GENETIC VARIATION IN THE TEXAS KANGAROO RAT, *DIPODOMYS ELATOR* MERRIAM

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ABSTRACT.—Electrophoretically detectable genetic variation for 19 enzymes and one non-enzymatic protein encoded by 29 loci was analyzed in 95 specimens of five species of kangaroo rats (*Dipodomys*). Six loci were polymorphic in *Dipodomys elator* and an additional 12 loci exhibited interspecific variation in *D. elator, D. merriami, D. spectabilis, D. ordii,* and *D. phillipsii. D. elator* has previously been reported as showing variability at one locus. Coefficients of genetic distance for conspecific populations of *D. elator* range from 0.028 to 0.039. *F*-statistics for *D. elator* indicated significant differentiation for three loci with an overall mean F_{ST} of 0.102. Interspecific coefficients of genetic distance ranged from 0.130 to 0.314. Relationships among the five species of *Dipodomys* indicate that *D. elator* is more similar to *D. phillipsii* than to *D. spectabilis, D. merriami,* or *D. ordii.* These results are contrary to some previous studies that placed *D. elator* in the *spectabilis* group.

The Texas kangaroo rat, *Dipodomys elator,* is known from nine counties in north-central Texas (Carter et al., 1985) and from one locality in southwestern Oklahoma (Bailey, 1905). *D. elator* is currently listed as threatened by the Texas Organization for Endangered Species and as protected by the Texas Department of Parks and Wildlife (Roberts and Mills, 1983). Within the past 50 years, habitat available to *D. elator* has been greatly reduced by clear-cutting and brush control.

Studies of *D. elator* have addressed distribution (Bailey, 1905; Blair, 1954; Dalquest, 1968; Martin and Matocha, 1972), reproduction (Webster and Jones, 1985), behavior (Packard and Roberts, 1973), ecology (Roberts and Packard, 1973), morphology (Best 1987; Webster and Jones, 1985), systematics (Best and Schnell, 1974; Dalquest and Collier,1964; Davis, 1942; Grinnell, 1922; Lidicker, 1960*a*, 1960*b*; Schnell et al., 1978; Setzer, 1949; Stock, 1974).Although there has been no extensive investigation of genetic variability within and among populations of *D. elator,* Johnson and Selander (1971) conducted an electrophoretic analysis of *D. elator* ($n = 23$) and 10 other species of *Dipodomys*. On the basis of their analysis of 17 enzymes and other proteins they concluded that *D. elator* was not closely related to any of the other species examined. Stock (1974) studied chromosomal evolution in the genus *Dipodomys* and Mazrimas and Hatch (1972) determined the amount of satellite DNA in *D. elator*. Both studies were unable to draw systematic conclusions concerning the relationship of *D. elator* to other species of *Dipodomys*.

Despite numerous systematic studies, the placement of *D. elator* within the genus *Dipodomys* has proved difficult. There are three major schools of thought concerning this question. Most studies have suggested that *D. elator* is either closely related to the *phillipsii* group or the *spectabilis* group (Best and Schnell, 1974). In contrast, several studies have suggested that *D. elator* is not closely related to the *phillipsii* or *spectabilis* groups (Best and Schnell, 1974; Blair, 1954; Lidicker, 1960*b*). Blair (1954) indicated that the baculum of *D. elator* is more similar to that of *D. merriami* than to *D. spectabilis*.

The rarity of the Texas kangaroo rat, threat of habitat destruction, and lack of information concerning the genetic structure of the species make *D. elator* an interesting and valuable subject for study. The purposes of this study were to investigate genetic variability within and among populations of *D. elator* and to determine the relationship of *D. elator* to *D. ordii, D. merriami, D. phillipsii,* and *D. spectabilis*.

