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MACROGEOGRAPHIC PATTERNS OF GENETIC DIFFERENTIATION IN THE POCKET GOPHER *THOMOMYS UMBRINUS*

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Abstract.—Electromorphic and chromosomal variation is analyzed in 26 populations of *Thomomys umbrinus* sampled from throughout the range of the species. Interpopulation levels of genic differentiation are extreme, generally exceeding values measured between conspecific populations of most animals or plants. Two principal groups of *T. umbrinus* are recognized based on chromosomal evidence, one with 2n = 76 chromosomes and the other with 2n = 78. Further, the 2n = 78 group (but not the 2n = 76 group) is bisected into geographic subgroups with respect to chromosome morphology and heterochromatin position. The kind and degree of chromosomal differentiation observed suggests that the three groups may be reproductively incompatible. Allozymic evidence corroborates the above groupings, and an analysis of patterns of allele sharing suggests the absence of gene flow among the groups. A cladistic analysis of electromorphic data indicates that the two 2n = 78 groups may be independently derived from the 2n = 76 lineage. The combined evidence supports the hypothesis that *T. umbrinus* is actually a composite of at least three biological species and confirms the observation that speciation in the genus *Thomomys* is unrelated to the level of genic differentiation between populations. [Evolutionary genetics; geographic variation; evolutionary concordance; pocket gophers; cladistic analysis; paraphyly; speciation.]

Biological species are generally viewed as comprised of populations that are interlinked by gene flow and that share a common ancestor relative to other species (e.g., Mayr, 1963). Indeed, the general relationship between genetic distance and taxonomic distance (Ayala, 1975; Avise, 1976) has been used to support this view. However, studies of pocket gopher populations (*Thomomys*; e.g., Patton and Yang, 1977; Patton, 1981) have shown that speciation and genetic differentiation are largely decoupled in this genus, such that population conspecificity (or lack thereof) cannot be inferred from genetic distance estimates alone. Moreover, as more is learned about the dynamics and mechanics of the speciation process, we should expect to see an increasing number of instances in which certain populations of one species, in fact, are genetically more similar to populations of another (e.g., Sage, 1981). This expectation follows from the observation that genetic distance is largely a function of time and degree of geographic separation of populations (see Soulé, 1976) and is not influenced by cladogenic events (e.g., Avise and Ayala, 1976). It is likely, therefore, that paraphyletic species may be common, perhaps the rule, in naturally occurring organisms (Patton, 1981; Patton and Smith, 1981).

It is not surprising that the above observations have emerged from studies of pocket gophers of the genus *Thomomys;* the genetic demography of natural populations of these animals is perhaps as well known as that of any other vertebrate, with the exception of *Mus* (see references herein and Patton [1981] for general review). Pocket gophers, by virtue of their fossorial habits and requisite restriction to isolated patches of friable soil, are characterized by fragmented distributions of small popu-

lations that show extreme levels of genetic (electromorphic and chromosomal) differentiation. The observation that species status and certain kinds of karyotypic changes in pocket gophers are often correlated has led to the conclusion that the two are causally related (Patton, 1972, 1981, 1985; Nevo et al., 1974; Thaeler, 1985). In contrast, the degree of electrophoretically detectable genetic differentiation appears unrelated to species status (Patton, 1985) but, instead, reflects levels of genetic "connectedness" between populations across geography (Patton and Yang, 1977). Thus, the overall picture in pocket gophers appears to be one of extreme interpopulation genetic differentiation, punctuated by the occasional chance fixation of a chromosomal rearrangement(s) in one population (regardless of its genic distance from others) of sufficient quality and magnitude to constitute a barrier to gene flow. Under this scenario, one would expect to see no relationship between genetic distance and species status in pocket gophers and, to date, none has been found (Patton, 1981; Hafner et al., 1983).

In this study, we examine macrogeographic patterns of electromorphic and karyotypic variation in the southern pocket gopher, *Thomomys umbrinus* (Richardson). This study expands on a previous one of this taxon by Patton and Feder (1978) and, for the first time, presents and assesses patterns of genetic differentiation across the entire geographic range of the species (Fig. 1). We treat *T. umbrinus* as distinct from *T. bottae* based on the cytological studies of Patton and Dingman (1968) and Patton (1973), which document reproductive incompatibility between the species where they meet in southern Arizona.

MATERIALS AND METHODS

We karyotyped 136 individuals from 23 populations using standard in vivo bone-marrow methods (Patton, 1967). Identity of populations sampled and the number and sex of individuals sampled per population are indicated in Table 1 and the Appendix.

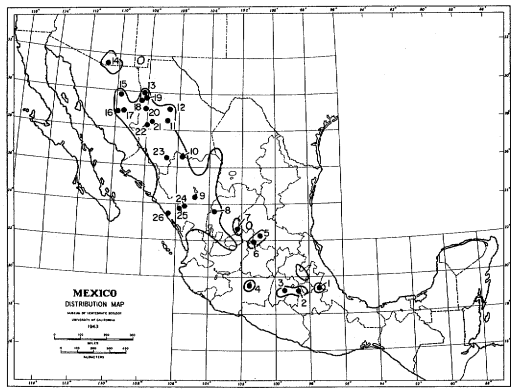

FIG. 1. Map of collecting localities, showing geographic range of *Thomomys umbrinus* (modified from Hall, 1981). Numbers refer to locality identifications given in text.

A total of 461 individuals representing 26 populations was analyzed for electrophoretically detectable protein variation (see Fig. 1 and the Appendix for localities and sample sizes). Blood samples and homogenates of liver and kidney were prepared according to the methods of Selander et al. (1971). Procedures for horizontal starch gel electrophoresis followed those of Selander et al. (1971), as modified by Patton et al. (1972) and Patton and Yang (1977). Nineteen enzymatic and four general proteins were examined as follows (abbreviations and IEC numbers from Harris and Hopkinson, 1976): malate dehydrogenase (MDH-1), MDH-2—1.1.1.37), glycerol-3-phosphate dehydrogenase (GPD—1.1.1.8), lactate dehydrogenase (LDH-1, LDH-2—1.1.1.27), isocitrate dehydrogenase (ICD-1, ICD-2—1.1.1.42), phosphogluconate dehydrogenase (PGD—1.1.1.44), alcohol dehydrogenase (ADH—1.1.1.1), sorbitol dehydrogenase (SORDH—1.1.1.14), glutamate-oxaloacetate transaminase (GOT-1, GOT-2—2.6.1.1), phosphoglucomutase (PGM—2.7.5.1), glucosephosphate isomerase (GPI—5.3.1.9), superoxide dismutase (SOD—1.15.1.1), peptidase [L-leucyl-L-alanine] (PEP-1, PEP-2—3.4.11 or 3.4.13), esterase (ES-1, ES-2—3.1.1.1), erythrocytic protein (Pt-A), prealbumin protein

TABLE 1. Chromosomal variation in *Thomomys umbrinus*.[a]

