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CONTACT ZONES AND THE GENETICS OF DIFFERENTIATION IN THE POCKET GOPHER *THOMOMYS BOTTAE* (RODENTIA: GEOMYIDAE)

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Abstract.—The genetic interaction between clinally varying populations of pocket gophers (*Thomomys bottae*) along the eastern flank of the Sangre de Cristo Mountains in Colorado and New Mexico is examined by comparative karyology, electromorphic analysis of proteins, and colorimetric and morphometric analyses of morphology. Diploid number varies clinally along the transected populations from 76 in the south to 88 in the north. The karyotypic change is unaccompanied by electromorphic divergence as all populations studied share greater than 95% similarity, although similar clines in pelage brightness and mean morphometric coefficient of variation are evident. Individuals with intermediate diploid numbers suffer no apparent fitness deficit.

The patterns of genetic interaction at the Sangre de Cristo contact are compared with four other *T. bottae* "contact zones" previously investigated. These five situations include differentiated parental forms which span the range of known genetic (karyological and electromorphic) divergence in the *T. bottae* species group, and involve both instances of reproductive isolation and extensive introgressive hybridization. Cline widths for *T. bottae* zones vary from approximately 1 km to 200 km, with the nature of the environmental setting at a contact being more predictive of cline width than gross measures of genetic differentiation (e.g., electromorphic distance values and chromosome numbers). [Pocket gophers; *Thomomys*; hybridization; chromosomes; electrophoresis; morphometrics; cline models.]

During the past 15 years, we have gathered information on the dynamics of genetic, phenetic, and ecologic interactions in hybrid zones of pocket gophers of the *Thomomys bottae* group (Fig. 1). The philosophy behind these studies has rested on the view that detailed analyses of character variation, at geographic sites where phenotypically and/or genetically differentiated populations are in contact, provide the best means to evaluate the types of changes that may be involved in speciation in the group. Thus, the Patagonia Mountains contact (for review see Patton, 1973), where the species *T. bottae* and *T. umbrinus* hybridize but produce only F_1, largely sterile offspring, emphasized the potential role of meiotic imbalance in mediating hybrid success in chromosomally differentiated forms. Other parapatric zones within *T. bottae,* involving both chromosomal and electromorphic differentiation (White-Sacramento Mts. [Patton et al., 1979]; Rio Grande [Smith et al., 1983]) or solely electromorphic differences (Colorado River [Smith and Patton, 1980]), emphasize that not all types of chromosomal changes will affect reproductive performance of hybrids, that hybridization potential is unrelated to the level of electromorphic differentiation, and that genic introgression may reflect only the local ecology and physiography of given regions (reviewed by Patton, 1981).

In this study genetic and morphologic information are evaluated for *T. bottae* character clines along a narrow peninsular distribution abutting the Sangre de Cristo Mountains of Colorado and New Mexico (Fig. 1). This situation involves the addition of up to 12 extra chromosomal elements to the diploid number, yet population samples lack electromorphic differentiation. This is an unusual system of cytological differentiation,

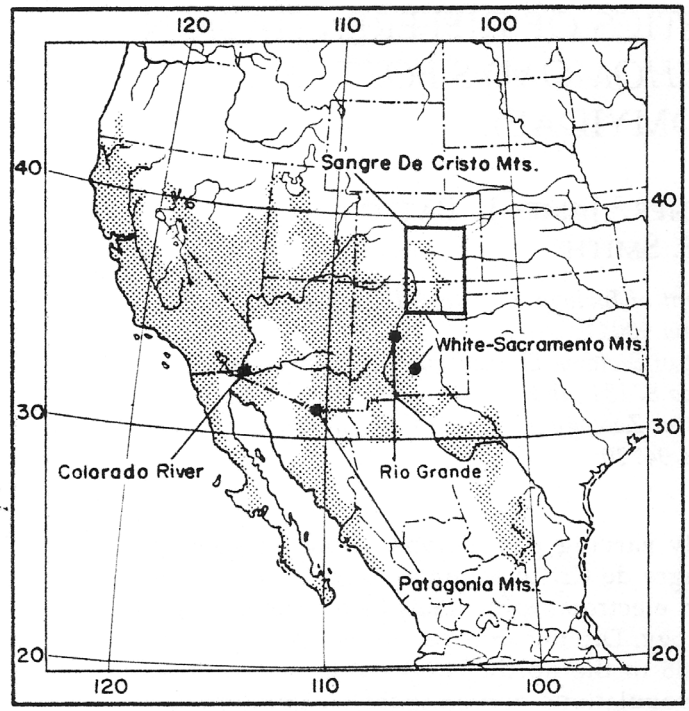


FIG. 1. Geographic distribution of *Thomomys bottae*; the position of the five contact zones examined to date are indicated.

not only for this species which almost invariably possesses 76 chromosomes, but for mammals in general. The combined analyses of *T. bottae* parapatric contacts permit us to develop a preliminary understanding of the tempo and mode of character change and to suggest possible ramifications of such change to speciation in the group.

MATERIALS AND METHODS

A total of 145 specimens comprising 10 populations of *T. bottae* was studied. Of the total sample, 116 specimens are from within or adjacent to the zone of contact defined on karyotypic grounds. All specimens are deposited in the Museum of Vertebrate Zoology (MVZ) or the Museum of Southwestern Biology (MSB) as skin-plus-skull or skin-plus-skeleton study preparations.

Karyotype analysis.—Fifty-five individuals were karyotyped, including 39 individuals from within the region of contact. Non-preferentially stained karyotypes were prepared using a modification of the in vivo bone-marrow technique described by Patton (1967). Determination of diploid numbers and chromosome morphology was made from photomicrographs, with an average of 15 cells examined per individual specimen. Approximately 60% of all scorable cells possessed the modal number of chromosomes judged to be the correct diploid number for an individual. Specific staining for constitutive heterochromatin (C-band analysis) was performed using Patton's (1977) modification of the general C-band technique of Cooper and Hsu (1972).

Electrophoresis.—Electromorphic variability was assayed in 109 individuals representing the 10 study localities using standard starch-gel electromorphic methods (Selander et al., 1971; Patton et al., 1972; Patton and Yang, 1977). Eighteen enzymes and other proteins were examined to reveal 22 presumptive gene loci following previous studies with pocket gophers (Patton and Yang, 1977; Smith and Patton, 1980; Patton and Feder, 1981). Rogers' (1972) coefficient of genetic similarity (*S*-value) and Nei's (1972) genetic distance (*D*) were used as indices of relatedness among populations. Cluster analysis of the matrix of genetic similarity values was performed by the unweighted pair-group method using arithmetic averages (UPGMA; Sneath and Sokal, 1973) as implemented in the NT-11 program on the CDC 6400 computer at the University of California, Berkeley.

Morphological analysis.—Pelage color, as well as cranial and external morphometric characters, was used to examine morphological variability. Variation in pelage color was measured using a Bausch and Lomb Spectronic 505 spectrophotometer. Visible reflectance of the middorsal pelage was recorded for each of 132 adult specimens representing the 10 study localities through a restricted port 8 mm in diameter; recordings were taken at 10% transmittance. Values for dominant wavelength (hue), relative brightness (value), and excitation purity (chroma or saturation) were computed from the recordings of reflectance curves for each specimen.

A total of 82 specimens (judged to be adult by closure of the basisphenoid-basioccipital suture) was used in the morphometric analyses. Of these, 22 from outside the contact zone (Tajique sample) served to assess the degree of non-geographic variation in the characters examined, which included: total

length (ToL), tail length (TaL), hind foot length (HF), ear length (EL), occipitonasal length (ONL), condyloincisor length (procumbancy measure; PRO), zygomatic breadth (ZB), mastoid breadth (MB), least width of interorbital constriction (IOC), nasal length (NL), rostral width (RW), bullar length (BuL), bullar width (BuW), alveolar length of maxillary tooth row (MTRL), palatal width (alveolar, at M^1; PW), and diastema length (DL). Cranial measurements were taken with dial calipers from cleaned skulls, while the four external measurements were read directly from specimen labels. A single classification analysis of variance (ANOVA; Statistical Analysis System, SAS; Helwig and Council, 1979) was applied to the Tajique sample to identify those characters either excessively variable (CV > 8; Long, 1970) or exhibiting secondary sexual dimorphism. Ratios derived by dividing all variables by ONL were employed to permit increased sample sizes by lumping sexes in the analyses. Subsequent to such division, only two variables (ZB and IOC) retained significant sex differences. Further, no remaining variables differed significantly from a normal distribution ($P > 0.50$), as indicated by the *W*-statistic of Shapiro and Wilk (1965).

Variation across the contact zone was assessed on the basis of discriminant function, factor, and regression analyses using programs of the Statistical Package for the Social Sciences (SPSS; Nie et al., 1975). A contour map based on *P*-values of intergroup *F*-statistics was constructed by hand from inspection of *F*-values for contiguous populations. This map indicated multivariate isoclines that unite populations, thus documenting patterns of morphometric variation over geography. The *P*-values rather than the *F* or Mahalanobis D^2 matrices were used because they conservatively correct for small sample size.

Specimens examined.—Localities for the specimens examined with sample sizes in parentheses are as follows (the 10 general locality names are italicized and correspond to usage in text and figures):

COLORADO: *Cañon City* (10): Cañon City, 5,300 ft, Fremont Co.; 5.3 mi N, 5.3 mi E Cañon City, 6,200 ft, Fremont Co.; *Walsenburg* (15): 4.1 mi W. Walsenburg (by road), Huerfano Co. NEW MEXICO: *Des Moines* (30): 5.1 mi S, 2.6 mi E Des Moines, 6,400 ft, Union Co.; 5.9 mi SE Des Moines (by road), Union Co.; *Raton* (8): 2.7 mi E Raton, 6,600 ft, Colfax Co.; *Cimarron* (18): 3.8 mi S Cimarron, 6,500 ft, Colfax Co.; *Ocate* (9): 0.2 mi S, 1.3 mi E Ocate, 7,200 ft, Mora Co.; *Mora* (2): 7.8 mi S, 1.5 mi W Mora, 7,400 ft, San Miguel Co.; *Las Vegas* (9): Las Vegas, 6,400 ft, San Miguel Co.; *Pecos* (15): 3.0 mi N Pecos, San Miguel Co.; *Tajique* (29): 7 mi NW Tajique, Manzano Mts., 7,400 ft, Torrance Co.; 0.5 mi S, 5 mi W Manzano, Red Canyon, Torrance Co.; 4 mi W, 1 mi S Manzano, Red Canyon, Torrance Co.