Materials and Methods

Dipodomys elator ($n = 21$) were live-trapped from seven localities in Texas on 12–13 March 1985. Specific localities were as follows: *Wilbarger Co.:* 2 mi. W Harrold ($n = 7$); *Wichita Co.:* 2 mi. W, 5 mi. N Iowa Park ($n = 2$); 9 mi. N Iowa Park ($n = 2$); *Hardeman Co.:* 4.1 mi. N, 3 mi. W jct. FM 2006 and US 287 ($n = 1$); 3.8 mi. N, 1.8 mi. E jct. FM 2006 and US 287 ($n = 3$); 3.5 mi. N, 2 mi. E jct. FM 2006 and US 287 ($n = 1$); 3.2 mi. N jct. FM 2006 and US 1287 ($n = 5$). Specimens are preserved as standard museum specimens (skin and skeleton) and are deposited in The Museum, Texas Tech University, Lubbock, Texas (TTU).

Liver, heart, and kidney samples were taken, labeled and immediately frozen in liquid nitrogen. Subsequently, tissue samples were homogenized in a buffered solution (pH 6.8) of Trizma base and EDTA and stored at −70°C until electrophoresis was performed. In addition to the 21 *D. elator*, samples of *D. ordii* ($n = 25$) from *TEXAS: Hemphill Co.:* 12 mi. E Canadian, Lake Marvin ($n = 1$); *Winkler Co.:* Winkler Co. Country Club ($n = 9$); fenceline S of Winkler Co. Airport ($n = 1$); 4.7 mi. S, 5 mi. W Wink ($n = 2$); *Culberson Co.:* 0.4 mi. SW jct. Hwys 2185 and 2424 ($n = 1$); 16.2 mi. SW jct. Hwys 2185 and 2424 ($n = 1$); *Yoakum Co.:* 23 mi. NE Plains ($n = 4$); *Oldham Co.:* 6 mi. W Boys Ranch Hq. ($n = 1$); *NEW MEXICO: Lincoln Co.:* Coyote ($n = 1$); 6.5 mi. N, 3 mi. W Carrizozo ($n = 1$); *DeBaca Co.:* 16 mi. S, 3 mi. E Taiban ($n = 3$); *D. merriami* ($n = 21$) from *TEXAS: Winkler Co.:* fenceline S of Winkler Co. Airport ($n = 1$); NW of Winkler Co. Airport ($n = 2$); beneath Winkler Co. Airport flight tower ($n = 1$); *Culberson Co.:* 23 mi. ENE Van Horn ($n = 9$); jct. Hwys 2185 and 2424 ($n = 2$); *Davis Co.:* Ft. Davis St. Park, Franklin Canyon ($n = 1$); *ARIZONA: Maricopa Co.:* 7.0 mi. N Gila Bend on Hwy 85 ($n = 2$); 20 mi. N Phoenix ($n = 1$); *NEW MEXICO: Socorro Co.:* 28 mi. S, 32 mi. W Socorro ($n = 2$); *D. spectabilis* ($n = 21$) from *TEXAS: Culberson Co.:* 23 mi. ENE Van Horn ($n = 2$); 0.4 mi. SW jct. Hwys 2185 and 2424 ($n = 1$); jct. Hwys 2185 and 2424 ($n = 2$); *NEW MEXICO: Lincoln Co.:* 4 mi. N, 3 mi. W Carrizozo ($n = 1$); *San Miguel Co.:* 13 mi. NE Anton and Chico ($n = 1$); *Socorro Co.:* 28 mi. S, 32 mi. W Socorro ($n = 1$); *Valencia Co.:* 1.5 km S, 13 km E jct. Hwys 6 and 47 ($n = 5$); 9.1 km S, 16.8 km E, jct. Hwys 6 and 47 ($n = 1$); 1.3 km S, 14.5 km E jct. Hwys 6 and 47 ($n = 4$); 1.6 km S, 15.2 km E jct. Hwys 6 and 47 ($n = 3$); and *D. phillipsii* ($n = 7$) from *MEXICO: Zacatecas,* 6.1 mi. S, 6.0 mi. E Villa de Cos ($n = 1$); *San Luis Potosi,* Las Cabras, 4.6 mi. NW Bledos ($n = 6$) were prepared in the same manner.