Locality number[b]	Population	Number of		2n	Autosomes[c]				X	Y
		♂♂	♀♀		SM	ST	A	Dots		
1	Boca del Monte	1	1	78	32	44	0	0	ST	dot
2	Amecameca	1	2	78	36	40	0	0	ST	dot
3	Toluca	0	1	78	36	42	0	0	?	?
4	Patzcuaro	0	1	78	28	48	0	0	?	?
5	Ventura	0	2	78	32	38	2	0	?	?
6	Arriaga	3	0	78	10	26	40	4	ST	dot
7	Ojocaliente	1	1	78	36	36	4	0	ST	dot
10	Las Nieves	1	0	78	34	42	0	0	ST	dot
11	Cuauhtemoc	0	3	78	10	16	52	10	?	?
12	Sierra del Nido	1	1	78	10	14	52	10	ST	dot
13	Colonia Garcia	3	7	78	12	12	52	10	ST	dot
14	Patagonia Mts.	28	43	78	10	10	56	6	ST	dot
15	Moctezuma	1	2	78	10	12	54	6	ST	dot
16	El Novillo	1	0	78	10	12	54	6	ST	dot
17	Bacanora	1	0	78	10	12	54	6	ST	dot
18	Chuhuichupa	0	1	76	42	34	0	0	?	?
19	Valle Moctezuma	0	6	76	42	34	0	0	?	?
21	Tomochic	1	2	76	42	32	0	0	ST	dot
22	Rancho El Pajarito	1	2	76	42	32	0	0	ST	dot
23	El Vergel	1	5	76	20	24	30	0	ST	dot
24	El Salto	0	3	76	40	36	0	0	?	?
25	La Ciudad	1	4	76	40	34	0	0	ST	dot
26	Siqueros	1	2	76	24	32	18	0	ST	dot

[a] Data for localities 6 and 10–25 from Patton and Feder (1978).
[b] Karyotype data not available for localities not included.
[c] SM = meta and submetacentric; ST = subtelocentric; A = acrocentric; dot = microchromosomes.

(preAlb), albumin (Alb), and transferrin (Trf). Alleles at each locus are designated by mobility relative to the most common allele at that locus in *T. bottae* (see Patton and Yang, 1977).

Rogers' (1972) coefficient of genetic similarity (S), Nei's (1971) genetic distance measure (D), and Wright's (1965) F-statistics were calculated using the BIOSYS-1 program of Swofford and Selander (1981). Clustering of similarity and distance matrices was performed using the unweighted pair-group method with arithmetic averages (UPGMA; Sneath and Sokal, 1973) and the method of Fitch and Margoliash (1967).

The electromorphic data set was subjected to a component analysis (Straney, 1980, 1981; Patton and Smith, 1981) to determine the probability of particular patterns of allele sharing (=components) across the taxa in question. This method differentiates between replications of an electromorph distribution that may result from chance associations—hence, having no phylogenetic significance—and those that are significant on a probabilistic basis and, therefore, likely contain phylogenetic information. Under the assumption of randomness in a data set, the probability of a particular component appearing by chance is:

$$p = 1/S_n,$$

where S_n is the number of possible components for n taxa. The probability of observing a given component r times is given by the binomial expansion:

$$b(r) = \binom{m}{r} p^r (1 - p)^{m-r},$$

where r is the number of replications of a given component, m is the number of characters (electromorphs), and $\binom{m}{r}$ is the number of combinations of m things taken r at a time.

All specimens are preserved as standard

museum vouchers and are deposited in the Museum of Vertebrate Zoology. See the Appendix for a list of specimens examined.

RESULTS AND DISCUSSION

Karyology

Chromosomal variation in 23 populations of *Thomomys umbrinus*, based on the analysis of nonpreferentially stained karyotypes, is presented in Table 1. Chromosomal variation in northern and western populations of this species was studied by Patton and Feder (1978); the present study expands this analysis to include populations from the southern and eastern portions of the species' geographic range.

Interpopulational variability.—The overall pattern of chromosomal variation in *T. umbrinus* is changed little from that presented by Patton and Feder (1978). Each population examined has a diploid number of either 78 or 76. Those with 2n = 78 inhabit both desert and forest from Arizona southward to the southern edge of the Mexican Plateau (Fig. 2), while 2n = 76 forms are restricted to the forested regions of the Sierra Madre Occidental in Chihuahua and Durango. A single, lowland population with 2n = 76 (sample 26, Fig. 1) inhabits the tropical deciduous forest of coastal Sinaloa.

Within the populations of *T. umbrinus* with 78 chromosomes, there is a sharp decrease in the number of acrocentric autosomes from Chihuahua south into northern Durango (Fig. 2). Only one southern plateau sample (Arriaga, population 6) possesses a moderately high number of uniarmed autosomes (20 pairs). This north-south gradient in acrocentric number in *T. umbrinus* is similar to, but somewhat more abrupt than, the east-west cline in uniarmed number in *T. bottae* through central Arizona and New Mexico (Patton and Yang, 1977). All but two of the *umbrinus* populations with 76 chromosomes (El Vergel and Siqueros, populations 23 and 26) have totally biarmed autosomal complements. El Vergel specimens have 15 pairs of acrocentrics, and those from Siqueros have nine pairs.

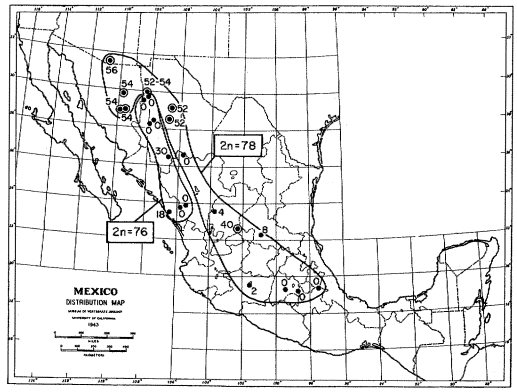

FIG. 2. Diploid number and number of acrocentric autosomes present in individuals representing 23 populations of *T. umbrinus*. Microchromosomes present in individuals from circled localities. See Figure 1 for locality designations.

Microchromosomes (tiny heterochromatic elements) are present in all northern populations with 2n = 78 (populations 11–17, Fig. 2), as well as in the central plateau Arriaga sample (population 6). All other populations of *T. umbrinus* sampled in this study lack microchromosomes, as do all populations of *T. bottae* sampled to date (Patton, 1972).