RESULTS

Karyotypic Analyses

Diploid number varies clinally along the transect from 76 in the south to 88 in the north (Fig. 2). A linear trend exists between mean diploid number and latitudinal position (kilometers north from Pecos) along the transect ($r = 0.921$; $P < 0.01$). The $2n = 88$ karyotype appears identical to the typical $2n = 76$ *T. bottae* karyotype from southern localities, differing only in the addition of 12 elements to the complement (Fig. 3). These extra chromosomes are heterochromatic (C-band positive) and, although variable in size, are smaller than the standard 13 pairs of acrocentric autosomes found in all *T. bottae* in this region. It is not possible to determine if these chromosomes represent pairs of homologs or a single class of elements. All diploid numbers between 76 and 88 were recorded, save $2n = 77$ and $2n = 87$. The lack of these two karyotypes likely reflects overall small samples. There is extensive intrapopulation chromosomal variability at nearly all localities across the transect (Fig. 2), and such variability is unrelated to the sex of the individual. Pecos and Cañon City, with no intrapopulational variability recorded, represent the chromosomally "parental" populations to the south and north, respectively. The chromosomal cline spans at least 200 km (Las Vegas to Walsenburg) and is sandwiched between the coniferous forests of the abruptly towering Sangre de Cristo Mountains and the short-grass prairie of the Great Plains. This region encompasses the

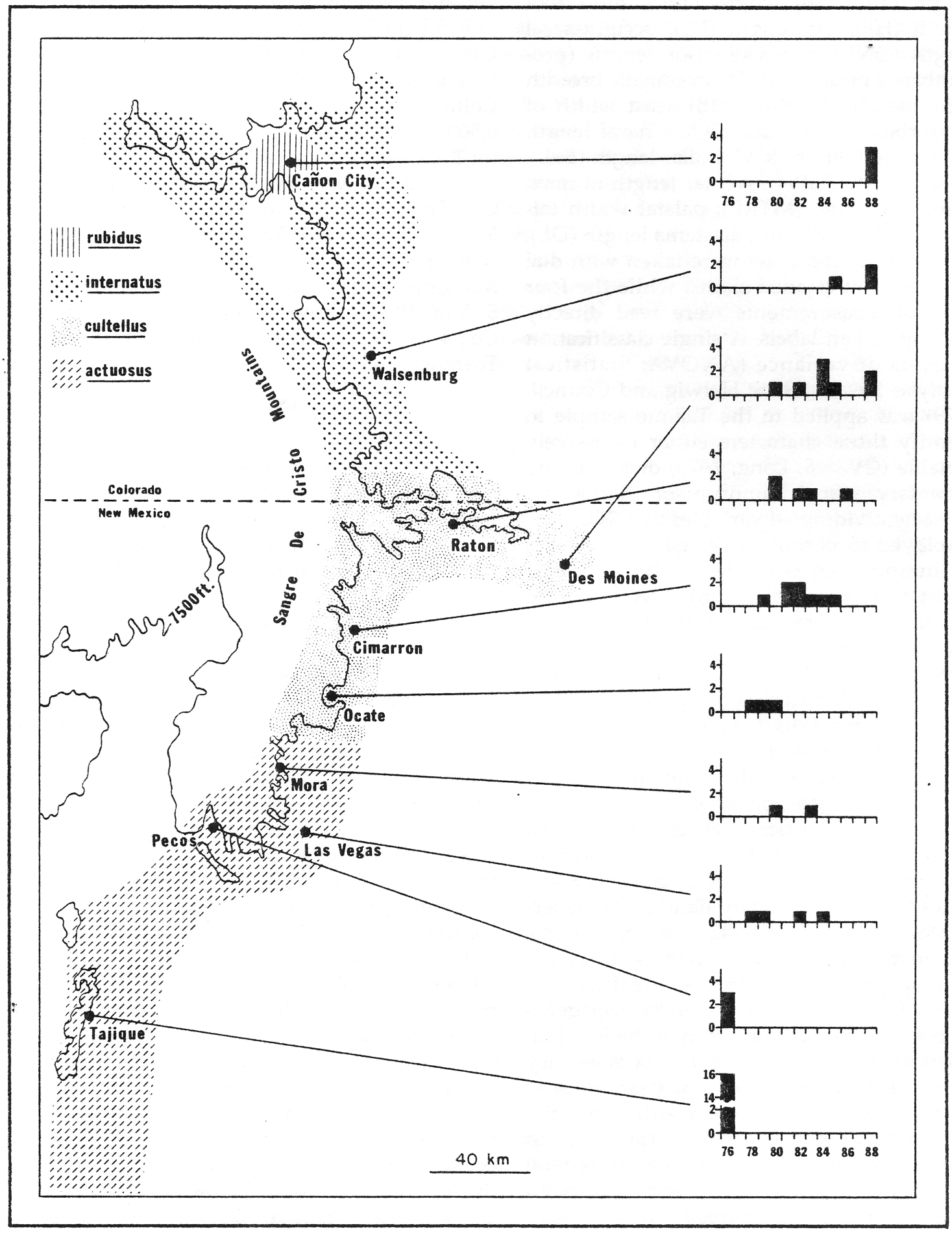


FIG. 2. Distribution of *T. bottae* across the Sangre de Cristo contact zone. Frequency histograms of variability in diploid number are indicated for each transect locality.

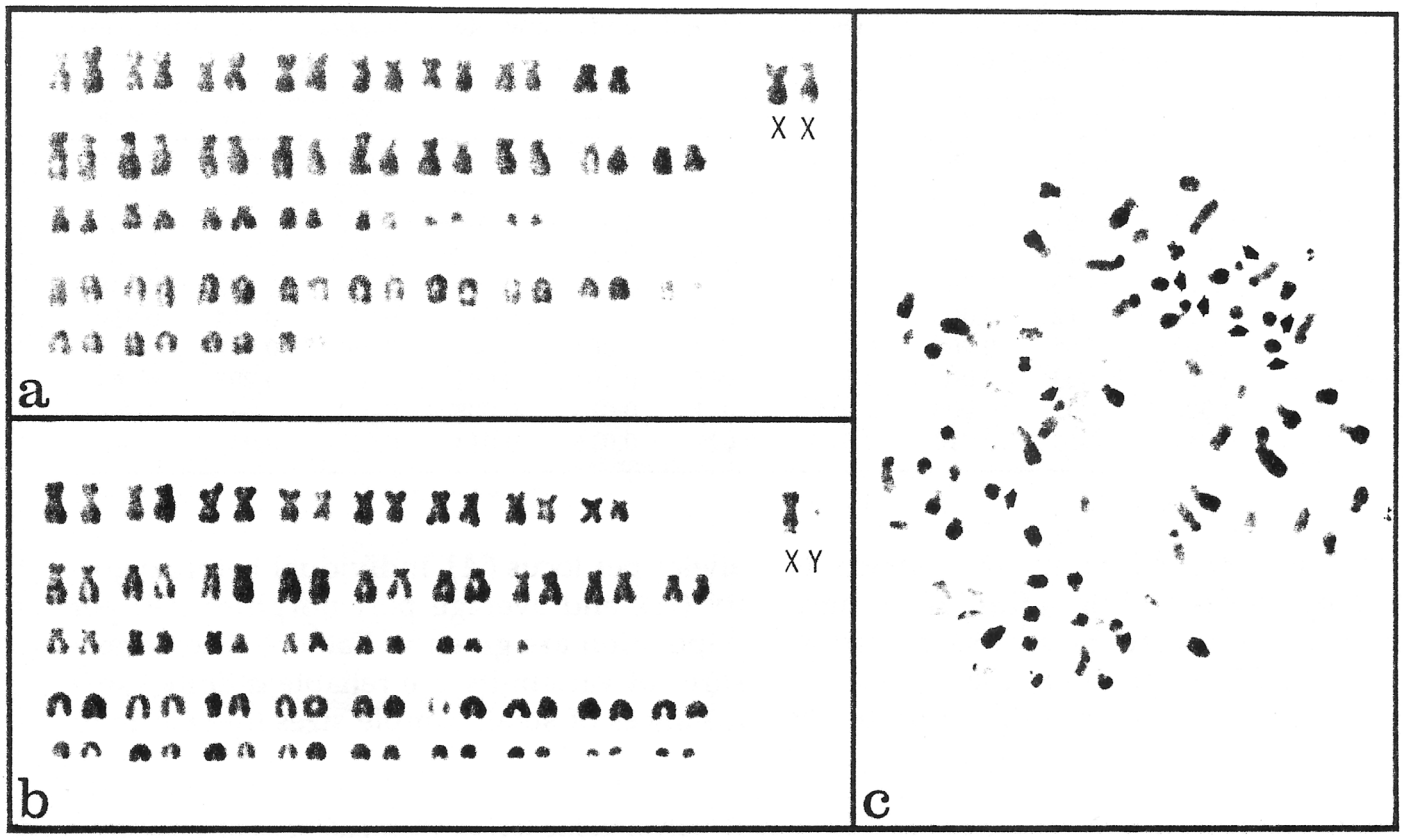


FIG. 3. Karyotypes of *T. bottae* at the Sangre de Cristo contact: (a) parental 2n = 76 karyotype from Pecos, San Miguel Co., New Mexico; (b) parental 2n = 88 karyotype from Cañon City, Fremont Co., Colorado; (c) C-banded mitotic metaphase from an individual with 2n = 84 from Walsenberg, Huerfano Co., Colorado, documenting the completely heterochromatic nature of the eight additional small acrocentric autosomes of the complement (arrows).

distributional ranges of four subspecies of *T. bottae* (Fig. 2): *T. b. actuosus* (Kelson, 1951), *T. b. cultellus* (Kelson, 1951), *T. b. rubidus* (Youngman, 1958), and *T. b. internatus* (Goldman, 1936). There is no apparent correspondence between chromosomal variation and currently recognized taxonomic boundaries.

