

GENIC AND CHROMOSOMAL DIFFERENTIATION IN POCKET GOPHERS OF THE *GEOMYS BURSARIUS* GROUP

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Received December 5, 1973

Recently there has been a surge of interest in karyotypic variation in the vertebrates, particularly in mammals (Benirschke, 1969; Ford, 1970; White, 1973), and in the relationships of chromosomal modification to ecological adaptation and speciation. Research on karyotypic diversity in rodents, including pocket gophers (Geomyidae) (Thaeler, 1968; Patton and Dingman, 1968; Patton, 1970, 1972; Patton et al., 1972; Davis et al., 1971), *Gerbillus* (Zahavi and Wahrman, 1957), *Spalax* (Wahrman et al., 1969), *Sigmodon* (Zimmerman, 1970), and *Peromyscus* (Hsu and Arrighi, 1968; Lee et al., 1972), has demonstrated that many morphologically defined species are in fact pairs or complexes of allopatric or parapatric semi-species and species isolated to varying degree in part at least by chromosomal differences.

Because extensive chromosomal reorganization can result in genetic isolation between populations as a consequence of hybrid sterility (White, 1969; Todd, 1970), it follows that speciation theoretically can occur without genic modification. Conversely, the recent discovery of homosequential species of *Drosophila* suggests that "it is possible for speciation and evolution to be based entirely on mutational changes occurring at the submicroscopic level" (Carson et al., 1967; Carson et al., 1970). It is therefore of interest to compare patterns of chromosomal and genic divergence in complexes of closely related species.

In a group of species with a wide range of variation in chromosome morphology and number, is there a correlated pattern of genic differentiation? To answer this

question, we have studied four morphologically defined species of pocket gophers of the *Geomys bursarius* group (Hall and Kelson, 1959; Baker and Williams, 1973), in which previous work has demonstrated an impressive range of karyotypic diversity (Davis et al., 1971; Kim, 1972; Baker et al., 1973).

Of the four species of the *Geomys bursarius* group (Fig. 1), *G. bursarius* is the most widely distributed, occurring in the Plains Region, where numerous subspecies are currently recognized (Hall and Kelson, 1959). *Geomys personatus* and *G. arenarius* have moderate-sized ranges, and each is divided into several subspecies. *G. personatus* is parapatric with *G. bursarius* in southern Texas (Kennerly, 1959), and *G. arenarius* has a disjunct range on the sandy areas along the Rio Grande and associated tributaries in New Mexico, Texas, and Chihuahua. The fourth species, *G. tropicalis*, is confined to an area of old sand-dune habitat of approximately 300 square kilometers near Altamira, Tamaulipas (Baker and Williams, 1973). *Geomys tropicalis* apparently is separated geographically from its nearest neighbor, *G. personatus*, which extends southward from the main part of its range in Texas on the narrow barrier islands of coastal Tamaulipas. Present information indicates a gap of 250 kilometers (Selander et al., 1962; Alvarez, 1963).

On the basis of morphological evidence and geographic considerations, Russell (1968) has proposed that *arenarius* is cladistically allied with *bursarius* and that geographic isolation was imposed in a post-Wisconsin period of increasing aridity.

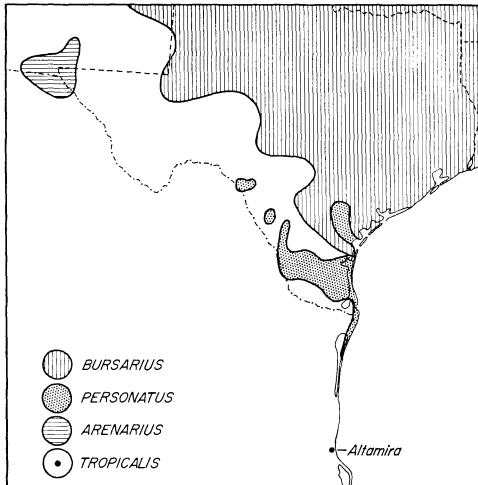


FIG. 1. Distribution of species of the *Geomys bursarius* group.