Reproductive compatibility.—Since pocket gophers possessing different diploid numbers are often unable to interbreed (Thaeler, 1974, 1985), the presence of two different diploid numbers in *T. umbrinus* (2n = 76 and 78) raises the possibility that cryptic species may exist. In addition, banding studies have shown that significant structural chromosomal differences may exist even among *umbrinus* populations with the same diploid number. Although the data are as yet incomplete, the *umbrinus* population in the Patagonia Mts. (population 14, 2n = 78) is known to have interstitial blocks of constitutive heterochromatin, whereas the population at Amecameca (population 2, also 2n = 78) possesses only whole-arm heterochromatin (Barros and Patton, 1985; unpubl. data). Similar differences in the chromosomal localization of heterochromatin (which indicate major structural rearrangements) characterize the complements of *T. umbrinus* and *T. bottae* where

they meet and hybridize in the Patagonia Mts. of southern Arizona. Male F_1 hybrids of these forms are sterile as a result of meiotic imbalances (Patton, 1973). Hence, if the heterochromatic differences within *T. umbrinus* are likewise indicative of significant underlying structural rearrangements, it is very likely that barriers to reproduction exist even between the two groups of 2n = 78 populations, as well as between these and 2n = 76 forms.

The northernmost sample with 2n = 76 (Valle Moctezuma, population 19) was trapped approximately 10 km (airline distance) south of the Colonia Garcia 2n = 78 sample (population 13). Although banding data are not available for these two karyotypes, the gross chromosomal complements are similar to those characterizing 2n = 76 *T. bottae* and 2n = 78 *T. umbrinus* where these taxa hybridize in southern Arizona (Patton, 1973). In the latter case, both the distribution of heterochromatin and degree of structural rearrangements are known, and hybrid sterility has been documented (Patton, 1973; Barros and Patton, 1985). We thus postulate that, if the Valle Moctezuma and Colonia Garcia forms were to contact one another somewhere along the continuously forested habitat between these localities, they would be similarly reproductively incompatible. This hypothesis is supported by the protein evidence (see below and Patton and Feder, 1978) suggesting that genetic introgression between these two populations is absent.

Macrogeographic patterns.—Three geographic units of *T. umbrinus* are thus defined by chromosomal features (Fig. 2). The 2n = 78 assemblage is divisible into northern and southern groups. The northern one (populations 11–17, Fig. 1) is characterized by karyotypes with high numbers of acrocentric autosomes, several pairs of microchromosomes, and (at least in populations 12, 14, and 15) interstitial blocks of heterochromatin. The southern group (populations 1–10, Fig. 1) shows low numbers of acrocentrics, no microchromosomes, and in the Amecameca population (locality 2) whole-arm heterochromatin distribution. Only the population at Arriaga (locality 6) departs from this general pattern. The third chromosomally defined group consists of those populations with 2n = 76 (populations 18–26, Fig. 1), all of which lack microchromosomes and only two of which (localities 23 and 26) possess uniarmed autosomes. The pattern of heterochromatin distribution in these karyotypes is unknown.

Electromorphic Variation

Nineteen of the 23 loci examined electrophoretically were polymorphic in one or more of the populations sampled (Table 2). Five of the variable loci (MDH-1, ICD-2, GOT-2, PEP-2, and Pt-A) were polymorphic in three or fewer populations. Four loci (MDH-2, ICD-1, SOD, and GPI) were monomorphic or showed only minor allelic variation (frequency <0.05) in one or a few populations.

Intrapopulation variability.—Table 2 lists allele frequencies at the 19 polymorphic loci and provides estimates of intrapopulation genetic variability for the 24 populations with sample sizes of six or more individuals. The average number of alleles per locus ranges from 1.09 in the Patzcuaro population (locality 4, Fig. 1) to 1.61 in the Colonia Garcia and Rancho El Pajarito populations (localities 13 and 22). The mean number of alleles per locus per population is 1.29. The proportion of loci polymorphic per population ranges from 4.3% (Patzcuaro) to 39.1% (Rancho El Pajarito). The unweighted mean polymorphism across all 24 populations is 18.3%. The proportion of loci heterozygous per individual per population ranges from 0.8% (Patzcuaro) to 10% (Rancho El Pajarito), with an unweighted mean across all samples of 5.1%. The mean polymorphism value (18.3%) is lower than all values previously reported for *Thomomys* (*T. talpoides*, $P = 23.5\%$ [Nevo et al., 1974]; *T. bottae*, $P = 33.4\%$ [Patton and Yang, 1977]). The mean heterozygosity value (5.1%) is only slightly higher than the lowest mean H value reported for *Thomomys* (*T. talpoides*, $H = 4.7\%$ [Nevo et al., 1974]),

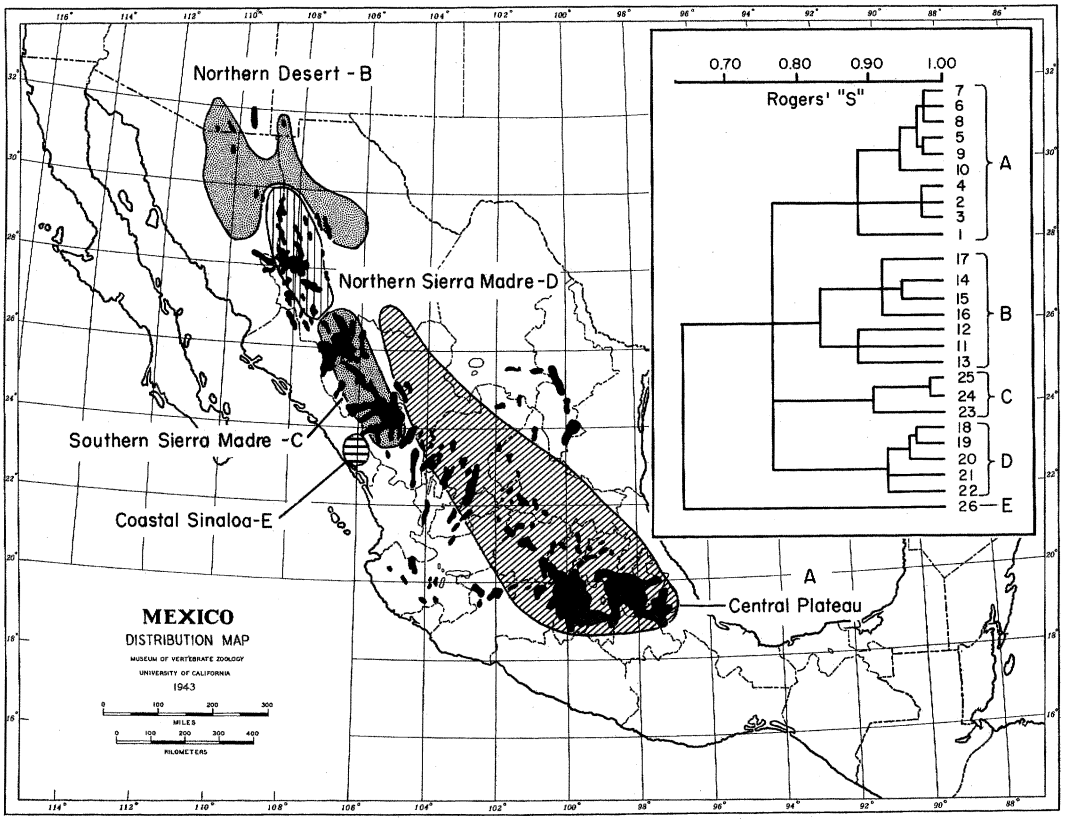

FIG. 3. Major geographic groups within *T. umbrinus* as identified by phenetic clustering of allozyme data by Fitch-Margoliash algorithm. Very short (Rogers' $D < 0.05$) and negative branch lengths are collapsed into a polychotomy linking groups A through D in dendrogram (standard deviation = 14.7%). Darkened areas on map represent regions above 2,100 m elevation. See Figure 1 for locality designations.

but is within the range characteristic of most mammalian species (Nevo, 1979).