Electromorphic Analyses

Interlocality differentiation.—Geographic variation in electromorphic characters for the 10 populations sampled is summarized in Table 1. The electromorphic analysis revealed no fixed allelic differences or even major frequency shifts among the sample populations, with 5% the most disparate pairwise divergence value obtained (Cimarron versus Walsenburg: Rogers' $S = 0.946$; Nei's $D = 0.023$). These populations of pocket gophers are the northern extension of a large and internally homogeneous (Rogers' $S > 0.90$) geographic unit that extends through the mountainous region of eastern New Mexico, western Texas, and southward into Coahuila, Mexico (Patton and Yang, 1977; Patton, 1981; Smith et al., 1983).

Populations at Cañon City and Pecos (the parental 2n = 88 and 2n = 76 localities) cluster at the highest similarity values while those at mid-transect are more distinctive (e.g., Raton, Des Moines, Ocate, and Cimarron; Fig. 4a). The electromorphic differentiation among the central populations is due not to fixation for alternative alleles, but to minor frequency differences among the populations and, more importantly, to the presence of rare and unique alleles at the mid-contact localities (Table 2). Alleles occurring in low frequency that characterize the center of the transect are those that are rare in the eastern region of *T. bottae* distribution (*IDH-1*^{117}, *IDH-2*^{138}, *Est-4*^{105}, *Alb*^{104}), or those entirely unique for the species (*Ga3PDH*^{119} and *ADA*^{83}). The distinctive Tajique locality (Fig. 4a and Table 2) was selected solely as a reference sample from outside the confines of

TABLE 1. Matrices of Rogers' similarity values (above the diagonal) and Nei's distance coefficients (below the diagonal) for 10 populations of *T. bottae*.

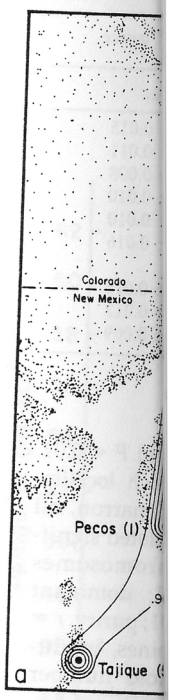
Locality	Cañon City	Walsenburg	Raton	Des Moines	Cimarron	Ocate	Mora	Las Vegas	Pecos	Tajique
Cañon City	—	0.991	0.981	0.974	0.955	0.965	0.989	0.994	0.999	0.970
Walsenburg	0.002	—	0.972	0.965	0.946	0.956	0.980	0.985	0.990	0.961
Raton	0.003	0.005	—	0.967	0.971	0.971	0.985	0.987	0.980	0.961
Des Moines	0.011	0.013	0.009	—	0.955	0.955	0.963	0.968	0.973	0.968
Cimarron	0.020	0.023	0.009	0.018	—	0.975	0.966	0.961	0.953	0.948
Ocate	0.010	0.012	0.005	0.015	0.005	—	0.977	0.971	0.964	0.950
Mora	0.003	0.005	0.002	0.014	0.012	0.004	—	0.995	0.987	0.958
Las Vegas	0.001	0.003	0.002	0.012	0.015	0.006	0.001	—	0.993	0.964
Pecos	0.000	0.002	0.003	0.011	0.021	0.010	0.003	0.001	—	0.968
Tajique	0.011	0.013	0.010	0.010	0.021	0.016	0.014	0.012	0.011	—

the chromosomal cline; its divergence is marked by alleles having affinities to more southernly distributed populations (Patton and Yang, 1977; Smith et al., 1983).

Intrapopulation variability.—The number of alleles per locus (A), individual heterozygosity (H), and average polymorphism (P) per population are given in Table 2. These measures of variability are reliable despite some instances of small sample sizes (see Gorman

TABLE 2. Allele frequencies and genic variability at 10 polymorphic loci in 10 populations of *T. bottae*. A = mean number of alleles per locus, H = mean proportion of 22 loci heterozygous per individual; P = proportion of 22 loci polymorphic per population.

Locus	Allele	Cañon City (10)	Walsenburg (15)	Des Moines (25)	Raton (6)	Cimarron (9)	Ocate (4)	Mora (2)	Las Vegas (4)	Pecos (15)	Tajique (19)
IDH-1	117			0.04							
	100	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00	1.00
IDH-2	138			0.04							
	100	1.00	1.00	0.96	1.00	1.00	1.00	1.00	1.00	1.00	1.00
6-PGD	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97
	67										0.03
PGM-1	131									0.03	
	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.97	1.00
PGI	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.82
	12										0.18
ADH	−114	1.00	1.00	1.00	0.83	0.50	0.62	0.75	0.87	1.00	1.00
	−100				0.17	0.50	0.38	0.25	0.13		
Est-4	106			0.02		0.25	0.25				
	105			0.11	0.17	0.25					
	104			0.41							
	100	1.00	1.00	0.46	0.83	0.50	0.75	1.00	1.00	1.00	0.50
	96										0.05
	95										0.40
	89										0.05
Alb	104						0.13				
	103	1.00	1.00	1.00	1.00	1.00	0.87	1.00	1.00	1.00	1.00
Ga3PDH	119		0.20								
	100	1.00	0.80	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
ADA	100	1.00	1.00	1.00	0.92	0.94	1.00	1.00	1.00	1.00	1.00
	83				0.08	0.06					
	A	1.000	1.045	1.227	1.136	1.182	1.136	1.045	1.045	1.045	1.227
	H	0.000	0.000	0.015	0.023	0.030	0.023	0.023	0.011	0.003	0.036
	P	0.000	0.045	0.136	0.136	0.136	0.136	0.045	0.045	0.045	0.136



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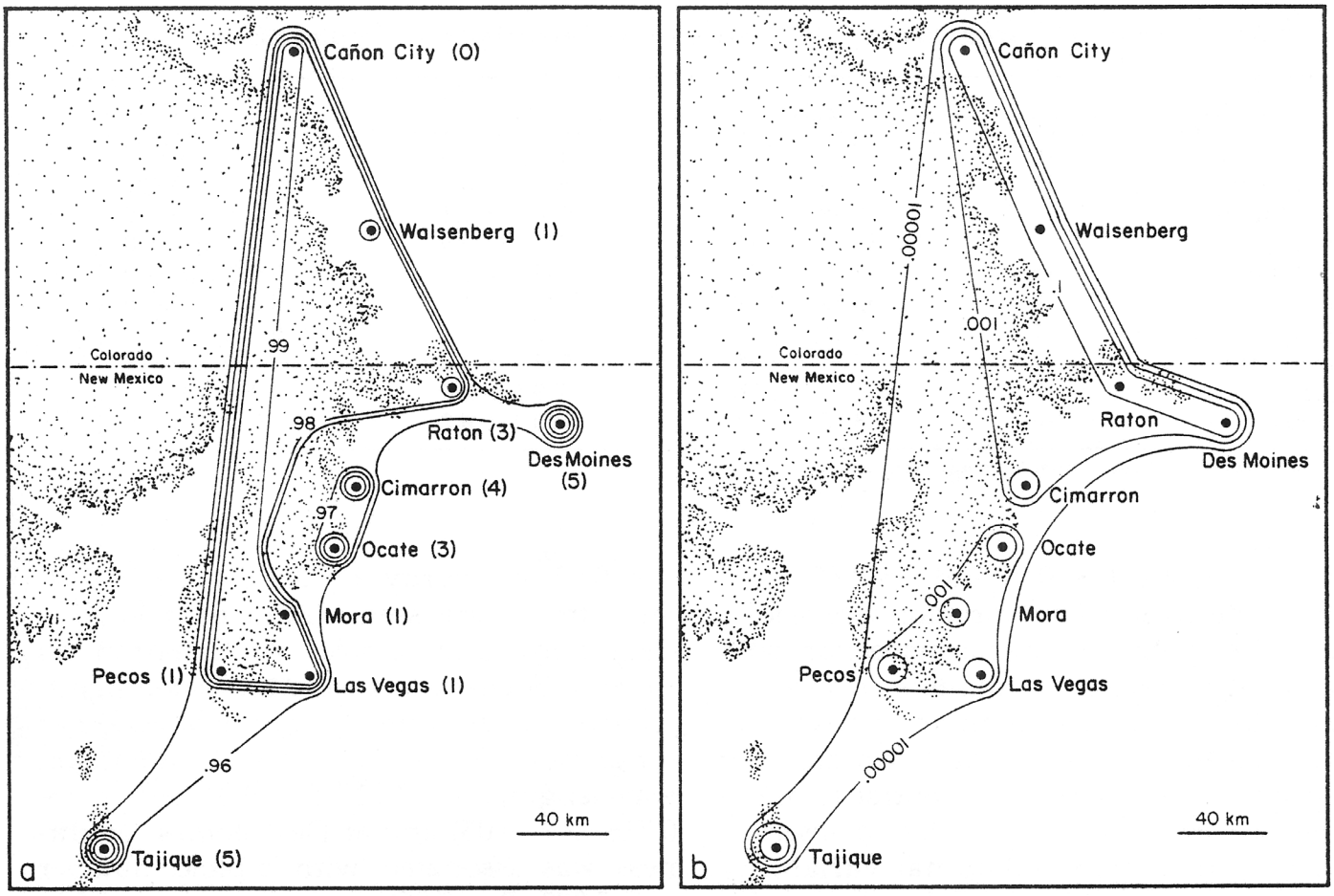

FIG. 4. (a) Isophene contours of electromorphic similarity values, based on UPGMA clustering of Rogers' similarity values, in the Sangre de Cristo contact region. The number of rare and/or unique alleles per locality is indicated in parentheses. (b) Isophene contours of morphometric similarity, based on *P*-values of intergroup multivariate *F*-statistics. The mountainous region above 7,500 ft (2,286 m) is illustrated by stippling.

and Renzi, 1979). Population variation over the entire region of study is significantly depressed for all three measures in comparison to the average sample of *T. bottae* from throughout its range ($P < 0.05$ in each case). Maximum heterozygosity and polymorphism values for these transect populations ($H = 0.036$ and $P = 0.136$) are, for example, less than one-third the values which are average for the species (Patton and Yang, 1977; unpubl. data). Intrapopulation variation does increase in magnitude towards the mid-transect region (between Pecos and Cañon City; Table 2). Again, this slight increase results from the presence of rare and/or unique alleles, not from increased levels of heterozygosity due to hybrid formation.