Geomys tropicalis presumably was derived from *personatus*, perhaps also as a consequence of isolation caused by late- or post-Wisconsin climatic changes (Selander et al., 1962). Species limits in the group remain questionable (Alvarez, 1963), even for *bursarius* and *personatus*, despite an attempt by Kennerly (1959) to determine their relationships in zones of contact. Both forms may consist of several cryptic species differing in karyotype (Kim, 1972).

For our purpose, the problem of species limits is not critical. It is sufficient that the *Geomys bursarius* group almost certainly represents a single, karyotypically diverse phyletic line. In *bursarius*, *personatus*, and *arenarius*, karyotypic variation is relatively minor, involving a $2N$ range of 68 to 74 mostly acrocentric chromosomes and a rather small number of changes (inversions and translocations) in individual chromosome morphology. But the karyotype of *tropicalis* is very distinctive, having $2N = 38$ biarmed chromosomes.

MATERIALS AND METHODS

Our understanding of genic and chromosomal variation in *bursarius* and *personatus* is based largely on a survey by Kim (1972), who examined 353 specimens from 12 areas

(ten in Texas and one each in Kansas and Colorado) within the range of *bursarius* and five areas within the range of *personatus* (Fig. 1). (A total of 118 individuals was karyotyped and all were used in an electrophoretic analysis of allozymic variation.) Two samples of *arenarius* were collected for the present investigation, one of 14 individuals at Las Cruces, New Mexico, and another of 23 at a point one mile south of Fabens, Texas. *Geomys tropicalis* was represented by 30 individuals from a point 2.5 miles southeast of Altamira, Tamaulipas, Mexico.

Genic variation at structural gene loci encoding enzymes and other proteins was assessed electrophoretically. Techniques of preparation of extracts of tissues (blood and kidney) and of electrophoresis and protein staining were similar to those employed by Selander et al. (1971), Patton et al. (1972), and Kim (1972). Alleles were designated alphabetically in order of decreasing mobility of their respective allozymes; a minus sign indicates a cathodally migrating protein.

Because the tissue extracts of *bursarius* and *personatus* on which Kim's (1972) work was based were no longer available at the time of our study, a complete analysis of genic identity, involving side-by-side comparisons of all allozymic variants on gels, between those species and *arenarius* and *tropicalis* was not possible. However, by resampling certain Texas populations studied by Kim, we were able to compare the predominant allele at each locus in *bursarius* and *personatus* with those of the other species.

RESULTS

Chromosomal Variation

Information on karyotypes in the *Geomys bursarius* group is presented in Table 1. When considered in light of Russell's (1968) interpretation of probable lines of phylogeny within the complex, these data suggest that the ancestral stock of *Geomys* had a karyotype of about 70 chromosomes, most of which were acrocentric elements;

TABLE 1. *Karyotypic variation in species of the Geomys bursarius group.*

Species	Number of karyotypes identified	2N	FN	Number of banded autosomes	Reference
<i>G. bursarius</i>	7	70, 72, 74	68-74	0-6	Kim (1972)
	10	69, 70, 71, 72	68-70	0-4	Baker et al. (1973)
<i>G. personatus</i>	5	68, 70	68-74	2-6	Kim (1972)
	8	68, 70, 72	70-76	2-8	Davis et al. (1971)
<i>G. arenarius</i>	1	70	102	34	Davis et al. (1971)
<i>G. tropicalis</i>	1	38	72	38	Davis et al. (1971)

this is the most frequent type in both *bursarius* and *personatus*. The number of chromosomes has changed in different populations through Robertsonian modifications (centric fusions and fissions); and variation in number of banded autosomes is attributed to inversions and trans-

locations. Derivation of the *arenarius* karyotype from the ancestral type apparently involved a series of inversions or translocations, converting about half the autosomes to banded forms. And the karyotype of *tropicalis* can be derived from the ancestral type by a series of centric