Interpopulation variability.—Table 3 lists coefficients of genic similarity and genetic distance for 26 populations of *T. umbrinus* (including populations 6 and 12, for which sample sizes were less than six individuals). In general, these data reveal a pattern of extremely high interpopulation genic differentiation. Genic similarity values range from a high of 0.991 (between Arriaga and Ojocaliente, populations 6 and 7) to a low of 0.610 (between Valle Moctezuma and Siqueros, populations 19 and 26). Although low levels of between-population genic similarity are the general rule for conspecific populations of *Thomomys* (Patton, 1981), several of the *S*-values in Table 3 are lower than any previously reported for the genus. For example, the lowest *S*-values previously measured are 0.67 for *T. bottae* (Patton and Yang, 1977) and 0.70 for *T. talpoides* (Nevo et al., 1974). Moreover, most of the genic similarity values in Table 3 are well below those typically measured between conspecific populations of animals or plants (Selander and Johnson, 1973; Avise, 1976).

Phenetic analysis.—Two phenetic clustering procedures (UPGMA and Fitch-Margoliash) identified the same genetic subgroups within *T. umbrinus*, but linked them differently. The Fitch-Margoliash dendrogram is illustrated in Figure 3, together with a map showing the geographic distribution of the five identified

TABLE 2. Allele frequencies, average number of alleles per locus (*A*), percent polymorphic loci (*P*), and average individual heterozygosity (*H*), in 24 populations of *Thomomys umbrinus* for which sample size is six or larger. Only polymorphic loci listed. Estimate of *P* includes only those loci for which dominant allele has a frequency less than 0.95. Estimate of *H* determined by direct count. Locality numbers refer to Figure 1 and Appendix.

Locus and allele		Population sample										
		1	2	3	4	5	7	8	9	10	11	13
LDH-1	104											
	102	1.0										.04
	100		1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.96
LDH-2	600	.53										
	500							.03	.04			
	224											
	100	.47	1.0	1.0	1.0	1.0	1.0	.97	.96	1.0	1.0	1.0
MDH-1	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	80											
	64											
ICD-2	138											
	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
GOT-1	135	.15										
	119								.08			
	100	.85	1.0	1.0	1.0	1.0	1.0	1.0	.92	1.0	1.0	1.0
	89											
	85											
GOT-2	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.95	1.0
	50										.05	
PGM	145											
	131											.04
	100	1.0	1.0	.88	1.0	1.0	1.0	1.0	1.0	.96	1.0	.96
	69			.12						.04		
	46											
ADH	−121											
	−114	1.0	1.0	.88	1.0	.93	1.0	1.0	1.0	1.0	1.0	.25
	−100			.12		.07						.75
ES-1	106	.85	.72	.95	.94	.32	.09		.08	.27	.13	
	100	.15	.28	.05	.06	.68	.89	.97	.58	.68	.84	.69
	97											
	94						.02	.03	.35	.04	.03	.31
ES-4	110										.08	
	106		1.0	1.0	1.0							
	102											
	100					.98	.96	.91	.92	.86	.32	.17
	96											
	95	1.0				.02	.04		.08	.14	.47	.08
	89							.09			.13	.73
	84											
	80											.02
GPD	181		.11					.18				
	154											.29
	119	1.0	.89	.95	1.0	1.0	1.0	.82	1.0	1.0	.92	.71
	109										.08	
	100			.05								
PEP-1	106							.03			.10	
	100	1.0	1.0	1.0	1.0	1.0	1.0	.82	1.0	1.0	.90	1.0
	95											
	89							.15				
PEP-2	116											
	108											
	110	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.98
	92											.02

TABLE 2. Continued.

Population sample												
14	15	16	17	18	19	20	21	22	23	24	25	26
			.08					.09	.03			
					.14							
1.0	1.0	1.0	.92	1.0	.86	1.0	1.0	.91	.97	1.0	1.0	1.0
				.04	.04							
								.03				
1.0	1.0	1.0	1.0	.96	.96	1.0	1.0	.97	1.0	1.0	1.0	1.0
1.0	1.0	.60	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.98	1.0	1.0
		.40										
										.02		
				.02						.14	.11	
1.0	1.0	1.0	1.0	.98	1.0	1.0	1.0	1.0	1.0	.86	.89	1.0
1.0	.94	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.97	1.0	1.0	1.0
	.06											
									.03			
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
				.65	.71	.50	.27	.12	.13			
				.35	.29	.25	.09	.06	.03			
1.0	1.0	.93	1.0			.08	.64	.68	.84	1.0	1.0	.77
		.07				.17		.15				.23
										.09		
		.31	.77	1.0	1.0	1.0	1.0	1.0	1.0	.91	.98	
1.0	1.0	.69	.23								.02	1.0
				1.0	1.0	.08	.04	.12	.53	.59	.57	
1.0	1.0	.50	1.0			.92	.77	.78	.47	.41	.43	
												1.0
		.50										
									.03			
.02										.04		1.0
.02		.40										
.05				.43	.11	.33	.04	.26	.91	.84	.87	
.01												
.88	.90	.52	.96	.41	.89	.67	.86	.50	.06	.11	.13	
.01		.07	.04	.17			.09	.24				
	.10											
	.02											
	.29	.17		1.0	1.0	1.0	.64	.88				
1.0	.69	.83	1.0				.36	.12	.72	1.0	1.0	1.0
									.28			
.88	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.94	.18		.81
												.19
.12									.06	.82	1.0	
												.08
												.73
1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.19

TABLE 2. Continued.

Locus and allele		Population sample 1	2	3	4	5	7	8	9	10	11	13
SORDH	−129											
	−116											
	−100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.97	1.0
	−80										.03	
PGD	143			.24								.04
	113											
	100	1.0	1.0	.76	1.0	1.0	1.0	1.0	1.0	1.0	1.0	.90
	86											.06
	67											
Alb	104	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0		.03	
	103.5									1.0	.97	.79
	103											.21
	100											
PreAlb	101											.17
	100	.77	.92	.98	.97	.80	.94	1.0	.88	1.0	.41	.77
	98	.23	.08	.02	.03	.20	.06		.12		.50	.06
	97										.09	
Trf	132	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0		
	121										1.0	1.0
Pt-A	100	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0
	90											
A		1.17	1.13	1.26	1.09	1.17	1.17	1.26	1.26	1.17	1.52	1.61
P		.174	.130	.130	.043	.130	.087	.130	.174	.087	.217	.304
H		.046	.036	.048	.008	.050	.018	.038	.030	.022	.060	.074

TABLE 3. Coefficients of genic similarity (*S*-values; Rogers, 1972) above diagonal, and Nei's genetic distance (*D*-values; Nei, 1971) below diagonal between 26 populations of *Thomomys umbrinus*. Numbers identifying samples refer to Figure 1 and Appendix.