Electromorphic and chromosomal variation.—As is evident in Figure 4a, chromosomally defined parental populations (Pecos and Cañon City) are not electromorphically separable. In fact, no concordance was found between pan-zonal patterns of protein and chromosomal variation (neither individual heterozygosity values versus diploid numbers, individual genotypes versus numbers of chromosomes, nor heterozygosity estimates per population versus coefficient of variation in diploid number; $P > 0.05$ in all comparisons).

Colorimetric Analysis

Interpopulational trends.—Summary statistics for the three colorimetric variables (brightness, dominant wavelength, and purity) for each transect locality are presented in Table 3. In parallel with diploid number, pelage color varies clinally through the transect area. From Pecos to Cañon City, both relative brightness and purity increase lin-

TABLE 3. Descriptive statistics ($\bar{x} \pm 2$ SE) for colorimetric variables in 10 populations of *T. bottae*.

Locality	*n*	Brightness	Dominant wavelength	Purity
Cañon City	10	57.49 ± 2.14	588.7 ± 0.5	0.101 ± 0.015
Walsenburg	15	55.29 ± 1.69	588.7 ± 0.8	0.097 ± 0.011
Des Moines	30	55.39 ± 1.50	588.4 ± 1.1	0.099 ± 0.008
Raton	8	53.52 ± 2.11	590.5 ± 0.9	0.103 ± 0.010
Cimarron	18	53.70 ± 1.68	592.1 ± 2.0	0.081 ± 0.010
Ocate	9	53.74 ± 2.79	591.1 ± 1.6	0.085 ± 0.016
Mora[a]	1	51.88	592.0	0.092
Las Vegas	9	49.60 ± 1.98	593.9 ± 2.6	0.069 ± 0.015
Pecos	15	52.74 ± 1.96	589.5 ± 0.9	0.088 ± 0.012
Tajique	16	48.83 ± 1.61	600.3 ± 6.2	0.042 ± 0.009

[a] One melanistic individual from Mora was excluded for the analysis.

early ($r = 0.864$, $P < 0.01$ and $r = 0.683$, $P < 0.05$, respectively). This variation was readily apparent by cursory visual inspection both in the field and in the museum: pocket gophers from southern localities appear dark and reddish, those from the north are light and buffy, and those from central localities intermediate in color. There was no observed increase in intrapopulational variability (based on sample CVs) of the three color variables in the mid-cline region.

Colorimetric variation and chromosome number.—Variation in both colorimetric and karyotypic data is aligned in a clinal array across the transect (Table 3 and Fig. 2). To eliminate the covariant effect of geography, we compared individual colorimetric variables and diploid numbers from only the three mid-transect localities (Cimarron, Raton, and Des Moines; $n = 21$). Justification for the pooling of these samples is two-fold: (1) they are in rather close proximity and are located at the same relative position along the cline, as evidenced by both geographic position and mean value equivalence in both colorimetric characters and diploid number; and (2) the environment in this region is homogeneous (moderately dark-colored soils supporting "plains region" vegetation) and without obvious physiographic disruptions to potential pocket gopher movement.

An individual's pelage color is strongly predictive of its diploid number (Fig. 5). All three colorimetric variables were associated significantly with karyotypes of the individuals: brightness, $r = 0.832$ and $P < 0.01$ (Fig. 5); dominant wavelength, $r = -0.534$ and $P < 0.05$; and purity, $r = 0.550$ and $P < 0.01$. Such trends are seen within each locality, despite low sample sizes. At Cimarron, all three color characters were correlated significantly with number of chromosomes (brightness, $r = 0.958$, $P < 0.01$; dominant wavelength, $r = -0.927$, $P < 0.01$; purity, $r = 0.716$, $P < 0.05$) and at Des Moines, brightness was associated with diploid number ($r = 0.820$, $P < 0.05$).

Morphometric Analysis

Geographic variation.—Summary statistics for the 12 cranial and external variables are presented in Table 4. A contour map based on *P*-values of intergroup *F*-statistics (Fig. 4b) indicates a high degree of interlocality differentiation between central and southern populations, while those from northern New Mexico and Colorado are not separated by abrupt morphological shifts. The indicated groupings do not coincide with the established subspecific boundaries (see Fig. 2).

The geographic pattern of morphometric variability was examined by the correlation analysis of sample mean coefficient of variation (CV) for the 12 ratio variables and geographic position. A strong south to north linear increase in average population variability was evident ($r = 0.884$, $P < 0.01$); no mid-transect increase in variability similar to that found for electromorphic characters was observed.

Morphologic variation and chromosome number.—As in the colorimetric analysis, comparison of an individual's diploid number and morphologic variation was restricted to

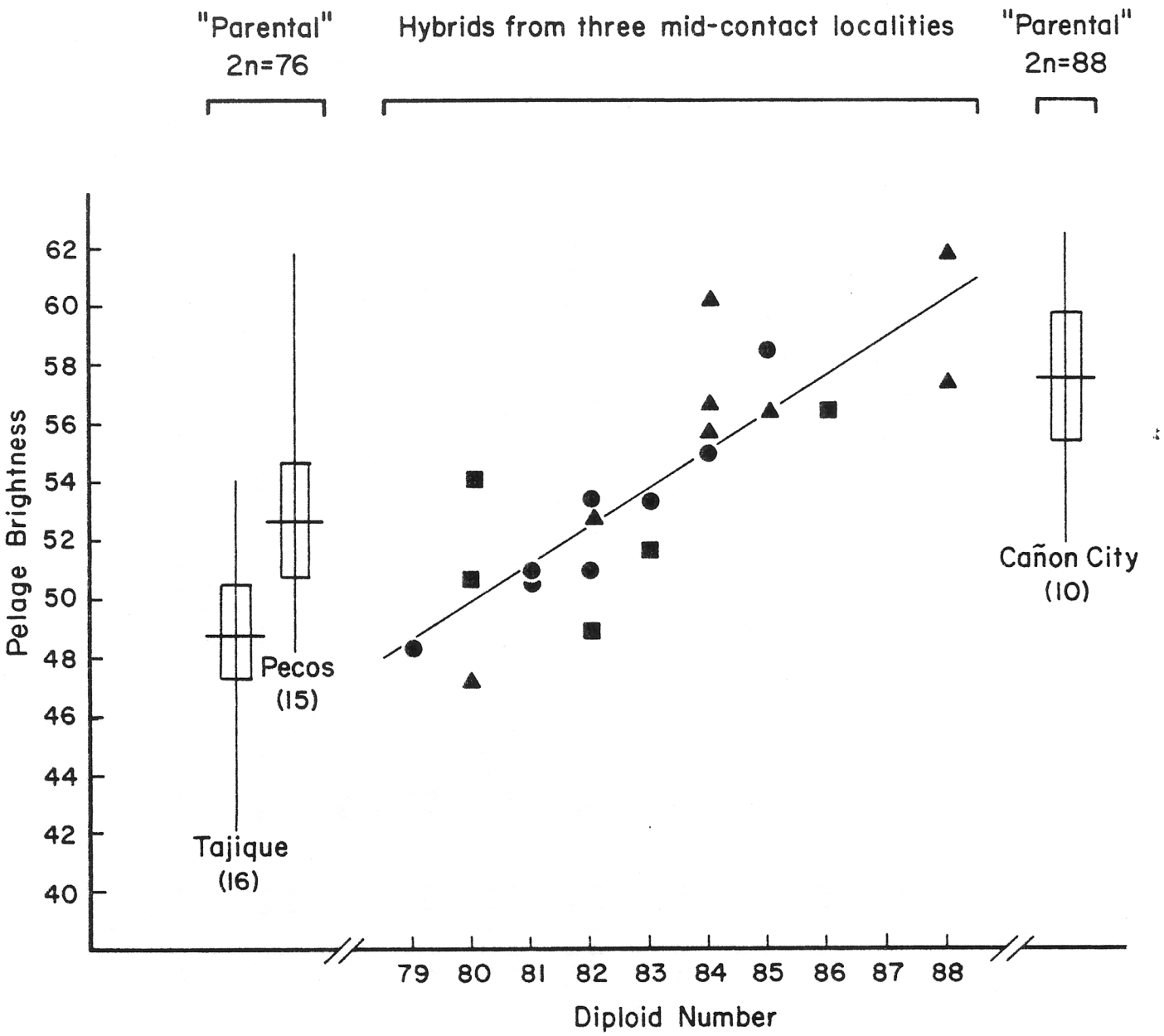

FIG. 5. Relationship between an individual's pelage color (brightness) and diploid number at the mid-contact region in the Sangre de Cristo transect ($r = 0.832$, $P < 0.01$). Pocket gophers from Cimarron are indicated by dots, those from Raton by squares, and those from Des Moines by triangles. Dice-Lerass graphs provide means and ranges (±2 SE in boxes) for the parental populations.

the three mid-transect localities (Cimarron, Raton, and Des Moines). Correlation analyses based on morphologic factor scores (from factor analysis) as well as individual character values revealed no significant associations ($P > 0.05$) between chromosome number and external or cranial characters.

Correspondence Among Data Sets

The pan-zonal patterns of chromosomal (2n), colorimetric (mean pelage brightness), and morphometric (mean CV) variation document south to north clinal trends (at $P <$ 0.01 level). The general level of correspondence among the three clines is good, with all pair-wise comparisons producing significant correlation coefficients (Table 5). On the average, geographic position is strongly correlated with karyology while less so with pocket gopher exomorphology. Although electromorphic comparisons detected no clinal trend, but instead high similarity throughout the region, the existence of rare and unique alleles in centrally located populations serves as an independent means in identifying the mid-contact or null region.