TABLE 2. *Genic variation in four species of the Geomys bursarius group.*

Protein locus	Allele and number of polymorphic populations ^a			
	<i>G. bursarius</i> (12 areas)	<i>G. personatus</i> (5 areas)	<i>G. arenarius</i> (2 populations)	<i>G. tropicalis</i> ^b (1 population)
Esterase-1	b (4)	c (3)	a, b	b
Esterase-2	b(11)	b (5)	d, e	d
Esterase-3	a (7)	a (3)	a, c	b
Esterase-4	a	a	a	a
Lactate dehydrogenase-A	a (3)	a	a	a
Lactate dehydrogenase-B	a (2)	a (1)	a	b
Malate dehydrogenase-1	a	a	a	a
Malate dehydrogenase-2	-a (2)	-a (2)	-a	-a
Isocitrate dehydrogenase-1	b (7)	b ^c	a	c
Isocitrate dehydrogenase-2	a (5)	a	a	a
6-Phosphogluconate dehydrogenase	a (2)	a (3)	a	a
α -Glycerophosphate dehydrogenase	a (4)	a (3)	a	a
Alcohol dehydrogenase	-b (2)	-a (2)	-a	-a
Sorbitol dehydrogenase	-b (1)	-c	-a	-c
Indophenol oxidase-1	a	a	a	a
Indophenol oxidase-2	—	—	-a	-a
Phosphoglucomutase-1	a (7)	a (3)	b	a
Phosphoglucose isomerase	a (3)	a (1)	a	a
Glutamate oxalate transaminase-1	a (1)	a	a	a
Glutamate oxalate transaminase-2	-a (1)	-a (2)	-a	-a
Erythrocytic protein-1	a (2)	a (1)	a	a
Erythrocytic protein-2	—	—	-a	-a
Albumin	a (5)	b ^c	a	a
Transferrin	a (3)	a	a	a
Hemoglobin ^d	a	a	a	a

^a For *G. bursarius* and *G. personatus*, predominant allele indicated; number of populations in which locus is polymorphic shown in parentheses.

^b Eight additional loci scored, all of which are monomorphic: Esterase-5, Leucine aminopeptidase-1, Leucine aminopeptidase-2, Phosphoglucomutase-2, Kidney protein-1, Kidney protein-2, Kidney protein-3, Post-albumin-1.

^c An alternate allele fixed in one population.

^d Phenotype for hemoglobin.

TABLE 3. *Genic variability in the Geomys bursarius group.*

Species	Number of populations sampled	Number of loci	Proportion of loci	
			Polymorphic per population	Heterozygous per individual
<i>G. bursarius</i> ^a	12	23	.226 (.13-.44)	.038 (.01-.08)
<i>G. personatus</i> ^a	5	23	.185 (.09-.26)	.044 (.02-.08)
<i>G. arenarius</i>	2	25	.120 (.12-.12)	.050 (.05-.05)
<i>G. tropicalis</i>	1	34	.000 —	.000 —

^a Calculated from data in Kim (1972).

fusions, reducing the $2N$ complement from 70 to 38 (Davis et al., 1971).

In all species of the complex, most local populations are monomorphic for a particular karyotype. However, chromosomal polymorphism has been detected in some populations of *bursarius* (Baker et al., 1973) and *personatus* (Davis et al., 1971). It is likely that additional karyotypes will be found in *bursarius*, *personatus*, and *arenarius*. But only a single karyotype has been found in *tropicalis*, and, in view of the very restricted geographic range of this species, it is unlikely that karyotypic variation exists.

Genic Variation

Twenty-two proteins encoded by 23 loci were scored in *bursarius* and *personatus* (Table 2), and 24 loci were scored in *arenarius*. For *tropicalis*, we studied 34 loci, including those scored in other species and eight more listed in the footnote to Table 2.