	Population	1	2	3	4	5	6	7	8	9	10	11	12
1	Boca del Monte	—	.867	.847	.871	.857	.836	.845	.825	.854	.810	.766	.720
2	Amecameca	.113	—	.963	.983	.926	.917	.925	.913	.923	.887	.821	.800
3	Toluca	.119	.007	—	.976	.902	.891	.896	.881	.893	.865	.789	.791
4	Patzcuaro	.111	.003	.004	—	.919	.914	.919	.901	.917	.885	.810	.798
5	Ventura	.124	.050	.070	.064	—	.973	.980	.955	.972	.936	.852	.861
6	Arriaga	.148	.070	.093	.086	.006	—	.991	.972	.970	.936	.846	.862
7	Ojocaliente	.136	.063	.083	.076	.003	.001	—	.974	.977	.939	.855	.861
8	Somberete	.149	.068	.092	.085	.009	.003	.003	—	.957	.921	.844	.842
9	Morcillo	.127	.059	.076	.070	.005	.008	.005	.010	—	.931	.843	.846
10	Las Nieves	.169	.098	.114	.108	.049	.050	.048	.053	.051	—	.892	.908
11	Cuauhtemoc	.212	.160	.186	.176	.121	.127	.122	.128	.125	.075	—	.892
12	Sierra del Nido	.273	.184	.196	.194	.119	.119	.118	.125	.125	.068	.055	—
13	Colonia Garcia	.273	.189	.202	.204	.158	.160	.158	.157	.157	.114	.060	.073
14	Patagonia Mts.	.235	.211	.231	.233	.166	.186	.178	.187	.180	.129	.116	.192
15	Moctezuma	.227	.199	.219	.221	.159	.174	.167	.174	.171	.130	.125	.197
16	El Novillo	.228	.185	.204	.202	.156	.181	.170	.181	.157	.116	.112	.189
17	Bacanora	.165	.151	.180	.172	.115	.128	.120	.130	.122	.087	.073	.170
18	Chuhuichupa	.385	.333	.339	.336	.325	.374	.356	.370	.345	.334	.237	.281
19	Valle Moctezuma	.350	.351	.357	.353	.362	.413	.393	.409	.380	.371	.252	.326
20	Madera	.393	.342	.377	.371	.293	.306	.298	.303	.303	.302	.184	.253
21	Tomochic	.313	.282	.316	.306	.251	.267	.257	.265	.254	.250	.128	.229
22	Rancho El Pajarito	.330	.280	.311	.304	.239	.256	.247	.252	.247	.242	.133	.201
23	El Vergel	.233	.164	.180	.172	.112	.131	.124	.133	.123	.122	.180	.201
24	El Salto	.258	.180	.192	.182	.140	.151	.147	.143	.147	.140	.223	.221
25	La Ciudad	.274	.198	.210	.201	.153	.164	.159	.152	.160	.154	.237	.240
26	Siqueros	.382	.228	.227	.232	.279	.292	.287	.294	.281	.276	.359	.344

TABLE 2. Continued.

Population sample												
14	15	16	17	18	19	20	21	22	23	24	25	26
				1.0	1.0	.91	1.0	.91	1.0	1.0	1.0	
												1.0
1.0	1.0	1.0	1.0			.09		.09				
								.12				
.01												
.99	1.0	1.0	1.0	.98	1.0	1.0	1.0	.88	1.0	1.0	.91	1.0
				.02							.09	
											.02	
1.0	.73	1.0	.71	.09			.14	.15				
				.91	1.0	1.0	.86	.85	1.0	1.0	.98	1.0
	.27		.29									
										.23	.23	
									.44	.77	.77	1.0
1.0	.56	1.0	.88	.91	.96	1.0	1.0	1.0	.56			
	.44		.12	.09	.04							
1.0	1.0	1.0	1.0				.04	.06	1.0	1.0	1.0	1.0
				1.0	1.0	1.0	.96	.94				
1.0	1.0	1.0	1.0	.82	.88	1.0	1.0	1.0	1.0	1.0	1.0	1.0
				.18	.12							
1.31	1.26	1.30	1.22	1.39	1.26	1.26	1.39	1.61	1.43	1.35	1.30	1.17
.087	.217	.261	.174	.217	.174	.174	.217	.391	.261	.261	.217	.130
.027	.056	.095	.061	.068	.034	.043	.052	.100	.071	.083	.059	.043

TABLE 3. Continued.

13	14	15	16	17	18	19	20	21	22	23	24	25	26
.718	.760	.762	.741	.810	.647	.673	.642	.689	.671	.752	.735	.728	.650
.793	.791	.796	.795	.832	.694	.684	.693	.727	.721	.820	.808	.800	.770
.779	.771	.773	.777	.811	.689	.678	.666	.700	.704	.792	.784	.778	.768
.781	.784	.783	.784	.824	.699	.689	.678	.714	.707	.807	.803	.795	.774
.813	.823	.821	.812	.863	.691	.670	.720	.745	.746	.858	.840	.835	.730
.807	.824	.823	.796	.864	.671	.649	.720	.740	.739	.838	.825	.821	.731
.812	.824	.822	.803	.864	.679	.658	.727	.747	.747	.846	.832	.828	.731
.806	.818	.817	.791	.849	.671	.649	.717	.738	.738	.837	.825	.820	.725
.816	.810	.811	.815	.850	.685	.664	.712	.745	.741	.847	.830	.826	.729
.845	.859	.841	.850	.882	.692	.669	.722	.751	.751	.852	.840	.837	.739
.880	.857	.839	.836	.878	.760	.742	.805	.830	.829	.804	.761	.755	.671
.871	.800	.782	.788	.808	.717	.693	.750	.763	.761	.775	.760	.749	.692
—	.827	.844	.839	.817	.713	.696	.745	.785	.786	.747	.730	.724	.713
.131	—	.944	.915	.936	.665	.687	.733	.755	.750	.767	.734	.726	.734
.122	.017	—	.887	.928	.672	.680	.732	.774	.749	.769	.723	.714	.727
.127	.032	.047	—	.890	.681	.679	.721	.767	.753	.769	.721	.710	.708
.144	.033	.038	.045	—	.704	.709	.765	.808	.789	.804	.764	.755	.701
.278	.376	.352	.328	.313	—	.961	.919	.884	.892	.808	.742	.737	.614
.308	.369	.345	.388	.302	.010	—	.924	.896	.884	.795	.726	.717	.610
.234	.287	.266	.274	.227	.047	.046	—	.935	.939	.817	.745	.738	.635
.185	.215	.207	.203	.158	.071	.062	.022	—	.950	.841	.770	.765	.660
.174	.233	.218	.213	.176	.061	.065	.018	.011	—	.835	.762	.760	.653
.230	.219	.219	.201	.162	.152	.176	.149	.118	.114	—	.908	.902	.745
.255	.272	.274	.270	.224	.243	.268	.246	.198	.200	.046	—	.979	.745
.273	.287	.292	.289	.239	.262	.287	.262	.214	.215	.060	.002	—	.732
.273	.287	.277	.294	.317	.456	.467	.433	.376	.386	.249	.250	.272	—

TABLE 4. Distributional patterns of seven electromorphs across five groups of *Thomomys umbrinus*.