Tissue homogenates were analyzed using standard starch-gel electrophoretic techniques (Harris and Hopkinson, 1977; Selander et al., 1971). Of 29 loci examined, six were polymorphic in *D. elator* (frequency of the common allele in at least one population <0.99); creatine kinase-4 (Ck-4), glutamate oxaloacetate transaminase-1 and -2 (Got-1, -2), peptidase-D (Pep-D; substrate used was phenylalanyl-L-proline), phosphoglucomutase-3 (Pgm-3), and 6-phosphogluconate dehydrogenase (6-Pgd). An additional 12 loci were found variable over all five species: aconitase-2 (Acon-2), albumin (Alb), Ck-2, esterase-2 (ES-2), alpha-glycerophosphate dehydrogenase-1 (α-Gpd-1), hexokinase (Hk), isocitrate dehydrogenase-2 (Icd-2), lactate dehydrogenase-2 (Ldh-2), mannose phosphate isomerase-1 (Mpi-1), Pgm-2, superoxide dismutase (Sod), and sorbitol dehydrogenase (Sdh). No variability was observed for 11 loci: Acon-1, catalase, Ck-1 and -3, Icd-1, malate dehydrogenase-1 and -2, nucleoside phosphorylase, Pep-A (substrate used was glycine-leucine), and Pgm-1. Pgm-3 was variable for all five species, but was not consistently scorable and therefore not included in the interspecific comparisons. In designating allelic differences for polymorphic loci, the common allele was designated as the "100" allele and additional alleles were numbered according to the mobility of their products relative to that of the common allele.

To analyze genetic variation within *D. elator*, animals from the seven localities were combined into three groups based on watersheds as described by Best (1987) (1-Wilbarger County, 2-Wichita County, 3-Hardeman County). Observed genotypic counts were used in calculation of Hardy-Weinberg statistics and estimates of heterozygosity values (H). Genetic variation among and within populations was analyzed by using F-statistics (Nei, 1977; Nei and Chesser, 1983; Wright, 1965). Genetic distances between each pair of populations of *D. elator* were calculated from data on allelic frequency (Nei, 1972; Rogers, 1972).

Relationships among *D. elator, D. ordii, D. spectabilis, D. merriami,* and *D. phillipsii* were analyzed by genetic distances (Nei, 1972; Rogers, 1972) and summarized in the form of a distance dendrogram obtained from the UPGMA (unweighted pair group method using arithmetic averages; Sneath and Sokal, 1973) clustering method. Phyletic relationships were also summarized in the form of an unrooted tree produced by a Fitch-Margoliash analysis of the distance matrix (Fitch and Margoliash, 1968).

Results

Allelle frequencies for the six polymorphic loci of *D elator* are presented in Table 1. *D. elator* has previously been reported as showing variability at only one locus, Got-1 (Johnson and Selander, 1971); however Ck-4 and Pep-D were not analyzed in their study. Genetic distances indicated

TABLE 1.—*Allelic frequencies of six variable loci for* Dipodomys elator *from three localities in north-central Texas. See text for locus abbreviations. The common allele is designated as the "100" allele and additional alleles are numbered according to the mobility of their products relative to that of the common allele. Alleles not listed in the table are as follows: CK-4-95, Got-1-90, Got-2-90, Pep-D-107, Pgm-3-90, and 6-Pgd-90.*

Location	No. in sample	Ck-4	Got-1	Got-2	Pep-D			Pgm-3	6-Pgd
		100	100	100	105	100	95	100	100
Wilbarger Co.	7	1.000	0.929	0.857	0.143	0.714	0.000	0.786	0.857
Wichita Co.	4	1.000	1.000	0.750	0.000	1.000	0.000	1.000	1.000
Hardeman Co.	10	0.700	0.700	0.800	0.000	0.900	0.100	0.950	1.000

a high degree of similarity for *D. elator* from the three locations. Nei's (1972) distances between locations 1 and 2, 1 and 3, and 2 and 3 were 0.005, 0.009, and 0.007, respectively. Rogers' (1972) distances values between locations 1 and 2, and 2 and 3 were 0.028 and 0.029, respectively, whereas the distance between 1 and 3 was 0.039.