Mean heterozygosity is 4% in *bursarius* and *personatus*, and the observed range is 1% to 8% (Table 3). In *bursarius*, variants were detected at most of the 23 loci, but only *Est-2*, *Est-3*, *Idh-1*, and *Pgm-1* were polymorphic in a majority of populations sampled by Kim (1972); and, in *perso-*

natus, only *Est-2* was polymorphic in all five populations sampled (Table 2). It is a common pattern in these species for variant minor alleles to be confined to single local populations.

Samples of *arenarius* show variation at only three loci, all esterases. Two alleles are represented at each locus, and frequencies of the alleles are as follows: *Est-1*^a = .61 at Las Cruces, .36 at Fabens; *Est-2*^a = .61, .81; *Est-3*^a = .79, .57. Because heterozygosity is fairly high at each locus (much more so than in the average population of *bursarius* or *personatus*), overall genic heterozygosity in *arenarius* is equivalent to that in *bursarius* and *personatus*, even though no other loci are polymorphic.

In *tropicalis*, no variation was detected at any of the 34 loci examined, all 30 individuals in the sample being genically identical.

DISCUSSION

There is little variation in degree of genic differentiation between species pairs of the *Geomys bursarius* group (Table 4). From 72% to 83% of predominant alleles are shared by all species pairs. Clearly, there is no close correspondence between patterns of genic differentiation and chromosomal

TABLE 4. *Proportion of predominant alleles at 23 loci shared by species pairs.*

Species	<i>G. bursarius</i>	<i>G. personatus</i>	<i>G. arenarius</i>	<i>G. tropicalis</i>
<i>G. bursarius</i>	1.000	.826	.718	.739
<i>G. personatus</i>		1.000	.761	.739
<i>G. arenarius</i>			1.000	.761
<i>G. tropicalis</i>				1.000

TABLE 5. *Genic heterozygosity in rodents.*

Species	Mean heterozygosity per population	Reference
Strongly fossorial		
<i>Spalax ehrenbergi</i>	.037	Nevo and Shaw (1972)
<i>Thomomys bottae</i>	.071	Patton et al. (1972)
<i>Thomomys umbrinus</i>	.031	Patton et al. (1972)
<i>Geomys bursarius</i>	.038	Present study
<i>Geomys personatus</i>	.044	Present study
<i>Geomys arenarius</i>	.050	Present study
Mean	.0452	
Others		
<i>Sigmodon hispidus</i> ^a	.036	Johnson et al. (1972)
<i>Sigmodon arizonae</i> ^a	.049	Johnson et al. (1972)
<i>Peromyscus polionotus</i>	.058	Selander et al. (1971)
<i>Peromyscus floridanus</i>	.053	Smith et al. (1973)
<i>Peromyscus gossypinus</i>	.051	Smith et al. (1974)
<i>Peromyscus leucopus</i>	.070	Smith et al. (1974)
<i>Peromyscus eremicus</i>	.040	Avise et al. (1974)
<i>Peromyscus californicus</i>	.065	Avise et al. (1974)
<i>Dipodomys ordii</i> ^a	.014	Johnson and Selander (1971)
<i>Dipodomys merriami</i> ^a	.087	Johnson and Selander (1971)
<i>Mus musculus</i>	.085	Selander et al. (1969)
Mean	.0553	

^a Values adjusted for absence of esterase loci; see Selander and Johnson (1973).

differentiation. It is especially noteworthy that *G. tropicalis* is not unusually divergent genically from other members of the complex, notwithstanding its highly reduced chromosome number. Our analysis thus supports the generalization emerging from previous studies of a variety of rodents (Johnson et al., 1972; Patton et al., 1972; Nevo and Shaw, 1972), that divergence of populations at the chromosomal level can occur without concomitant allelic differentiation at structural gene loci. The processes underlying chromosomal and genic divergence apparently are largely independent.