No. replicates	Allele	Groups linked by pattern				
		Northern Sierra Madre	Southern Sierra Madre	Northern Desert	Central Plateau	Coastal Sinaloa
2	PGM^{145}, $SORDH^{-129}$	X	X			
2	GPD^{109}, $ES\text{-}4^{110}$		X	X		
3	PGD^{143}, $LDH\text{-}1^{102}$, $Alb^{103.5}$	X		X	X	

subgroups. One of these occurs in the northern desert region (populations 11–17; hereafter referred to as Northern Desert group), another inhabits the Central Plateau of Mexico (populations 1–10; Central Plateau group), a third is found only in coastal Sinaloa (population 26; Coastal Sinaloa), a fourth inhabits the northern Sierra Madre Occidental (populations 18–22; Northern Sierra Madre group), and a fifth is found in the southern Sierra Madre Occidental (populations 23–25; Southern Sierra Madre group). These groups delineate geographic units that are very similar to those defined by chromosomal characters (compare Figs. 2 and 3). For example, the Northern Desert electromorphic group contains only populations with 2n = 78 and high numbers of acrocentric autosomes, and the Central Plateau subgroup is exactly concordant with the 2n = 78 biarmed karyotypic form (with the single exception of population 6, the Arriaga sample). The 2n = 76 karyotypic form, however, is divisible into three electromorphic units, with Coastal Sinaloa being the most distinctive.

To gain a better understanding of the relative reliability of different portions of the electromorphic data set, the data were subjected to a component analysis. Of the 74 alleles detected (Table 2), 27 (36%) were unique to individual groups and 13 (18%) were common to all. The remaining 34 electromorphs formed 12 components, or patterns of allele sharing. Based on the formulae presented above, a component must be replicated at least six times to be statistically corroborated; that is, to be recognized as potentially nonrandom information. For example, given five groups and 74 electromorphs, a component with five replicates has a probability of nonrandom association of 0.058, whereas that for six replicates has a probability of 0.022. Thus, the only components that can be distinguished from chance associations include that linking all five groups together (supported by 13 alleles; Table 2) and that linking all groups exclusive of the Coastal Sinaloa one (six replicates). This information is consistent with that based on the phenetic analysis (Fig. 3), but it reveals no information on intergroup phylogenetic relationships in *T. umbrinus*.

Cladistic analysis.—To focus the probability analysis on the phylogenetically informative portions of the electromorphic data set, we repeated the analysis omitting the 27 alleles that were unique to individual *umbrinus* groups. In so doing, we departed from the component procedure advocated by Straney (1980, 1981). Our reasoning was that unique (autapomorphic) alleles are phylogenetically devoid of information (i.e., they do not constitute components, or patterns of allele sharing) such that their inclusion in a probability analysis will bias against the detection of significant underlying patterns of relationship in those taxa whose history and/or genetic structure has resulted in the generation of a large number of unique alleles. We further refined the electromorphic data set prior to the probability analysis by omitting all *umbrinus* alleles shared with any other species of *Thomomys* (outgroup data from Patton and Smith, 1981); the resulting data set consisted of seven presumed synapomorphic alleles that define three components across the five *umbrinus* groups (Table 4).

The statistical reliability of each of the patterns in Table 4 was examined by substituting $p = 0.0385$ (reciprocal of the total number of possible patterns) and $m = 7$

(number of electromorph characters) in the component-analysis formulae. Because all electromorphs unique to individual groups were eliminated a priori from the analysis, the value S_n (the number of possible components for n taxa) was reduced by n prior to calculation of p. Based on these calculations, the probability of any one of the 26 possible components appearing twice by chance alone (given only 7 electromorphs) is 0.027, and that of a given pattern being replicated three times by chance alone is remote (0.0017). Thus, all three components shown in Table 4 are highly significant on a probabilistic basis and likely represent actual relationships.

The three components (Table 4) can be used to construct two dendrograms (Fig. 4), each of which requires the evolutionary loss (or change) of five electromorphs across the various groups. Thus, simple parsimony cannot be used to select between the two trees. For example, both trees require that the Southern Sierra Madre populations have lost the PGD^{143}, LDH-1^{102}, and Alb$^{103.5}$ alleles (Table 4). In addition, the tree shown in Figure 4a requires that the Northern Sierra Madre populations have lost the GPD^{109} and ES-4^{110} alleles, whereas the tree in Figure 4b indicates that the Northern Desert populations have lost the PGM^{145} and SORDH^{-129} alleles. Considering that the alleles uniting the Northern and Southern Sierra Madre groups occur at moderately high frequencies and are widespread throughout the two groups (Table 2), it is unlikely that these alleles were present in the Northern Desert group, yet went undetected due to sampling error. The same cannot be said for the two alleles linking the Southern Sierra Madre and Northern Desert groups; these alleles occur at low frequencies in only a few populations and may very well have gone undetected in the Northern Sierra Madre populations due to sampling error. Thus, of the two alternatives shown in Figure 4, the electromorphic evidence is somewhat more supportive of dendrogram 4a. Note also that the two Sierra Madre groups linked together in Figure 4a also share a common diploid number (Fig. 2).

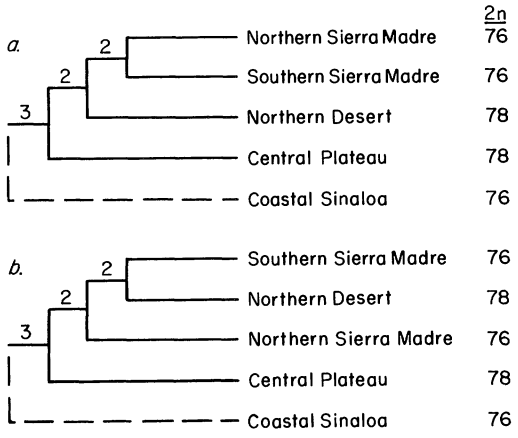

FIG. 4. Two possible dendrograms based on distribution of shared alleles unique to *T. umbrinus*. Numbers on branches indicate number of replications supporting branching sequence (see Table 4). All nodes are significant nonrandom associations at the 0.05 probability level.