Significant ($P < 0.05$) deviations from Hardy-Weinberg proportions were observed, with the Got-2 locus significant at all three locations. In addition, 6-Pgd and Pep-D were significant at location 1 and the Ck-4 locus was significant at location 3. These deviations from Hardy-Weinberg were a result of heterozygote deficiencies for the four loci. Because of small samples we used the *F*-statistics of Nei and Chesser (1983). F_{IS}, which is the correlation of alleles coming together to form an individual within a subpopulation, can range from a value of -1 to $+1$. F_{IS} values calculated for *D. elator* ranged from 0.107 to 1.000 with an overall mean value of 0.769. Significant F_{ST} values were reported for three of the six polymorphic loci of *D. elator* (Got-1, Pep-D, Ck-4). Values ranged from 0.085 to 0.193 with an overall mean F_{ST} value of 0.102. This value indicates significant differentiation among the three locations sampled and of the total amount of genetic variation found in *D. elator*, 10% ($F_{ST} = 0.102$) is attributable to differences among populations and 90% is due to variation within populations.

Allelic frequencies for the five species of *Dipodomys* are presented in Table 2. Rogers' (1972) distance values and Nei's (1972) identity values for interspecific comparisons of *Dipodomys* are given in Table 3. Genetic distance relationships among the five species of *Dipodomys* are summarized in the form of a distance dendrogram (Fig. 1). Based on the electrophoretic data, *D. elator* is more similar to *D. phillipsii* than to *D. merriami*, *D. ordii*, or *D. spectabilis*. *D. elator* and *D. phillipsii* cluster together at about 0.130, *D. merriami* joins at about 0.195, and *D. spectabilis* and *D. ordii* are the least similar to *D. elator*, clustering at about 0.280. The average value of *H* for the five species of *Dipodomys* is 0.006. Heterozygosity values are as follows: *D. phillipsii* ($H = 0.005$), *D. spectabilis* ($H = 0.0114$), *D. ordii* ($H = 0.007$), *D. merriami* ($H = 0.0003$), and *D. elator* ($H = 0.008$). Phyletic relationships were also summarized using a Fitch-Margoliash analysis which generates an unrooted tree that reflects the actual observed genetic distance in the lengths of the branches (Fig. 2). This analysis also shows *D. elator* to be more closely related to *D. phillipsii* and *D. merriami* than to *D. ordii* or *D. spectabilis*. In relation to the hypothetical taxonomic unit (HTU) created by the Fitch-Margoliash analysis, *D. spectabilis* has diverged the most and *D. elator* and *D. ordii* have diverged the least. Also, *D. elator* and *D. phillipsii* share a common ancestor which diverged subsequent to *D. merriami*, *D. ordii*, and *D. spectabilis*.

DISCUSSION

The *F*-statistics indicate that significant differentiation has occurred among populations of *D. elator*. The average differentiation was about 10% which is comparable to differentiation among prairie dogs (10%—Chesser, 1983), moose (9%—Ryman et al., 1980) and house mice from different populations (12%—Nei, 1975). High positive F_{IS} values, such as those reported here, are usually an indication of inbreeding or Wahlund (1928) effect. However, the lack of hetero-

TABLE 2.—*Allelic frequencies of 17 variable loci for five species of* Dipodomys. *See text for locus abbreviations. The common allele is designated as the "100" allele and additional alleles are numbered according to the mobility of their products relative to that of the common allele. Alleles not listed in the table are as follows: Acon-2-95, Alb-105, Ck-2-105, Ck-4-98, Es-2-110, Got-1-105, Got-2-95, α-Gpd-1-105, Hk-98, Icd-1-110, Ldh-2-107, Mpi-1-95, Pep-D-107, 6-Pgd-102, Pgm-2-95, Sod-110, Sordh-110.*

