (see Hall, 1981) exhibit traits that more closely resemble *D. o. medius*. Kangaroo rats from east of the Llano Estacado exhibit traits similar to those of *richardsoni* even though there is a zone where intermediate individuals occur. It is here proposed that the boundary between the two subspecies in Texas be redefined as the northern and eastern boundaries of the Llano Estacado, and that the subspecific name *medius* be used henceforth to include all populations on the Llano Estacado that previously were referred to as *richardsoni*. Those populations from east of the Llano that previously were referred to as *medius* should be assigned to *richardsoni*. To the southwest, the Llano merges with the Monahans Sand Hills and probably does not pose a barrier to gene flow between kangaroo rats on the Llano and those to the southwest. The southern boundary of the Llano merges with the Edwards Plateau where an area of unsuitable habitat separates populations east of the Llano from those to the southwest, and we propose that this also be recognized as a point of separation between the two subspecies.

Accounts of Subspecies

Dipodomys ordii medius Setzer

Dipodomys ordii medius Setzer, Univ. Kansas Publ., Mus. Nat. Hist., 1:519, 1949. Holotype from Santa Rosa, Guadalupe Co., New Mexico.

Distribution.—In Texas, from the northern boundary of the Llano Estacado south at least to the Pecos River, and from eastern New Mexico to the breaks on the eastern margin of the Llano.

Comparisons.—Compared to *D. o. richardsoni*, geographically adjacent to the north and east, *D. o. medius* is smaller in overall external measurements and all cranial measurements except postorbital constriction. Respective means of selected cranial measurements for adult males and adult females are: greatest length skull, 39.41, 39.45; maxillary breadth, 21.37, 21.38; basal length, 28.79, 28.96; and length of diastema, 8.89, 8.82.

Remarks.—Schmidly (1971) noted that specimens from Needmore, Bailey Co., Texas (part of group 1 on Fig. 1), located on the Llano Estacado, were intermediate between specimens from north of the Canadian River and those he examined from localities to the south of Needmore. He did note, however, that the Needmore population was