TABLE 4. Descriptive statistics ($\bar{x} \pm 2$ SE) for the morphometric variables in 10 populations of *T. bottae*.

Population	*n*	ToL	TaL	HF	EL	ONL	PRO	ZB	MB
Cañon City									
♂	3	237.7 ± 20.5	79.0 ± 7.0	32.7 ± 2.4	8.0 ± 1.2	41.5 ± 3.5	42.0 ± 4.3	25.4 ± 2.9	20.9 ± 1.7
♀	2	215.5 ± 5.0	73.0 ± 0.0	30.0 ± 0.0	7.0 ± 0.0	37.7 ± 1.5	37.5 ± 0.9	22.7 ± 0.3	19.2 ± 0.1
Walsenburg									
♂	1	234.0	70.0	31.0	6.0	41.6	41.2	25.2	20.6
♀	2	217.5 ± 15.0	66.0 ± 4.0	29.5 ± 1.0	5.0 ± 0.0	37.5 ± 1.1	36.9 ± 1.6	22.2 ± 0.8	18.8 ± 0.3
Des Moines									
♂	12	229.1 ± 6.8	73.9 ± 2.5	29.9 ± 0.8	6.5 ± 0.4	39.6 ± 0.9	39.4 ± 0.8	24.1 ± 0.6	19.8 ± 0.4
♀	5	213.4 ± 11.3	68.0 ± 6.9	27.8 ± 1.2	6.4 ± 0.5	36.9 ± 1.1	36.6 ± 1.1	21.9 ± 0.8	18.3 ± 0.5
Raton									
♂	2	237.0 ± 10.0	78.0 ± 6.0	30.5 ± 1.0	7.5 ± 1.0	40.9 ± 0.7	41.3 ± 1.5	23.5 ± 3.6	20.6 ± 0.6
♀	5	209.8 ± 3.2	66.0 ± 2.8	28.6 ± 1.0	7.0 ± 0.6	38.2 ± 0.5	38.2 ± 0.5	23.6 ± 0.3	19.3 ± 0.2
Cimarron									
♂	4	240.3 ± 10.9	84.5 ± 5.7	31.8 ± 1.0	7.5 ± 1.0	41.6 ± 2.3	42.4 ± 2.6	25.8 ± 1.6	20.9 ± 0.9
♀	4	223.8 ± 6.1	73.5 ± 3.4	29.8 ± 0.5	7.8 ± 0.5	38.9 ± 0.8	39.2 ± 0.9	23.8 ± 0.5	19.4 ± 0.3
Ocate									
♂	2	234.5 ± 5.0	77.5 ± 5.0	31.0 ± 2.0	8.0 ± 0.0	41.4 ± 2.0	40.5 ± 2.2	25.4 ± 1.2	20.2 ± 0.5
♀	4	216.3 ± 6.3	71.8 ± 4.5	29.8 ± 1.3	6.3 ± 1.3	37.6 ± 1.1	36.9 ± 1.2	22.3 ± 0.5	18.4 ± 0.5
Mora									
♀	2	221.5 ± 7.0	76.0 ± 6.0	28.5 ± 1.0	8.0 ± 0.0	38.4 ± 0.5	38.5 ± 0.2	23.3 ± 0.8	18.8 ± 0.3
Las Vegas									
♂	1	235.0	74.0	30.0	8.0	41.7	41.9	26.7	20.8
♀	5	215.2 ± 6.7	70.2 ± 3.0	29.2 ± 0.7	6.8 ± 0.4	38.4 ± 0.5	38.0 ± 0.6	23.1 ± 0.5	19.2 ± 0.4
Pecos									
♂	3	250.3 ± 4.1	86.3 ± 7.3	31.3 ± 0.7	6.7 ± 0.7	42.2 ± 1.1	42.5 ± 1.1	26.6 ± 0.5	20.7 ± 0.4
♀	3	238.0 ± 9.2	75.7 ± 5.3	30.7 ± 0.7	6.3 ± 0.7	39.8 ± 1.1	39.9 ± 1.5	24.4 ± 0.7	20.1 ± 0.5
Tajique									
♂	7	221.3 ± 9.0	69.0 ± 6.3	28.7 ± 0.8	5.9 ± 0.3	39.1 ± 1.3	38.7 ± 1.4	24.0 ± 1.2	19.6 ± 0.7
♀	15	209.1 ± 5.2	59.5 ± 4.0	28.0 ± 0.6	5.8 ± 0.3	37.5 ± 0.4	36.8 ± 0.4	22.4 ± 0.3	18.8 ± 0.2

TABLE 4. Continued.

Population	*n*	IOC	NL	RW	BuL	BuW	MTRL	PW	DL	$\overline{CV}$[a]
Cañon City										5.58
♂	3	6.5 ± 0.1	14.7 ± 1.5	8.5 ± 1.0	8.1 ± 1.5	5.4 ± 0.8	8.0 ± 0.3	1.9 ± 0.1	8.1 ± 1.8	
♀	2	6.7 ± 0.1	13.2 ± 1.0	7.7 ± 0.5	8.0 ± 0.1	4.7 ± 0.4	7.8 ± 0.4	1.8 ± 0.1	6.5 ± 0.4	
Walsenburg										5.57
♂	1	6.5	15.3	8.2	7.9	4.6	8.0	1.7	8.0	
♀	2	6.4 ± 0.3	12.9 ± 0.5	7.5 ± 0.3	8.2 ± 0.5	5.2 ± 1.0	7.9 ± 0.3	1.6 ± 0.1	6.1 ± 0.8	
Des Moines										4.22
♂	12	6.5 ± 0.1	14.2 ± 0.6	7.6 ± 0.2	8.1 ± 0.2	5.3 ± 0.3	8.0 ± 0.2	1.8 ± 0.1	6.9 ± 0.3	
♀	5	6.4 ± 0.1	12.9 ± 0.4	7.0 ± 0.1	7.7 ± 0.3	5.2 ± 0.5	7.7 ± 0.2	1.7 ± 0.2	6.3 ± 0.2	
Raton										4.54
♂	2	6.3 ± 0.3	14.4 ± 0.4	7.9 ± 0.3	8.3 ± 0.4	4.7 ± 0.2	8.3 ± 0.1	1.7 ± 0.5	7.7 ± 0.6	
♀	5	6.7 ± 0.2	13.2 ± 0.4	7.6 ± 0.3	8.1 ± 0.2	4.7 ± 0.1	7.9 ± 0.5	1.9 ± 0.2	6.9 ± 0.3	
Cimarron										4.55
♂	4	6.4 ± 0.3	14.6 ± 1.4	8.1 ± 0.5	8.2 ± 0.7	5.9 ± 0.1	8.0 ± 0.2	1.9 ± 0.2	8.4 ± 1.0	
♀	4	6.6 ± 0.5	13.4 ± 0.3	7.5 ± 0.3	8.4 ± 0.1	5.5 ± 0.4	7.7 ± 0.4	2.1 ± 0.2	7.4 ± 0.3	
Ocate										4.64
♂	2	6.4 ± 0.3	15.4 ± 0.8	8.1 ± 0.5	8.0 ± 0.5	5.5 ± 0.8	8.3 ± 0.3	1.9 ± 0.1	7.5 ± 1.2	
♀	4	6.4 ± 0.2	12.9 ± 0.5	7.4 ± 0.3	8.1 ± 0.5	4.8 ± 0.6	8.2 ± 0.3	1.7 ± 0.1	6.6 ± 0.5	
Mora										3.25
♀	2	6.6 ± 0.4	13.4 ± 0.8	7.2 ± 0.0	7.6 ± 0.4	5.8 ± 0.2	8.0 ± 0.0	1.9 ± 0.3	6.6 ± 0.3	
Las Vegas										3.52
♂	1	6.8	14.5	8.0	8.2	4.8	8.3	2.0	7.7	
♀	5	6.5 ± 0.2	13.1 ± 0.6	7.4 ± 0.2	8.2 ± 0.2	5.2 ± 0.2	7.5 ± 0.2	1.8 ± 0.1	7.1 ± 0.2	
Pecos										3.73
♂	3	6.7 ± 0.3	15.5 ± 0.4	8.1 ± 0.4	8.1 ± 0.3	5.4 ± 0.1	8.4 ± 0.3	1.8 ± 0.2	8.0 ± 0.3	
♀	3	6.9 ± 0.2	13.6 ± 1.1	7.6 ± 0.4	8.3 ± 0.1	5.2 ± 0.3	8.2 ± 0.4	1.9 ± 0.1	7.1 ± 0.6	
Tajique										4.52
♂	7	6.3 ± 0.1	14.1 ± 0.8	7.5 ± 0.4	8.2 ± 0.3	5.3 ± 0.4	7.8 ± 0.3	1.7 ± 0.1	6.6 ± 0.3	
♀	15	6.6 ± 0.1	13.1 ± 0.2	7.1 ± 0.1	8.1 ± 0.1	5.0 ± 0.1	7.8 ± 0.1	1.8 ± 0.1	6.4 ± 0.2	

[a] $\overline{CV}$ computed for ratio data (original variable divided by ONL) with sexes pooled, but not including TaL, EL, ONL, or ZB (see text).

TABLE 5. Pearson product-moment correlation coefficients documenting the relationships among mean diploid number, mean pelage brightness, mean morphometric CV, and geographic position of *T. bottae* populations along the Sangre de Cristo transect.

	Variables			
Variables	Mean diploid number	Mean pelage brightness	Mean morphometric CV	Mean *r*
Distance north (km)	0.921**	0.864**	0.884**	0.890
Mean diploid number		0.683*	0.697*	0.767
Mean pelage brightness			0.830**	0.792
Mean morphometric CV				0.804

* $P < 0.05$; ** $P < 0.01$.