Locus	Allele	*D. phillipsii* $n = 7$	*D. elator* $n = 21$	*D. merriami* $n = 21$	*D. spectabilis* $n = 21$	*D. ordii* $n = 25$
Acon-2	100	1.00	1.00	1.00	0.00	1.00
Alb	100	1.00	1.00	1.00	1.00	0.00
Ck-2	100	1.00	1.00	0.95	0.00	1.00
Ck-4	100	1.00	0.86	1.00	1.00	1.00
Es-2	95	0.57	0.00	0.00	0.00	0.20
	100	0.29	0.00	1.00	0.00	0.80
	104	0.14	0.00	0.00	1.00	0.00
Got-1	100	0.14	0.17	0.95	0.00	0.96
	110	0.86	0.83	0.05	0.00	0.04
Got-2	100	0.86	0.80	0.85	0.90	0.84
α-Gpd-1	100	0.36	1.00	0.95	0.95	1.00
	110	0.00	0.00	0.05	0.05	0.00
Hk	100	1.00	1.00	0.00	1.00	1.00
Icd-1	100	1.00	1.00	0.95	0.93	1.00
Ldh-2	95	0.29	0.00	0.00	0.00	0.04
	100	0.29	0.00	0.90	1.00	0.96
	105	0.43	1.00	0.05	0.00	0.00
Mpi-1	100	0.50	1.00	0.90	0.98	0.72
	105	0.50	0.00	0.10	0.00	0.00
Pep-D	95	0.00	0.05	0.05	0.00	0.04
	100	1.00	0.85	0.95	0.88	0.96
	105	0.00	0.05	0.00	0.05	0.00
6-Pgd	98	0.00	0.95	0.52	0.00	0.00
	100	0.93	0.05	0.48	0.00	0.98
	105	0.00	0.00	0.00	1.00	0.00
Pgm-2	100	1.00	1.00	1.00	0.00	0.00
Sod	100	1.00	1.00	1.00	0.00	0.00
Sordh	100	1.00	1.00	0.00	1.00	1.00

zygotes for the Got-2, Pep-D, 6-Pgd, and Ck-4 loci, as well as the small samples, have probably inflated the F_{IS} values; thus they are not indicative of inbreeding.

Rogers' distance values between populations of *D. elator* are quite low. There are several explanations for this high genetic similarity. Gene flow between populations may be sufficient to maintain high similarity, or perhaps populations of *D. elator* have not been separated for a sufficient period of time to have developed a great amount of genetic distance. In their electrophoretic analysis of *Dipodomys*, Johnson and Selander (1971) analyzed one population (Texas: Wichita County) of *D. elator;* therefore, we have no information for meaningful comparison to our results.

Rogers' distance values between the five species of *Dipodomys* ranged from 0.130 to 0.314 with the least disparate pairwise divergence values occurring between *D. phillipsii* and *D. elator*

Table 3.—*Coefficients of genetic distance* (D; *Rogers, 1972) below the diagonal and genetic identity* (I, *Nei, 1972) above the diagonal among five species of* Dipodomys.

	D. elator	*D. phillipsii*	*D. spectabilis*	*D. merriami*	*D. ordii*
D. elator	—	0.906	0.721	0.829	0.769
D. phillipsii	0.130	—	0.725	0.844	0.821
D. spectabilis	0.288	0.299	—	0.691	0.792
D. merriami	0.195	0.196	0.314	—	0.805
D. ordii	0.247	0.209	0.221	0.214	—