Wright's F-statistics.—Wright's (1965) standardized variance in gene frequency (F_{ST}) provides a measure of among-population genetic heterogeneity, and the inbreeding coefficient (F_{IS}) permits examination of within-population breeding structure. The mean F_{ST} for *T. umbrinus*, calculated among those populations with sample sizes of six or more individuals, is 0.752 (including only polymorphic loci with frequency of the dominant allele $<$ 0.95). This value approaches 1.00 (fixation for alternative alleles at each locus); it is nearly an order of magnitude higher than typical F_{ST} values reported for animal species (Wright, 1978), and is twice that for populations of *T. bottae* (Patton and Yang, 1977).

Together, the magnitude of the F_{ST} value in *T. umbrinus* and the large number of unique alleles (23 of 74; Table 2) indicate an extremely high level of among-population genetic heterogeneity. This is consistent with the low levels of genic similarity measured among many populations (Table 3). Moreover, the presence of fixed allelic differences between populations (Table 2) suggests that gene flow between them has been either extremely low or nonexistent in the recent past.

TABLE 5. Population-genetic statistics for five subgroups of *Thomomys umbrinus*. Only populations with sample sizes of six or larger included.

Group	No. populations	*H* (range)	*P* (range)
Northern Desert	6	0.062 (0.027–0.095)	0.210 (0.087–0.304)
Central Plateau	9	0.033 (0.059–0.083)	0.120 (0.043–0.174)
Northern Sierra Madre	5	0.059 (0.034–0.100)	0.235 (0.174–0.391)
Southern Sierra Madre	3	0.071 (0.059–0.083)	0.246 (0.217–0.261)
Coastal Sinaloa	1	0.043	0.130

Estimates of average individual heterozygosity (H) and percent polymorphic loci (P) for each of the five *T. umbrinus* groups (Table 5) are low relative to those calculated for 23 populations of *T. bottae* (H = 0.093, P = 0.334; Patton and Yang, 1977). Heterozygosity and polymorphism are particularly low in the Central Plateau group, which also has a low average number of alleles per locus (1.19; compare with 1.85 for *T. talpoides* [Nevo et al., 1974]) and several fixed allele differences among populations.

The low levels of genetic variation in *T. umbrinus* populations in general, and in the Central Plateau group in particular, do not appear to result from extreme current inbreeding. The average inbreeding coefficient estimated for each of the 24 populations is near zero (F_{IS} = 0.051), and the mean F_{IS} for the Central Plateau populations is −0.005. These data clearly indicate an absence of substantive inbreeding in these populations today, as well as in the recent past.

Considered in total, the population-genetic statistics (high F_{ST} estimates accompanied by low F_{IS}, H, and P values) are consistent with the hypothesis that past population bottlenecks, including founder events, resulted in the chance loss of certain alleles and chance fixation of others. This explanation simultaneously accounts for both the low number of alleles per locus in nearly all populations and the high incidence of fixation for alternative alleles, even in geographically adjacent ones. Between bottleneck events, the populations appear to expand in size, and the F-statistics suggest that inbreeding is minimal. A similar scenario has been presented for populations of *T. bottae* (Patton and Yang, 1977), one which is also supported by detailed genetic demographic analyses of local populations for this species (Patton and Feder, 1981).

Speciation in T. umbrinus

Overall patterns in the genus Thomomys.— All available data on electromorphic variation in *Thomomys* suggest that speciation in the genus is unrelated to the level of genic differentiation between populations (Patton and Yang, 1977; Patton, 1981; Hafner et al., 1983). Rather, genic differentiation appears to be more a function of time and degree of separation of populations (Soulé, 1976), than a reflection of the degree of reproductive compatibility among them. Thus, populations of pocket gophers with very low genic similarity (S as low as 0.65) are able to interbreed freely across contact zones (Patton et al., 1979; Smith et al., 1983), whereas others showing more than 80% genic similarity are distinct species on biological grounds (Nevo et al., 1974; Patton and Yang, 1977).

Patton (1981) argued that a major mode of speciation in *Thomomys* is the fixation of structural chromosomal rearrangements, such as reciprocal translocations (as opposed to additions or deletions of constitutive heterochromatin), that lead to meiotic imbalance and hybrid sterility. For example, meiotic and banding studies have shown that *T. bottae* and *T. umbrinus* possess a large number of structural chromosome differences (Patton, 1973; Barros and Patton, 1985). Where the two species meet and hybridize in southern Arizona, multivalents are formed during meiosis in F_1 hybrids, resulting in complete to partial ste-

rility (Patton, 1973). In contrast, hybrids formed between *T. bottae* populations with radically different amounts of heterochromatin show normal meiosis (Patton, 1972; Patton and Yang, 1977; Patton and Sherwood, 1982).

In pocket gophers, additions or deletions of heterochromatin usually result only in changes in arm number (Patton and Sherwood, 1982); in contrast, structural rearrangements generally are manifest in diploid number differences (Patton, 1973). Thus, diploid number differences between populations of pocket gophers may signal underlying structural variations of sufficient magnitude to result in meiotic imbalances in hybrids. Indeed, there are only a few known cases where pocket gopher populations with different diploid numbers freely interbreed; in one case (Hafner et al., 1983), the diploid number difference is the result of the addition of entire heterochromatic chromosomes to the genome (i.e., structural rearrangements are not involved). In the other cases (Thaeler, 1974, 1985), the cause and nature of the diploid number differences are unknown.

Possible contact zones in T. umbrinus.—Knowledge of the exact nature of the chromosomal differences between 2n = 76 and 2n = 78 populations of *T. umbrinus* must await future banding studies. Nevertheless, because diploid number differences are so often coincident with *Thomomys* species boundaries (Thaeler, 1974, 1985), we postulate that at least the two diploid number classes of *T. umbrinus* are reproductively incompatible and, thus, genetically isolated. Unfortunately, populations of these two forms have not as yet been found in contact and, while it is possible to document gene flow between even geographically distant populations using electromorphic data (Slatkin, 1985), it is not possible to document the *absence* of gene flow unless the populations are actually in contact.

Data from the near-contact populations of Valle Moctezuma (locality 19) and Colonia Garcia (locality 13) in the northern Sierra Madre of Chihuahua are suggestive, however, of genetic isolation between them. For example, the $SORDH^{-129}$ allele, which is a synapomorphy linking the Southern and Northern Sierra Madrean groups (Fig. 4 and Table 4), is fixed at Valle Moctezuma but absent at Colonia Garcia. It seems unlikely that this allele could arise in one Sierra Madre population and spread to all others (in which it is nearly fixed), but never enter the Colonia Garcia population, unless the latter has been either genetically or physically isolated for most of its history. The same argument can be made for the PGM^{145} allele, a derived feature of the Northern Sierra Madrean group (Table 4) but conspicuously absent from the Northern Desert populations, including Colonia Garcia. On the other hand, evidence indicative of probable gene flow is lacking. Such evidence would come from alleles shared by these two populations, but in every case those alleles which are shared are also those which are pleisiomorphic for *T. umbrinus*. These cannot be used either to support or reject a gene flow hypothesis; their presence in both populations can be as easily explained as a retention from a common ancestor as by introgressive hybridization.