DISCUSSION

Sangre de Cristo Cline

Distribution, environment, and history.— Pocket gophers of the narrow peninsular distribution along the eastern flank of the Sangre de Cristo Mountains (Figs. 1 and 2) are the only populations of *T. bottae* known to encroach on and inhabit the environs of the Great Plains biotic region. In general, these populations are found at the ecotone of coniferous forests and prairie. Although this habitat is continuous along the front range of the Sangre de Cristos, *T. bottae* populations in the region appear rather small and well isolated from one another. Average estimates of pocket gopher densities at collecting localities (based on the number of active individual pocket gopher mound systems) were on the order of 2.5 individuals per hectare. This estimate is considerably below published figures in other regions, where maximal densities reach 60 breeding adults per hectare (Howard and Childs, 1959; Hansen and Remmenga, 1961; Patton and Feder, 1981).

These populations may be small and isolated due both to biotic (competition with other species of pocket gophers) and abiotic (climate and geography) factors. Species and even genera of pocket gophers are largely contiguously allopatric in distribution because of an apparent inability to subdivide the fossorial niche (for review see Nevo, 1979). Populations of *T. bottae* in the study region are wedged between those of three other pocket gophers: *T. talpoides* occurs in the mountains to the west, *Geomys bursarius* is found in the plains to the northeast, and *Pappogeomys castanops* inhabits the prairie to the southeast (Miller, 1964; Best, 1973). Importantly, Miller's (1964) classic study which encompassed this region concluded that, in respect to a dominance hierarchy, *T. bottae* was subordinant to both *G. bursarius* and *P. castanops.* It is likely, therefore, that competitive interactions and concomitant distributional adjustments have punctuated the history of *T. bottae* populations in this region.

The habitat of *T. bottae* through the study area seems to be interrupted only by a physiographic baffle of basaltic tableland that extends eastward from the Sangre de Cristo Mountains well onto the Great Plains (northern Oklahoma) along the Colorado-New Mexico state boundary (see Fig. 2). This geologic formation appears to be an ineffective barrier to north–south pocket gopher movement since pocket gophers are present around and on the mesas (Best, 1973; Moulton et al., 1979), and the genic similarity values are near identity for populations on either side of the basaltic prominences. Hence, physiography per se does not seem to have contributed greatly to the fragmentation of *T. bottae* distribution in the area. Climatic changes associated with Pleistocene glaciations, however, may have had a profound effect on pocket gophers. The Sangre de Cristo Mountains held glaciers during various junctures of the Pleistocene (Ray, 1940; Richmond, 1963, 1965), and life zones in the region were lowered thousands of feet (Harris and Findley, 1964; Harris, 1970). We can only speculate as to the exact influence the Pleistocene glaciations may have had, although range shifts of pocket gophers would certainly have occurred in response to fluctuating climate and consequent vegetation zones. Populations of *T. bottae* very likely

became fragmented and isolated in east-central New Mexico, separated from conspecifics by both inhospitable habitats and the inescapable competitive interactions with other species of pocket gophers.

Population structure and genetic variability.—Populations of *T. bottae* along the Sangre de Cristo transect appear to be both small and unevenly distributed. This geographic pattern, in combination with the small measured individual dispersal distances for the species (Howard and Childs, 1959; Vaughan, 1963), suggests reduced effective population sizes which, theoretically, would facilitate rapid fixation of differing genetic characteristics (Wright, 1931, 1940; Mayr, 1970; Carson, 1971; Bush, 1975). This theoretical view is supported by the breeding structure of pocket gophers, where skewed sex ratio, unequal male reproductive success, and small census numbers result in a highly non-random mating system (Patton and Feder, 1981). However, while the populations sampled here did display both very low within population genic variability and a high degree of similarity to one another ($S > 0.95$), they are chromosomally quite polymorphic.

There are two predominant hypotheses to explain these contradictions in genetic variability levels across the transect. The first is a vicariant model of population isolation in two refugia (one in the north and the second in the south), where bottleneck effects lower genic variation and where differentiation in karyotypes results. Genic variation would remain low even following secondary contact because drift in fragmented populations would eliminate new mutants. A chromosomal cline could result from low gene flow despite drift due either to (1) a higher mutation rate than that for electromorphs or (2) meiotic drive. A cline could also result from active spread due to positive karyotypic selection. The alternative explanation is that former population isolation (if any) is irrelevant, with the electromorphs selectively neutral and the extra chromosomal elements selected for in the northern part of the range. We favor the first of these two general hypotheses, for reasons given below, although adequate tests for either have not been performed.

Population cytogenetics.—Chromosomal data are available from well over 2,000 individuals, representing approximately 150 populations from throughout the range of *T. bottae*. Karyotypic variation, although extensive, consists almost exclusively of shifts in arm number due to addition and/or deletion of whole-arms of heterochromatin; nearly all individuals examined have 76 chromosomes (Patton and Sherwood, 1982; Sherwood and Patton, 1982). The Sangre de Cristo populations are chromosomally aberrant with respect to our earlier understanding of *T. bottae* cytogenetics (Patton, 1972, 1981).

The direction of chromosome evolution in this case undoubtedly involved an increase in diploid number. This is supported by both commonality (in-group analysis) and outgroup comparison with the other three species in the subgenus *Megascapheus*, each of which is either $2n = 76$ or 78 (Thaeler, 1980; Patton, 1981). The only difference between the $2n = 76$ and other karyotypes in the Sangre de Cristo area is the addition of up to 12 small acrocentric and totally heterochromatic chromosomes to the complement (Fig. 3). The karyological mechanism(s) responsible for the increase in chromosome number are not immediately apparent but, clearly, simple centric dissociations are not involved. With respect to size, heterochromatic nature, and variability within and between populations, this additional complement of chromosomes resembles a supernumerary (or B-chromosome) system (reviewed by Jones and Rees, 1982).

Width of the contact zone.—Three separate clines, or linear trends (at $P < 0.01$), were observed in this study: mean diploid number, pelage brightness, and mean morphometric CV. The width of any cline, w, is the distance between points where the gradient varies from 0.2 to 0.8 (e.g., May et al., 1975; Endler, 1977; Barrowclough, 1980; Hafner, 1982). In the present case, therefore, w is approximately 200 km for each cline. Further, clinal null points are roughly coincidental and fall within the mid-contact region (vicinity of Cimarron, Raton, and Des Moines) delineated in the electromorphic analysis (see above).

The relative size of each cline (w/l, where

l is the gene flow parameter) is the appropriate measure for comparison of cline widths across different situations or taxa. Gene flow estimates for pocket gophers suggest that l is on the order of 0.1 km/generation, with a single generation per year (Howard and Childs, 1959; Vaughan, 1963). Thus, the relative width of the Sangre de Cristo contact is approximately 2,000, which is an exceedingly broad cline (Endler, 1977: 165–167).

Selection across the cline.—Several kinds of selection may be in operation along the Sangre de Cristo transect: (1) selection gradients which can balance gene flow and maintain each cline; (2) selection against heterozygotes (i.e., diploid numbers other than 76 or 88) due to coadaptive breakdown; and (3) heterozygote advantage, or heterosis. The hypothesis that the clines are selectively maintained is testable through the application of static cline models involving gene flow-selection equilibria (Slatkin, 1973; May et al., 1975; Nagylaki, 1975; Endler, 1977). The available single-locus models are generally appropriate, even for traits such as those observed here that are likely to be under polygenic control (Slatkin, 1975, 1978).

In single locus clines with homogeneous gene flow, sizable populations, and no dominance, the selection gradient (b) is described by the relationship $b = l^2(1.66/w)^3$. We use Endler's (1977) gradient model to estimate b since the terminal habitats along the transect were ecologically similar and without a sharp ecotone. Using the estimates for l and w given above, b is approximately 5.7×10^{-9} km^{-1} for each of the three clines. Thus, the level of selection necessary to maintain a cline is so weak as to be impossible to demonstrate in the field. Even if published gene flow estimates are grossly underestimated (a likely possibility; see below), an l of 1 km/generation still yields a very weak selection gradient. Clearly, there is no reason to invoke a large selection gradient for the maintenance of the three observed clines.

Coadaptive differentiation, which may accompany hybridization following secondary contact, might result in negatively heterotic effects. We evaluated this possibility by comparing the observed array of diploid numbers across the transect (Fig. 2) with that predicted from simple probability distributions. Table 6 compares the observed chromosome number frequencies with those expected from the expansion of the binomial $(a + b)^x$, where a and b represent the probabilities of the 2n = 76 and 2n = 88 phenotypes, respectively. The probabilities of a (and hence, b) were determined by the position of the populations in the zone. For example, we predict (extrinsic of the data) that in the center of the cline (Cimarron, Raton, and Des Moines) there would be an equal probability of finding a 2n = 76 or 88 individual. Therefore, the study populations were divided into three geographic regions reflecting regions where $a = 0.75$, $a = 0.50$, and $a = 0.25$ (Table 6). Classes were pooled when expected frequencies were less than five (following Sokal and Rohlf, 1969:565). In each of the three regions the chi-square value is non-significant (Table 6). We cannot, therefore, reject the null hypothesis that the observed array of diploid numbers results from simple neutral diffusion due to hybridization. This does not preclude, however, the possibility of weak selection on a cline at or near equilibrium. Increased sample sizes will be necessary to resolve these possibilities.

Finally, a cline may be very broad, not by virtue of response to a selection gradient, but if there is any heterozygous advantage. That advantage can be estimated as $h = wb/1.2$ (Endler, 1977). However, in this context, b cannot be determined directly from the cline in question as was done above, and this possibility cannot be evaluated at the moment.

Primary intergradation or secondary contact.—The three clinal patterns in *T. bottae* along the Sangre de Cristo Mountains may be due either to primary divergence within a continuous distribution or to secondary contact, as noted above. In either case, the differences across the gradients may have developed by selection and/or drift. The possibility of random divergence among contiguous populations (see Endler, 1977) can be discounted because of the highly coincidental nature of the three clines (Table 5).