An unusual aspect of our findings is the total absence of heterozygosity at 34 loci assayed in *tropicalis* (Table 3). Although our sample of 30 individuals was collected in a small area (a strip of dunes 200 meters × 1 kilometer), we believe it is representative of the species as a whole, for we found no evidence that *tropicalis* is divided into geographically isolated subunits.

Geomys tropicalis inhabits an area of

approximately 300 square kilometers. If the average density of individuals is one per acre (estimates for other species of *Geomys* range from 1 to 15 per acre; Butcher, 1929; Downhower and Hall, 1966; Kennerly, 1954), the total species number is ~74,000. This estimate may be off by an order of magnitude, but, in any event, the species number must surely be in the thousands, and thus well above the level at which random genetic drift could have an important effect in reducing genic heterozygosity over any reasonable time span. A similar absence or severely reduced level of heterozygosity has been reported for insular or continental populations of other vertebrates, including *Mus* (Hunt and Selander, 1973), *Peromyscus* (Selander et al., 1971; Avise et al., 1974), seals (Bonnell and Selander, 1974), lizards (Webster et al., 1973), and cave fish (Avise and Selander, 1972). Some combination of founder effect and intermittent drift in periods of low population numbers has been advanced as a probable cause of reduced

genic variability in these populations, but in no case has the alternate possibility of adaptive response to uniform environmental conditions been ruled out. The drift and niche-width hypotheses are, of course, not mutually exclusive.

On the basis of work with the mole rat (*Spalax*), Nevo and Shaw (1972) suggested that rodents that are well adapted to the fossorial habitus may have unusually low levels of genic heterozygosity as a reflection of selectively mediated responses to a "monotonous subterranean niche." In Table 5, we have summarized all available estimates of heterozygosity in rodents, excluding only those species or populations occupying very small islands or, as in the case of *G. tropicalis*, having relictual distributions. Genic heterozygosity in the fossorial pocket gophers (*Thomomys* and *Geomys*) and *Spalax* does in fact average less than in other rodents, but the difference in means is not significant ($t = .900$, with 15 df; $P \sim .16$). Much additional data will be required for an adequate test of the niche-width hypothesis.

If, for the sake of argument, we tentatively exclude the possibility that the loss of genic variability in *tropicalis* represents an adaptive response, how can we account for it? One way is to postulate a series of founding events, involving one or a few pairs (or even single pregnant females) along the narrow barrier islands of the Tamaulipas coast when a *personatus*-like ancestor was extending its range southward from Texas. With a narrow, discontinuous, linear distribution on these islands, there would be little chance for restoration by gene flow of the variability lost at each founder event. Hence, the ancestor of *tropicalis* could have lost most or all of its genic variability before reaching the Altamira region. Perhaps some insight into the problem would be provided by examination of heterozygosity levels in contemporary populations of *personatus* on the barrier islands of Tamaulipas (Selander et al., 1962).

Karyotypic variation in the *G. bursarius*

group illustrates White's (1973) principle of karyotypic orthoselection, which describes the tendency for chromosomes to undergo the same type of structural change, thus preserving a similar morphology (Table 1). At one extreme are *bursarius* and *personatus*, with the great majority of chromosomes acrocentric, and at the other extreme, *tropicalis*, with all autosomes biarmed. *G. arenarius* is exceptional in having approximately equal proportions of the two chromosome types.

It is widely held, particularly among plant cytogeneticists (Darlington, 1939; Stebbins, 1950, 1971; Grant, 1971), that the restriction in genetic recombination resulting from a reduction in chromosome number may facilitate adaptation to restricted ecological niches. Because *tropicalis* is confined to an extremely uniform habitat type, the marked reduction in chromosome number in this species has been viewed as an adaptive character by Davis et al. (1971). However, much more important factors regulating recombination are the number and degree of localization of chiasmata, about which, unfortunately, we have no information for *tropicalis* or other members of the *G. bursarius* group. In another pocket gopher, *Thomomys bottae*, Patton (1971, 1972) found a very low chiasma frequency (an average of 1.03 per bivalent) and a strong tendency for localization of chiasmata at or near the end of each bivalent. The resulting tightening of linkage groups is interpreted as a means of evolving specific gene complexes adapted to local environmental conditions. Particularly, in view of the apparent monogenic character of *tropicalis* at structural gene loci, it would be most interesting to determine the frequency and distribution of chiasmata in comparison with the other, more widely distributed and genically variable species of the complex.