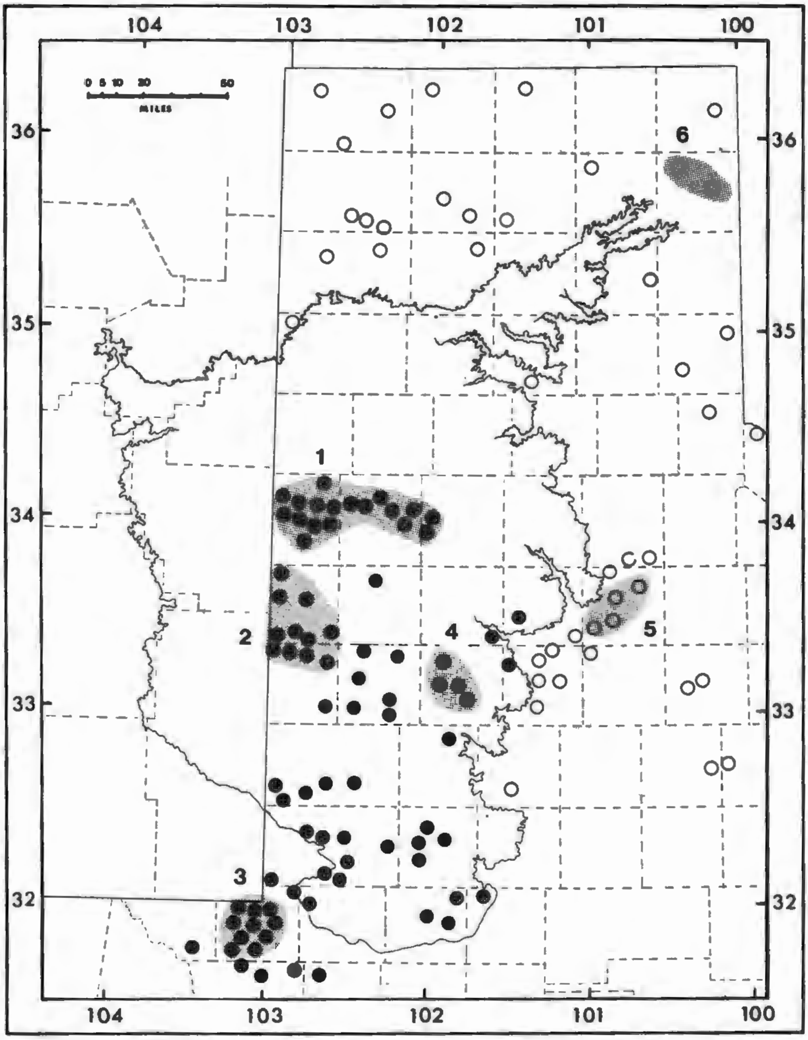

FIG. 1. Map of the Llano Estacado and adjacent regions showing the location of places from which specimens were examined (dots), and the areas encompassed by the six pooled samples (see text). Solid symbols represent *Dipodomys ordii medius*, whereas open symbols denote *D. o. richardsoni*.

significantly different from the population north of the Canadian. Specimens from both locations were examined during this study and specimens from Needmore showed no affinity for samples from north or east of the Llano. Rats in the sample from the Muleshoe Sand Hills and vicinity resemble *richardsoni* only in maxillary breadth in both males and females and in length of maxillary toothrow in males. Some individuals in group 3 from the Monahans Sand Hills did resemble *richardsoni* in some features, but this population is isolated from that race by the Llano Estacado to the north and the northwestern part of the Edwards Plateau to the east.