Endler (1977) noted that it is impossible to distinguish between primary and secondary contact for any single cline by merely ex-

TABLE 6. Comparison of observed distribution of diploid numbers with that expected from the binomial probability distribution (see text for discussion).[a]

Chromosomes per individual	Las Vegas, Mora, Ocate ($a = 0.75$; $b = 0.25$)				Cimarron, Raton, Des Moines ($a = 0.50$; $b = 0.50$)				Walsenburg ($a = 0.25$; $b = 0.75$)			
	f		$\hat{f}$	Deviation from $\hat{f}$	f		$\hat{f}$	Deviation from $\hat{f}$	f		$\hat{f}$	Deviation from $\hat{f}$
76	0		0.29		0		0.01		0		0.00	
77	0		1.14		0		0.06		0		0.00	
78	2	4	2.09	5.84 –	0	4	0.34	4.07 0	0		0.00	
79	2		2.32		1		1.13		0		0.00	
80	2		1.74		3		2.54		0		0.01	
81	0		0.93		2		4.06	–	0	1	0.03	1.83 –
82	1		0.36		4		4.74	0	0		0.12	
83	1		0.10		2		4.06	–	0		0.31	
84	1	5	0.02	3.16 +	4		2.54		0		0.58	
85	0		0.00		2		1.13		1		0.77	
86	0		0.00		1	9	0.34	4.07 +	0		0.70	
87	0		0.00		0		0.06		0	2	0.38	1.17 +
88	0		0.00		2		0.01		2		0.10	
Total	9		9.00		21		21.00		3		3.00	
	$\chi^2 = 1.649$ $\chi^2_{0.05[1]} = 3.841$				$\chi^2 = 8.177$ $\chi^2_{0.05[4]} = 9.488$				$\chi^2 = 0.096$ $\chi^2_{0.05[1]} = 3.841$			

[a] f = observed frequencies; $\hat{f}$ = expected frequencies from binomial expansion.

amining the cline's characteristics. Barrowclough (1980) and Hafner (1982) have argued, however, that the coincidence of several independent clines suggests secondary contact, as primary intergradation would require either mutual dependence of the characters examined (epistatic interactions or tight linkage) or identical selection gradients generating homogeneous cline widths. The possibility of character dependence cannot be ruled out in the present case because the strong relationship between an individual's pelage color and diploid number in mid-transect localities suggests linkage disequilibrium. Further, while the three clines are identical in cline width, many more localities need to be examined before the statistical concordance of the observed clines can be tested (Endler, 1977). Finally, a general environmental gradient does exist along the transect (Hopkins, 1938), and it is always possible that the three variables examined are independently responding to this gradient.

Nevertheless, the data available do not rule out the possibility that the clines result from genetic interaction following secondary contact. Certainly, the selection gradient necessary to balance gene flow and maintain any of the clines appears quite small. Furthermore, the existence of regionally rare and/or unique alleles in the mid-transect region (see Table 2, Fig. 4a) is suggestive of the mutator release phenomenon resulting from hybridization between differentiated strains of *Drosophila* and geographic populations of several vertebrates (see Sage and Selander, 1979).

A secondary contact hypothesis does imply that the clines are dynamic with the observed variability resulting from hybridization between previously allopatric northern and southern populations. Time since secondary contact can be estimated by the relationship $T = 0.35(w/l)^2$ (Endler, 1977:93); this provides an estimate of 1.4 million years BP using the values of zone width given above and gene flow estimates from the literature. While the early Pleistocene was doubtlessly a time of species multiplication for *Thomomys* (the genus dates from the late Pliocene; Russell, 1968), such an early time of contact between chromosomal forms which are virtually identical electromorphically appears to be off by two or more orders of magnitude. There are several possible reasons for this seemingly unrealistic estimate, not the least of which may be the inappli-

cability of this equation in situations involving broad clines. Endler (1977:165–167) noted that in all broad clines examined (where $w/l = 250$–$4{,}000$), the clines are so flat that the estimates of age of secondary contact are too high to be real. It is also very likely that literature estimates of the gene flow parameter (l) of 0.1 km/generation are too small (e.g., Howard and Childs, 1959; Vaughan, 1963). A value for l of 0.5 km/generation would reduce the estimated time since contact to 72,000 years BP. We have argued elsewhere that gene flow in pocket gophers is considerably higher than commonly believed (Patton and Yang, 1977; Patton, 1983; see also Slatkin, 1981), and this view is supported by recent dispersal studies (J. C. Daly, pers. comm.).

Synthesis of T. bottae Contact Zones

Genetic data of two types (chromosomal and electromorphic) as well as morphological information are available from each of five parapatric zones of contact in *bottae*-group pocket gophers (Fig. 1, Table 7). Zone widths were estimated using conventional boundary limit criteria (see above and May et al., 1975; Endler, 1977); that for the Sangre de Cristo contact was derived from all three phenotypic gradients discussed above while width estimates for the Rio Grande and White-Sacramento Mountains contacts relied on extrapolation from genic index scores. No widths could be estimated for either the Patagonia Mountains or Colorado River contacts; the former involves reproductively isolated species and in the latter gopher populations are not now in direct contact, but are separated by physiographic barriers.

The width of the zone reported in this paper (ca. 200 km) is considerably larger than the estimates for either the Rio Grande (ca. 5 km) or White-Sacramento Mountains (ca. 1 km) contacts, although each of these may represent a situation of hybridization following secondary contact (Table 7). In Endler's (1977:91–93) neutral diffusion model, the width of a cline is a function of the rate of gene flow and the time since contact. The greater width of the Sangre de Cristo zone, then, would result from either a much higher rate of gene flow or a considerably longer time since secondary contact (about 10^6 years as opposed to less than 10^4 years). The very high genic similarity values among populations in this area support recency of divergence, but not unequivocably. There is, however, no reason to invoke a higher rate of gene flow. Although gene flow rates undoubtedly vary throughout the species' range, as suggested earlier (Patton and Yang, 1977), it seems unlikely that pocket gophers disperse much farther on the average in this area than in other parts of their distribution. Dispersal distances would have to vary by one or more orders of magnitude in order to affect the calculations presented. Therefore, a simple neutral diffusion model does not by itself explain the observed gradients.

Contact zone widths may also be maintained by a dynamic balance between gene flow and selection (Fisher, 1937, 1950; Haldane, 1948; Basykin, 1969; Slatkin, 1973; May et al., 1975; Endler, 1977; Barton and Hewitt, 1981). Accepting that gene flow rates are uniform across the species range, the marked differences in width among these three pocket gopher contacts seem best explained by a combination of the environmental setting and the fitness deficit of hybrids at the zones. The narrowness of the Rio Grande contact is readily explained by the rather pronounced physiographic constriction that undoubtedly restricts pocket gopher movement along the river terrace (Table 7; see Smith et al., 1983); a steep selection gradient need not be invoked for this relatively abrupt 5-km cline. The White-Sacramento Mountains and the Sangre de Cristo contacts, by comparison, contain no barriers to gopher dispersal. The significant distinction between these zones, other than their widths, is the clearly demarcated and rather abrupt ecological transition (2 km) between the parental habitats at the White-Sacramento Mountains contact (Patton et al., 1979) but not across the Sangre de Cristo zone. Cline models based on a balance between gene flow and selection yield estimates of the selection coefficient (s) on the order of 8 to 9% against hybrids in the former region, a significant value compared to the diminutive s of 2×10^{-6} estimated for the latter (where $s =$

TABLE 7. Characteristics of contact zones in *bottae*-group pocket gophers.

Extent of divergence		Geographic and ecological setting	Zone width (km)	Genetic interaction	Reference
Chromosomal	Genic[a]				
Patagonia Mountains (*T. bottae–T. umbrinus*)					
Extensive (structural transpositions and 2n: 76 vs. 78)	Moderate $\bar{S} = 0.845$	Extensive habitat differences; no topographic barrier	N.A.[b]	Reproductive isolation	Patton and Dingman (1968), Patton et al. (1972), Patton (1973)
White-Sacramento Mountains (*T. b. ruidosae–T. b. actuosus*)					
Extensive (uniarm range 0–32)	Moderate $\bar{S} = 0.807$	Extensive habitat differences; no topographic barrier	ca. 1	Introgressive hybridization	Patton et al. (1979)
Colorado River (*T. bottae* populations)					
Minimal	Extensive $\bar{S} = 0.670$	Minimal habitat difference; extensive topographic barrier	N.A.	Introgressive hybridization possible via peripheral populations	Smith and Patton (1980)
Rio Grande (*T. b. connectens–T. b. opulentus*)					
Extensive (uniarm range 0–34)	Extensive $\bar{S} = 0.687$	Minimal habitat difference; moderate topographic barrier	ca. 5	Low level of introgressive hybridization	Smith et al. (1983)
Sangre de Cristo Mountains (*T. bottae* populations)					
Extensive (2n range 76–88)	Minimal $\bar{S} > 0.950$	No habitat difference; topographic barrier	ca. 200	Introgressive hybridization	This paper

[a] Average of Rogers' similarity values between the differentiated units.
[b] N.A. = not applicable; zone width cannot be estimated because the situation does not fit the assumptions of the model.

$2[2l/w]^2$; Barton, 1979; Barton and Hewitt, 1981).

Earlier hybrid zone studies of fossorial rodents often relied on the morphologically defined geographical limits of the hybrid zone and number of identifiable hybrids as principal indicators of the actual dynamics of a particular zone (e.g., Thaeler, 1968, 1974; Patton, 1973; Nevo and Bar-El, 1976). Patton et al. (1979) urged caution in utilizing these criteria in the absence of genetic data, as a morphologically defined zone width is often strongly influenced by ecological gradients and may actually be a poor indication of the genetic dynamics of a given zone. Indeed, this point is illustrated well by the White-Sacramento Mountains, Rio Grande, and Sangre de Cristo contacts (Table 7); while each of these zones is characterized by extensive hybridization, the ecogeographic settings and the zone widths vary markedly.

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REFERENCES

BARROWCLOUGH, G. F. 1980. Genetic and phenotypic differentiation in a wood warbler (genus *Dendroica*) hybrid zone. Auk, 97:655–668.