SUMMARY

The processes of karyotypic and genic differentiation have proceeded independently in the evolution of pocket gophers

of the *Geomys bursarius* group. In the peripheral relict *G. tropicalis*, a reduction in $2N$ chromosome number from ~ 70 to 38 was not accompanied by an unusual degree of allelic substitution at structural gene loci. The possibility that a reduction in number of linkage groups and an apparent loss of variability at structural gene loci in *G. tropicalis* represent adaptation to an unusually uniform environment is discussed.

ACKNOWLEDGMENTS

We thank John C. Patton and Steve Tennison for assistance in the field.

This research was supported by NIH Grant GM-15769 and NSF Grant GB-15664 (to R. K. Selander), an Organized Research Grant from Texas Tech University (to R. J. Baker), and the Institute for Museum Research. D. W. Kaufman was supported by NIH Training Grant 5T01-00337.

LITERATURE CITED

- ALVAREZ, T. 1963. The recent mammals of Tamaulipas, Mexico. Univ. Kans. Publ. Mus. Nat. Hist. 14:363-473.
- AVISE, J. C., AND R. K. SELANDER. 1972. Evolutionary genetics of cave-dwelling fishes of the genus *Astyanax*. *Evolution* 26:1-19.
- AVISE, J. C., M. H. SMITH, R. K. SELANDER, T. E. LAWLOR, AND P. R. RAMSEY. 1974. Biochemical polymorphism and systematics in the genus *Peromyscus*. V. Insular and mainland species of the subgenus *Haplomylomys*. *Syst. Zool. (in press)*.
- BAKER, R. J., AND S. L. WILLIAMS. 1973. *Geomys tropicalis*. *Mammalian Species*.
- BAKER, R. J., S. L. WILLIAMS, AND J. C. PATTON. 1973. Chromosomal variation in the plains pocket gopher, *Geomys bursarius major*. *J. Mammal.* 54:765-769.
- BENIRSCHKE, K. (ed.). 1969. *Comparative mammalian cytogenetics*. Springer-Verlag, New York.
- BONNELL, M. L., AND R. K. SELANDER. 1974. Elephant seals: genetic variation and near extinction. *Science* 184:908-909.
- BUTCHER, F. D. 1929. *Rodent pests of Iowa*. Iowa State Coll. Agr. Mech. Arts, Ext. Serv. Bull. 153. 20 p.
- CARSON, H. L., F. E. CLAYTON, AND H. D. STALKER. 1967. Karyotypic stability and speciation in Hawaiian *Drosophila*. *Proc. Nat. Acad. Sci.* 57:1280-1285.
- CARSON, H. L., D. E. HARDY, H. T. SPIETH, AND W. S. STONE. 1970. The evolutionary biology of the Hawaiian Drosophilidae, p. 437-543. In M. K. Hecht and W. C. Steere (eds.), *Essays in evolution and genetics in honor of Theodosius Dobzhansky*. Appleton-Century-Crofts, New York.
- DARLINGTON, C. D. 1939. *The evolution of genetic systems*. 1st ed. Cambridge Univ. Press.
- DAVIS, B. L., S. L. WILLIAMS, AND G. LOPEZ. 1971. Chromosomal studies of *Geomys*. *J. Mammal.* 52:617-620.
- DOWNHOWER, J. F., AND E. R. HALL. 1966. The pocket gopher in Kansas. *State Biol. Surv., Kansas* 44:1-32.
- FORD, C. E. 1970. The population cytogenetics of other mammalian species, p. 221-239. In P. A. Jacobs, W. H. Price, and P. Law (eds.), *Human population cytogenetics*. Williams and Wilkins, Baltimore.
- GRANT, V. 1971. *Plant speciation*. Columbia Univ. Press, New York.
- HALL, E. R., AND K. R. KELSON. 1959. *The mammals of North America*. Ronald Press, New York.
- HSU, T. C., AND F. E. ARRIGHI. 1968. Chromosomes of *Peromyscus* (Rodentia, Cricetidae). I. Evolutionary trends in 20 species. *Cytogenetics* 7:417-446.
- HUNT, W. G., AND R. K. SELANDER. 1973. Biochemical genetics of hybridisation in European house mice. *Heredity* 31:11-33.
- JOHNSON, W. E., AND R. K. SELANDER. 1971. Protein variation and systematics in kangaroo rats (genus *Dipodomys*). *Syst. Zool.* 20:377-405.
- JOHNSON, W. E., R. K. SELANDER, M. H. SMITH, AND Y. J. KIM. 1972. Biochemical genetics of sibling species of the cotton rat (*Sigmodon*). *Studies in Genetics VII*, Univ. Texas Publ. 7213:297-305.
- KENNERLY, T. E., JR. 1954. Local differentiation in the pocket gopher (*Geomys personatus*) in southern Texas. *Texas J. Sci.* 6:297-329.
- . 1959. Contact between the ranges of two allopatric species of pocket gophers. *Evolution* 13:247-263.
- KIM, Y. J. 1972. *Studies of biochemical genetics and karyotypes in pocket gophers (family Geomyidae)*. Ph.D. Dissertation, Univ. of Texas, Austin.
- LEE, M. R., D. J. SCHMIDLY, AND C. H. HUHEEY. 1972. Chromosomal variation in certain populations of *Peromyscus boylii* and its systematic implications. *J. Mammal.* 53:697-707.
- NEVO, E., AND C. R. SHAW. 1972. Genetic variation in a subterranean mammal, *Spalax ehrenbergi*. *Biochem. Genet.* 7:235-241.
- PATTON, J. L. 1970. Karyotypic variation following an environmental gradient in the pocket