Specimens examined.—Total of 920, all from Texas and housed in The Museum of Texas Tech University. ANDREWS Co.: 1 mi. S Frankel City, 1; *1 mi. S, 1 mi. E Frankel City*, 2; *4 mi. N, 9 mi. W Andrews*, 1; 4 mi. N, 3-5 mi. E Andrews, 4; 3 mi. N, 10-11 mi. W Andrews, 3; *5-6 mi. S, 6 mi. E Andrews*, 7; *7 mi. S, 3-4 mi. E Andrews*, 3; 8.5 mi. S, 4 mi. E Andrews, 2; 14 mi. S Andrews, 1; 18 mi. N, 2 mi. E Kermit, 2. BAILEY Co.: 7 mi. N Muleshoe, 17; 0.5-2.5 mi. S, 18 mi. W Muleshoe, 4; *2 mi. S, 10 mi. W Muleshoe*, 4; *3.2 mi. S, 2.7-3.1 mi. W Muleshoe*, 2; *4 mi. SW Muleshoe*, 1; 4 mi. S Muleshoe, 1; *4 mi. S, 1-2 mi. W Muleshoe*, 15; *4 mi. S, 1 mi. E Muleshoe*, 1; *5 mi. S, 18 mi. W Muleshoe*, 4; 5.5 mi. S, 10 mi. W Muleshoe, 4; 6 mi. S, 1-3 mi. E Muleshoe, 24; 8.5 mi. S, 16.5 mi. W Muleshoe, 2; 9.5 mi. S, 13 mi. W Muleshoe, 15; 9.5 mi. S, 8.5-9 mi. W Muleshoe, 2; 3.5 mi. N Needmore, 62; *3.5-5.7 mi. S, 2-2.7 mi. W Needmore*, 12; Muleshoe Nat. Wildlife Refuge, 6. COCHRAN Co.: 18 mi. W Morton, 2; 1 mi. W Bledsoe, 1; 2 mi. E Lehman, 1; 1-2.5 mi. W FM 1780 on FM 1585, 4; 13 mi. S Lehman, 3; 5 mi. E State Hwy. 214, 6 mi. S FM 1585, 5; 11 mi. N Bronco, 4. CRANE Co.: 17 mi. N, 19 mi. W Crane, 1; *FM 1053, 5 mi. S Interstate 20*, 1; *5 mi. N, 17 mi. W Crane*, 7. CROSBY Co.: 12.5-13.5 mi. S, 1.1-2.1 mi. W Ralls, 8. DAWSON Co.: 9 mi. N, 4 mi. E Lamesa, 2. ECTOR Co.: 4 mi. N Notrees, 1. GAINES Co.: 4 mi. S, 9 mi. E Seminole, 4; 5 mi. S Seminole, 1; 7 mi. S, 10.3 mi. W Seminole, 3; 10 mi. S, 20 mi. W Seminole, 1; *unidentifiable locality*, 1. GARZA Co.: 6 mi. S Southland, 2; *no specific locality*, 1. GLASSCOCK Co.: 0.5 mi. S, 11 mi. W Lees, 2. HALE Co.: 0.5 mi. N, 12 mi. W Hale Center, 1; 4-4.5 mi. N, 5.5 mi. W Cotton Center, 12. HOCKLEY Co.: *10 mi. N, 0.5 mi. W Levelland*, 2; 12 mi. N Levelland, 4. LAMB Co.: *4-5.5 mi. S, 2.5 mi. E Earth*, 27; 6-6.5 mi. S Springlake, 9; 7.2-7.6 mi. S Earth, 5; 6-7.5 mi. N Sudan, 6; *7 mi. S Olton*, 5; 8-8.5 mi. S, 1-2 mi. E Olton, 3; 6.5 mi. N, 0.5 mi. E Fieldton, 1; *3-4 mi. N Fieldton*, 30; *14.1 N Littlefield*, 1; 10.6 mi. N Spade, 2. LOVING Co.: 2 mi. N, 5 mi. E Mentone, 3; *4.1 mi. E Mentone*, 1; *8.5 mi. E Mentone*, 2. LUBBOCK Co.: *1 mi. E Tahoka Hwy.*, 1; 3.5 mi. N Slaton, 1. LYNN Co.: 3 mi. S New Home, 4; 6 mi. W Tahoka, 2; *2.6 mi. W Tahoka*, 1; Tahoka, 8; *3.5 mi. S Tahoka*, 1; *6.5 mi. SW Tahoka*, 3; 7 mi. SW Tahoka, 64; *5 mi. S, 3-4 mi. W Tahoka*, 7; *5 mi. S Tahoka*, 4. MARTIN Co.: 7 mi. N, 1 mi. E Tarzan, 3; 15 mi. S Flower Grove, 2; 19-19.9 mi. S Patricia, 10; 7 mi. N, 17 mi. W Stanton, 1. MIDLAND Co.: 6.5 mi. S, 1 mi. E Stanton, 2; 7 mi. SE Midland, 1; 5 mi. S, 15 mi. E Midland, 1. TERRY Co.: 3.5 mi. N, 12 mi. W Meadow, 2; *3.5 mi. N, 10 mi. W Meadow*, 2; 3 mi. S, 2 mi. E Meadow, 2; 4 mi. N Gomez, 1; 2 mi. S, 8 mi. E Brownfield, 1; 2 mi. N, 3 mi. W Wellman, 1; *1 mi. S Wellman*, 1; *10 mi. S Brownfield*, 1; 12 mi. S, 2 mi. E Brownfield, 1. UPTON Co.: *3.5 mi. N, 2.5 mi. E Crane*, 4. WARD Co.: 8.2-8.6 mi. S Wink, 7; *9.5 mi. S Wink*, 6; *9 mi. NE Monahans*, 1; *6 mi. NE Monahans*, 1; *Monahans State Park*, 2; 9 mi. W Monahans, 7; *11 mi. WSW Monahans*, 1. WINKLER Co.: 10 mi. NW Notrees, 1; *6.7 mi. N, 4 mi. W Notrees*, 4; 9.1