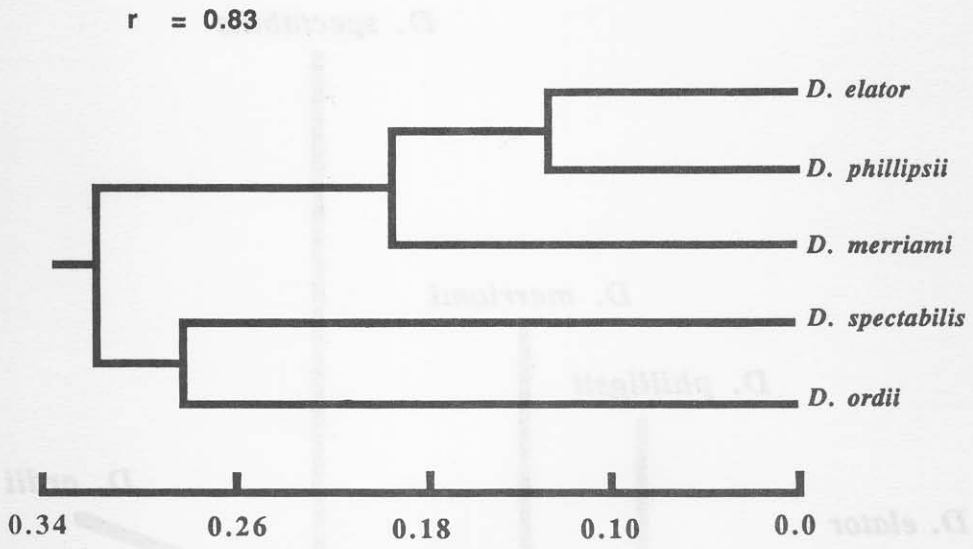

FIG. 1.—Dendrogram depicting relationship of *Dipodomys elator*, *D. phillipsii*, *D. merriami*, *D. spectabilis*, and *D. ordii* derived from UPGMA of Rogers' distance coefficients.

(D = 0.130). In contrast, Johnson and Selander (1971) reported greater amounts of genetic distance between these four species with Rogers' values ranging from 0.34 (*D. spectabilis* vs. *D. ordii*) to 0.64 (*D. elator* vs. *D. spectabilis*). This may be a result of the larger number of loci we analyzed (Gorman and Renzi, 1979). Johnson and Selander (1971) reported *Dipodomys* to have unusually low levels of heterozygosity compared to values reported for continental species of rodents and other organisms. The heterozygosity values reported here are of the same magnitude as those reported by Johnson and Selander (1971) with the exception of *D. merriami*. Johnson and Selander (1971) reported a value of 0.051 as compared to 0.0003 reported in the present study. Johnson and Selander (1971) included four subspecies of *D. merriami* whereas the present study included two. Also, they analyzed the transferrin-1 (Trf-1) locus which contributed a great deal of heterozygosity (10 to 31% of the individuals were heterozygous for this locus). Both of these factors could account for the higher levels of heterozygosity they observed.

Historically, the placement of *D. elator* within the genus *Dipodomys* has varied greatly. Most authors placed the species of *Dipodomys* into "groups" which are essentially equivalent to the subgenera of other taxa (Schnell et al., 1978). Grinnell (1922) assigned *D. elator* to the *phillipsii* group along with the Mexican species *D. phillipsii*. Setzer (1949) recognized six groups, which were based on indices of osteologic differences and visceral arrangements. He merged the *merriami* and *phillipsii* groups of Grinnell and placed *D. elator* next to *D. phillipsii*. Davis (1942) removed *D. elator* from the *phillipsii* group, placed it in a separate group, and suggested it was more closely related to *D. spectabilis* than to *D. phillipsii*. Davis thought the larger size of *D. elator* and the great distance between the ranges of these species warranted this decision. Lidicker (1960*a*) placed *D. elator* in the *spectabilis* group with *D. spectabilis*, *D. nelsoni*, and *D. deserti*. However, he later removed *D. elator* from this group based upon an observation by Blair (1954) who found the baculum of *D. elator* was more similar to that of *D. merriami* than to *D. spectabilis*. Lidicker (1960*b*) concluded that *D. elator* was not particularly close to either the *phillipsii* or *spectabilis* groups, an interpretation supported by bacular data of Best and Schnell (1974). Dalquest and Collier (1964) considered *D. elator* and *D. phillipsii* to be closely related. On the basis of karyotypic data, Stock (1974) supported the alliance of *D. elator* with *D. spectabilis* by Davis (1942) and Lidicker (1960*a*). In contrast, protein variation analysis by Johnson and Selander (1971) suggested that *D. elator* was quite dissimilar to the 10 other species studied, including