BARTON, N. H. 1979. The dynamics of hybrid zones. Heredity, 43:341–359.

BARTON, N. H., AND G. M. HEWITT. 1981. A chromosomal cline in the grasshopper *Podisma pedestris*. Evolution, 35:1008–1018.

BASYKIN, A. D. 1969. A hypothetical mechanism of speciation. Evolution, 23:685–687.

BEST, T. L. 1973. Ecological separation of three genera of pocket gophers (Geomyidae). Ecology, 54: 1311–1319.

BUSH, G. L. 1975. Modes of animal speciation. Ann. Rev. Ecol. Syst., 6:339–364.

CARSON, H. L. 1971. Speciation and the founder principle. Stadler Symp., 3:51–70.

COOPER, J. E. K., AND T. C. HSU. 1972. The C-band and G-band patterns of *Microtus agrestis* chromosomes. Cytogenetics, 11:295–304.

ENDLER, J. A. 1977. Geographic variation, speciation, and clines. Princeton Univ. Press, Princeton, New Jersey.

FISHER, R. A. 1937. The wave of advance of an advantageous gene. Ann. Eugen., 7:355–369.

FISHER, R. A. 1950. Gene frequencies in a cline determined by selection and diffusion. Biometrics, 6: 353–361.

GOLDMAN, E. A. 1936. New pocket gophers of the genus *Thomomys*. J. Wash. Acad. Sci., 26:111–120.

GORMAN, G. C., AND J. RENZI, JR. 1979. Genetic distance and heterozygosity estimates in electrophoretic studies: Effects of sample size. Copeia, 1979: 242–249.

HAFNER, J. C. 1982. Genetic interactions at a contact zone of *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Evolution, 36:852–862.

HALDANE, J. B. S. 1948. The theory of a cline. J. Genet., 48:277–284.

HANSEN, R. M., AND E. E. REMMENGA. 1961. Nearest neighbor concept applied to pocket gopher populations. Ecology, 42:812–814.

HARRIS, A. H. 1970. The Dry Cave mammalian fauna and late pluvial conditions in southeastern New Mexico. Texas J. Sci., 22:3–27.

HARRIS, A. H., AND J. S. FINDLEY. 1964. Pleistocene-Recent fauna of the Isleta Caves, Bernalillo County, New Mexico. Am. J. Sci., 262:114–120.

HELWIG, J. T., AND K. A. COUNCIL. 1979. SAS user's guide, 1979 edition. SAS Institute, Cary, North Carolina.

HOPKINS, A. D. 1938. Bioclimates. A science of life and climate relations. U.S. Dep. Agric., Misc. Publ. no. 280.

HOWARD, W. E., AND H. E. CHILDS, JR. 1959. Ecology of pocket gophers with emphasis on *Thomomys bottae mewa*. Hilgardia, 29:277–358.

JONES, R. N., AND H. REES. 1982. B chromosomes. Academic Press, New York.

KELSON, K. R. 1951. Two new subspecies of *Thomomys bottae* from New Mexico and Colorado. Univ. Kans. Publ., Mus. Nat. Hist., 5:59–71.

LONG, C. A. 1970. An analysis of patterns of variation in some representative Mammalia. Part III. Some equations on the nature of frequency distributions of estimated variabilities. Acta Theriol., 15: 517–520.

MAY, R. M., J. A. ENDLER, AND R. E. MCMURTRIE. 1975. Gene frequency clines in the presence of selection opposed by gene flow. Am. Nat., 109:659–676.

MAYR, E. 1970. Populations, species, and evolution. Harvard Univ. Press, Cambridge, Massachusetts.

MILLER, R. S. 1964. Ecology and distribution of pocket gophers (Geomyidae) in Colorado. Ecology, 45:251–272.

MOULTON, M. P., J. R. CHOATE, AND S. J. BISSELL. 1979. Sympatry of pocket gophers on Mesa de Maya, Colorado. Trans. Kans. Acad. Sci., 82:194–195.

NAGYLAKI, T. 1975. Conditions for the existence of clines. Genetics, 80:595–615.

NEI, M. 1972. Genetic distance between populations. Am. Nat., 106:282–292.

NEVO, E. 1979. Adaptive convergence and divergence of subterranean mammals. Ann. Rev. Ecol. Syst., 10:269–308.

NEVO, E., AND H. BAR-EL. 1976. Hybridization and speciation in fossorial mole-rats. Evolution, 30:831–840.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. Statistical package for the social sciences. McGraw-Hill Book Co., New York.

PATTON, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). J. Mammal., 48:27–37.

PATTON, J. L. 1972. Patterns of geographic variation in karyotype in the pocket gopher, *Thomomys bottae* (Eydoux and Gervais). Evolution, 26:574–586.

PATTON, J. L. 1973. An analysis of natural hybridization between the pocket gophers, *Thomomys bottae* and *Thomomys umbrinus*, in Arizona. J. Mammal., 54:561–584.

PATTON, J. L. 1977. B-chromosome systems in the pocket mouse, *Perognathus baileyi*: Meiosis and C-band studies. Chromosoma, 60:1–14.

PATTON, J. L. 1981. Chromosome and genic divergence, population structure, and speciation potential in *Thomomys bottae* pocket gophers. Pages 255–295 *in* Ecologia y genetica de la especiacion animal (O. A. Reig, ed.). Equinoccio, Caracas, Venezuela.

PATTON, J. L. 1983. Population structure and the genetics of speciation in pocket gophers, genus *Thomomys*. Acta Zool. Fennica (in press).

PATTON, J. L., AND R. E. DINGMAN. 1968. Chromosome studies of pocket gophers, genus *Thomomys*. I. The specific status of *Thomomys umbrinus* (Richardson) in Arizona. J. Mammal., 49:1–13.

PATTON, J. L., AND J. H. FEDER. 1981. Microspatial genetic heterogeneity in pocket gophers: Non-random breeding and drift. Evolution, 35:912–920.

PATTON, J. L., J. C. HAFNER, M. S. HAFNER, AND M. F. SMITH. 1979. Hybrid zones in *Thomomys bottae* pocket gophers: Genetic, phenetic, and ecologic concordance patterns. Evolution, 33:860–876.

PATTON, J. L., R. K. SELANDER, AND M. H. SMITH. 1972. Genic variation in hybridizing populations of gophers (genus *Thomomys*). Syst. Zool., 21:263–270.

PATTON, J. L., AND S. W. SHERWOOD. 1982. Genome evolution in pocket gophers (genus *Thomomys*). I. Heterochromatin variation and speciation potential. Chromosoma, 85:149–162.

PATTON, J. L., AND S. Y. YANG. 1977. Genetic variation in *Thomomys bottae* pocket gophers: Macrogeographic patterns. Evolution, 31:697–720.

RAY, L. L. 1940. Glacial chronology of the southern Rocky Mountains. Geol. Soc. Am. Bull., 51:1851–1917.

RICHMOND, G. M. 1963. Correlation of some glacial deposits in New Mexico. U.S. Geol. Surv. Prof. Papers, 450-D:121–125.

RICHMOND, G. M. 1965. Glaciation of the Rocky Mountains. Pages 217–230 *in* The Quaternary of the United States (H. E. Wright and D. G. Frey, eds.). Princeton Univ. Press, Princeton, New Jersey.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Stud. Genet. VII, Univ. Texas Publ., 7213:145–153.

RUSSELL, R. J. 1968. Evolution and classification of pocket gophers of the subfamily Geomyinae. Univ. Kans. Publ., Mus. Nat. Hist., 16:473–579.

SAGE, R. D., AND R. K. SELANDER. 1979. Hybridization between species of the *Rana pipiens* complex in central Texas. Evolution, 33:1069–1088.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. R. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). Stud. Genet. VI, Univ. Texas Publ., 7103:49–90.

SHAPIRO, S. S., AND M. B. WILK. 1965. An analysis of variance test for normality (complete sample). Biometrika, 52:591–611.

SHERWOOD, S. W., AND J. L. PATTON. 1982. Genome evolution in pocket gophers (genus *Thomomys*). II. Variation in cellular DNA content. Chromosoma, 85:163–179.

SLATKIN, M. 1973. Gene flow and selection in a cline. Genetics, 75:733–756.

SLATKIN, M. 1975. Gene flow and selection in a two locus system. Genetics, 81:787–802.

SLATKIN, M. 1978. Spatial patterns in the distributions of polygenic characters. J. Theor. Biol., 70: 213–228.

SLATKIN, M. 1981. Estimating levels of gene flow in natural populations. Genetics, 99:323–335.

SMITH, M. F., AND J. L. PATTON. 1980. Relationships of pocket gopher (*Thomomys bottae*) populations of the lower Colorado River. J. Mammal., 61:681–696.

SMITH, M. F., J. L. PATTON, J. C. HAFNER, AND D. J. HAFNER. 1983. *Thomomys bottae* pocket gophers of the central Rio Grande Valley, New Mexico: Local differentiation, gene flow, and historical biogeography. Occas. Papers, Mus. Southwestern Biol., Univ New Mexico (in press).

SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco.

THAELER, C. S., JR. 1968. An analysis of three hybrid populations of pocket gophers (genus *Thomomys*). Evolution, 22:543–555.

THAELER, C. S., JR. 1974. Four contacts between ranges of different chromosome forms of the *Thomomys talpoides* complex (Rodentia: Geomyidae). Syst. Zool., 23:343–354.

THAELER, C. S., JR. 1980. Chromosome numbers and

systematic relations in the genus *Thomomys* (Rodentia: Geomyidae). J. Mammal., 61:414–422.

VAUGHAN, T. A. 1963. Movements made by two species of pocket gophers. Am. Midland Nat., 69: 367–372.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics, 16:97–159.

WRIGHT, S. 1940. Breeding structure of populations in relation to speciation. Am. Nat., 74:232–248.

YOUNGMAN, P. M. 1958. Geographic variation in the pocket gopher, *Thomomys bottae*, in Colorado. Univ. Kans. Publ., Mus. Nat. Hist., 9:363–384.

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