mi. NW Kermit, 1; 4.1 mi. N, 5.1 mi. E Kermit, 18; 4 mi. N Kermit, 1; *4 mi. NW Kermit*, 1; *2 mi. N, 3 mi. E Kermit*, 1; 6 mi. W Kermit, 1; vic. Kermit, 1; 6-6.6 mi. E Kermit, 15; *1.6 mi. S Kermit*, 1; 6-6.7 mi. SE Kermit, 52; *7 mi. SW Kermit*, 1; *4 mi. S, 3 mi. E Kermit*, 2; *2.5 mi. NE Winkler County Airport*, 1; *Winkler County Airport*, 109; *6 mi. S Kermit*, 33; *6 mi. S, 2 mi. E Kermit*, 71; Wink and localities within 4.5 mi. thereof, 14; *6.5 mi. E Wink*, 1; 10 mi. S Kermit, 2; 4.7 mi. S, 0.5 mi. W Wink, 11; *6 mi. S Wink*, 3. Yoakum Co.: 8 mi. N Bronco, 3; 7 mi. N, 6.5 mi. E Bronco, 6; *22.9 mi. S, 3.7 mi. E Lehman*, 16; 13-14 mi. N Plains, 16; 9.5 mi. N, 13 mi. E Plains, 1; 6 mi. S, 12 mi. E Plains, 6.

Dipodomys ordii richardsoni (J. A. Allen)

Dipodops richardsoni J. A. Allen, Bull. Amer. Mus. Nat. Hist., 148:317, 1891. Holotype from confluence of Cienquilla and Currumpaw creeks, sec. 32, T. 2 N, R. 2 E, Cimarron Co., Oklahoma (Glass, 1971:498).

Dipodomys ordii richardsoni, Grinnell, J. Mamm., 2:96, 1921.

Distribution. North of the Canadian River breaks that form the northern border of the Llano Estacado, east of the Llano Estacado to the eastern margin of the range of *D. ordii*, and south to the edge of, but not on, the Edwards Plateau.

Comparisons. See account of *D. o. medius*. Means of selected cranial measurements for adult males and adult females are, respectively: greatest length of skull, 40.03, 40.01; maxillary breadth, 21.74, 21.72; basal length, 29.67, 29.55; and length of diastema, 9.25, 9.16.

Remarks.—Although there is no apparent evidence for gene flow between *medius* and *richardsoni* along the northern margin of the Llano Estacado, there is evidence of gene flow between the two races on the eastern margin of the Llano. This may be because the northern boundary between *medius* and *richardsoni* is characterized by inhospitable rocky breaks on both sides of the Canadian River, and the river itself may pose a partial barrier. On the eastern boundary, gene flow may be facilitated by contact through canyons that open off the caprock onto the Rolling Plains to the east. Although *D. ordii* prefers sandy loam soils to deep sandy dunes, Dalquest *et al.* (1990) noted that it is a surprisingly adaptable species. They examined a specimen of *D. o. richardsoni* from an area of extensive volcanic cinders with no apparent soil development, and also noted that a specimen was taken from the north side of Capulin Mountain, New Mexico, in an area with little exposed soil.

Specimens examined.—Total of 435, all from Texas and housed in The Museum of Texas Tech University. Armstrong Co.: 18.5 mi. S, 3 mi. W Claude, 1. Borden Co.: 12 mi. S, 1 mi. W Gail, 1. Childress Co.: 11 mi. N Childress, 1. Collingsworth Co.:

2 mi. N, 9 mi. E Lutie, 9; 1 mi. N, 9 mi. W Wellington, 2. CROSBY Co.: *vic. Crosbyton [White River] Lake*, 1; 2 mi. S White Lake Village, 1. DALLAM Co.: *2 mi. N, 13 mi. E Texline*, 1; 12 mi. E Texline, 11; 10.6 mi. W Stratford, 1; 1 mi. N, 6 mi. W Dalhart, 1. DEAF SMITH Co.: 4.9 mi. S, 4.8 mi. E Glenrio, 1; *7 mi. S, 3 mi. E Glenrio*, 2. DICKENS Co.: 4 mi. S, 5 mi. E Roaring Springs, 2; 6 mi. N, 9 mi. E Dickens, 6; *5 mi. N, 6 mi. E Dickens*, 4; 3.5 mi. N Dickens, 1; 5 mi. N Spur, 2; *3 mi. N, 8 mi. W Spur*, 7; 7-7.5 mi. S, 10-10.5 mi. W Dickens, 76; *1 mi. E FM 836, 1 mi. N FM 2565*, 1. FISHER Co.: 3 mi. E Sylvester, 2; *2 mi. S, 5 mi. E Sylvester*, 2. FOARD Co.: *6 mi. E Thalia*, 12. GARZA Co.: 23-25 mi. S Crosbyton, 3; 9 mi. N Post, 1; *10 mi. E Southland*, 32; *6 mi. N Post*, 1; Post, 1; 7 mi. E Post, 1; 14 mi. S, 1 mi. E Post, 2. GRAY Co.: 11 mi. N McLean, 4. HANSFORD Co.: 13 mi. N Gruver, 1. HARDEMAN Co.: 20.3 mi. N Goodlett, 2. HARTLEY Co.: 11 mi. W Channing, 3; 1.5 mi. S, 6 mi. W Channing, 1; 3 mi. S Channing, 9. HEMPHILL Co.: 7 mi. N Canadian, 11; *Gene Howe Wildlife Manag. Area*, 92; *1.5 mi. N, 13 mi. E Canadian*, 1; 12 mi. E Canadian, 17. HUTCHINSON Co.: 3.5-4.8 mi. NW Sanford, 11; *below dam, 1 mi. N, 1 mi. W Sanford*, 1. JONES Co.: 13 mi. S, 0.5 mi. W Hamlin, 2. KENT Co.: 26 mi. W Girard, 8. LIPSCOMB Co.: 2 mi. N, 8 mi. E Lipscomb, 3. MOORE Co.: 3 mi. S Dumas, 3; 7 mi. S, 14 mi. E Dumas, 1. MOTLEY Co.: 8 mi. S, 9 mi. E Matador, 3; 3 mi. E Roaring Springs, 8; *25 mi. N Dickens*, 1. OLDHAM Co.: 6 mi. W Boys Ranch, 6; 17 mi. N, 1 mi. W Adrian, 1. POTTER Co.: *4 mi. S, 6 mi. W Fritch*, 1; 7 mi. S, 7 mi. W Fritch, 4. ROBERTS Co.: 13-16 mi. S, 11 mi. E Spearman, 19. SHERMAN Co.: 10 mi. N Stratford, 2. STONEWALL Co.: 2 mi. E Swenson, 1; 0.5 mi. S, 0.5 mi. E Peacock, 2. WICHITA Co.: *10 mi. N Electra*, 2; *7.5 mi. N, 2 mi. E Electra*, 2; *1-4 mi. NW Brukburnett*, 4. WILBARGER Co.: *15 mi. N, 1 mi. E Vernon*, 4; *5 mi. N, 6 mi. W Vernon*, 13; *2 mi. N, 1 mi. E Elliot*, 3.

Discussion

The characteristics of two subspecies of *Dipodomys ordii* on the Llano Estacado and in adjacent areas of Texas have been examined and redefined. The two are differentiated principally on the basis of cranial dimensions. Specimens from north of the Canadian River are significantly larger than those from the Llano Estacado to the south, indicating that populations in these two areas are effectively isolated from each other. The Canadian River itself does not appear to be a hindrance to gene glow in the area to the east of the Llano because there are no significant differences between specimens from the two sides of the river there. Kangaroo rats from south of the river near the Oklahoma border as well as those from near the eastern boundary of the distribution of *D. o. richardsoni* in Texas clearly should be classified with *richardsoni*, showing little if any affinity to *medius*.

There is a zone of intergradation recognized along the southern part of the eastern boundary of the Llano. Those specimens from east of the Llano are now recognized as *richardsoni*; they average larger than rats from the Llano. Those specimens from atop the Llano that previously were assigned by Setzer (1949) to *richardsoni* are herein recognized as *medius*.

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Addressses of authors: *Division of Range Animal Science, Sul Ross State University, Alpine, Texas 79832 (RNR); Department of Biological Sciences, Central Connecticut State University, New Britian 06050-4010 (RRH); and The Museum and Department of Biological Sciences, Texas Tech University, Lubbock 79409-3191 (JKJ).* *Received 18 March 1992; accepted 13 May 1992.*

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