We are left, then, with a considerable amount of negative evidence (electromorphs) as well as circumstantial evidence (chromosomes) suggesting that the populations at Valle Moctezuma and Colonia Garcia are reproductively incompatible and, thus, genetically isolated. Detailed analyses of contact zones are required to test this hypothesis.

Banding evidence.—Available fluorochrome chromosomal-banding data (Barros and Patton, 1985; P. Garvey, unpubl. data) suggest that major structural chromosomal differences exist between the Northern Desert and Central Plateau populations, even though all share a diploid number of 78. If, in fact, these structural differences lead to meiotic imbalances in F_1 hybrids, the two assemblages may be reproductively isolated and, thus, represent different biological species. Although additional chromosomal-banding data together with analyses of contact zones are needed to resolve this issue, the available

karyotypic and allozymic data are concordant in showing marked differentiation between the two 2n = 78 subgroups (Figs. 2, 3).

CONCLUSIONS

On the basis of a cladistic assessment of the electromorphic data (Fig. 4), we have argued that the two Sierra Madrean assemblages (both 2n = 76) are the immediate sister group to the Northern Desert set of populations (2n = 78). The Central Plateau group (also 2n = 78) is considered to lie outside the Sierra Madre-Northern Desert clade, and the phylogenetic position of the Coastal Sinaloa population is basal to these four groups. We also have postulated, on the basis of both electromorphic and chromosomal evidence, that the 2n = 76 and 2n = 78 populations of *T. umbrinus* are specifically distinct, as are the 2n = 78 Northern Desert and Central Plateau groups. If, indeed, this hypothesis is correct, then the 2n = 76 complex would constitute a paraphyletic taxon. Paraphyly at the species level is apparently a common phenomenon in pocket gophers, as evidenced by the case of *T. bottae* and *T. townsendii* (see Patton and Smith, 1981).

A large body of evidence suggests that a diploid number of 76 is primitive within the *bottae* species-group, or subgenus *Megascapheus*, of *Thomomys* (reviewed by Patton [1981] and Hafner et al. [1983]). Thus, the primitive diploid number has been retained in the Sierra Madre and Coastal Sinaloa groups, and the 2n = 78 condition is derived. Based on electromorphic evidence, we postulate that the Coastal Sinaloa and Sierra Madre groups diverged early in the history of the assemblage. Although the Coastal Sinaloa animals are morphologically (unpubl. data) and electromorphically (this study) very different from the higher-elevation 2n = 76 forms, we have no evidence to suggest that the two would be reproductively incompatible were they to come into contact. For the moment, therefore, the observed morphologic and genic differentiation between these two 2n = 76 groups is more readily explained as a result of a long history of geographic, as opposed to genetic, isolation.

The pattern of shared, derived alleles (Table 4 and Fig. 4) suggests that the two 2n = 78 groups (Central Plateau and Northern Desert) were independently derived from the ancestral 2n = 76 Sierra Madrean complex. This view is reinforced by the trenchant chromosomal differences between the 2n = 78 groups (including banding differences discussed above). Regardless of the sequence for the origin of either 2n = 78 geographic group (Fig. 4a or 4b), the populations inhabiting the conifer forests of the Sierra Madre Occidental have differentiated into northern and southern units, possibly effected by the presence of the Barranca del Cobre (the "Grand Canyon of Mexico") in south-central Chihuahua.

If chromosomal differentiation is a dominant mode of speciation in the genus *Thomomys*, and if structural rearrangements are usually (but not always; see 2n = 78 case above) accompanied by changes in diploid number, then it is possible that the 2n = 76 populations of *T. umbrinus* are reproductively compatible with the 2n = 76 populations of *T. bottae* inhabiting the coastal regions of northwestern Mexico. To date, populations of *umbrinus* and *bottae* possessing the same diploid number have not been found in contact, so this hypothesis remains to be tested. Nevertheless, this possibility serves to emphasize several points with regard to this particular study, and to general aspects of cladogenic diversification in pocket gophers. For one, many species of gophers traditionally recognized on morphological grounds are instead complex composites of genetically differentiated geographic units, some of which have clearly reached the stage of complete genetic isolation, others of which are nearing that stage. This is certainly the case for the specific entity we have called *T. umbrinus* here; it most likely comprises several distinct biological species that should be recognized as such.

These data highlight the fact that tem-

poral patterns of cladogenesis will often result, for example, in two population units of one species being phyletically more distantly related to one another than either may be to a second species that is demonstrably isolated on genetic grounds. This apparent paradox stems from a species concept based on criteria of reproductive compatibility and a simultaneous recognition that the mechanisms effecting genetic isolation can vary widely both in mode and in timing, even within the same complex of organisms.

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APPENDIX

Sample Localities

Localities are listed below by number and are indicated on the map (Fig. 1). Sample sizes for each analysis are indicated (K = karyotypic, E = electrophoretic). Detailed locality information and specimen catalog numbers are available on request from J. L. Patton.

PUEBLA: [1] Boca del Monte (K = 2, E = 17); **MEXICO: [2]** Amecameca (K = 3, E = 18); **[3]** Toluca (K = 1, E = 21); **MICHOACAN: [4]** Patzcuaro (K = 1, E = 17); **SAN LUIS POTOSI: [5]** Ventura (K = 2, E = 22); **[6]** Arriaga (K = 3, E = 2); **ZACATECAS: [7]** Ojocaliente (K = 2, E = 24); **[8]** Somberete (E = 17); **DURANGO: [9]** Moncillo (E = 13); **[10]** Las Nieves (K = 1, E = 14); **[24]** El Salto (K = 3, E = 22); **[25]** La Ciudad (K = 5, E = 23); **CHIHUAHUA: [11]** Cuauhtemoc (K = 3, E = 19); **[12]** Sierra del Nido (K = 2, E = 2); **[13]** Colonia Garcia (K = 10, E = 26); **[18]** Chuhuichupa (K = 1, E = 27); **[19]** Valle Moctezuma (K = 6, E = 14); **[20]** Madera (E = 6); **[21]** Tomochic (K = 3, E = 11); **[22]** Rancho El Pajarito (K = 3, E = 17); **[23]** El Vergel (K = 6, E = 16); **SINALOA: [26]** Siqueros (K = 3, E = 13); **SONORA: [15]** Moctezuma (K = 3, E = 24); **[16]** El Novillo (K = 1, E = 21); **[17]** Bacanora (K = 1, E = 12); **ARIZONA: [14]** Patagonia Mts. (K = 71, E = 43).