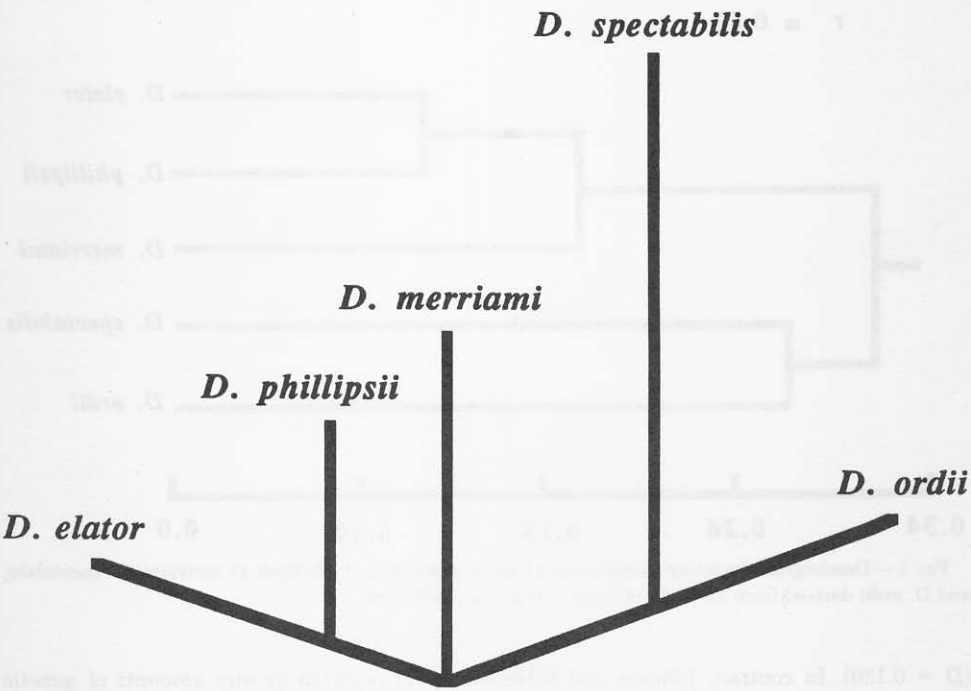

FIG. 2.—Unrooted tree generated by a Fitch-Margoliash analysis based on genetic distance for *Dipodomys elator, D. phillipsii, D. merriami, D. spectabilis,* and *D. ordii.*

D. spectabilis (*D. phillipsii* was not included). Jannett (1976) thought that *D. elator* was an early offshoot in the evolution of the genus and not merely a specialized form to be fitted into a *merriami* or a *spectabilis* group.

Based on our electrophoretic data, *D. elator* should remain in the *phillipsii* group as suggested by Grinnell (1922) and Setzer (1949). Our conclusions do not agree with several studies which placed *D. elator* in the *spectabilis* group (Davis, 1942; Lidicker, 1960*a*; Stock, 1974); it appears that genically, *D. elator* has diverged markedly from *D. spectabilis*. Stock (1974) determined that members of the *merriami* group had the greatest degree of karyotypic modification from the hypothesized ancestral condition and concluded that *D. merriami* evolved separately from the other kangaroo rats for a considerable length of time. Our data indicate there is a close alliance of *D. elator* and *D. phillipsii* with *D. merriami,* as is supported by Blair (1954) and Setzer (1949), and they also indicate that *D. merriami* should be included in the *phillipsii* group.

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