- gopher, *Thomomys bottae grahamensis* Goldman. *Chromosoma* 31:41-50.
- . 1972. Patterns of geographic variation in karyotype in the pocket gopher, *Thomomys bottae* (Eydoux and Gervais). *Evolution* 26: 574-586.
- . 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., 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., R. K. SELANDER, AND M. H. SMITH. 1972. Genic variation in hybridizing populations of gophers (genus *Thomomys*). *Syst. Zool.* 21:263-270.
- RUSSELL, R. S. 1968. Evolution and classification of the pocket gophers of the subfamily Geomyinae. *Univ. Kans. Publ. Mus. Nat. Hist.* 16:473-579.
- SELANDER, R. K., W. G. HUNT, AND S. Y. YANG. 1969. Protein polymorphism and genic heterozygosity in two European subspecies of the house mouse. *Evolution* 23:379-390.
- SELANDER, R. K., AND W. E. JOHNSON. 1973. Genetic variation among vertebrate species. *Ann. Rev. Ecol. Syst.* 4:75-91.
- SELANDER, R. K., R. F. JOHNSTON, B. J. WILKS, AND G. G. RAUN. 1962. Vertebrates from the barrier islands of Tamaulipas, Mexico. *Univ. Kans. Publ. Mus. Nat. Hist.* 12:309-345.
- SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, AND J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*. I. Variation in the old-field mouse (*Peromyscus polionotus*). *Studies in Genetics* VI. *Univ. Texas Publ.* 7103:49-90.
- SMITH, M. H., R. K. SELANDER, AND W. E. JOHNSON. 1973. Biochemical polymorphism and systematics in the genus *Peromyscus*. III. Variation in the Florida deer mouse (*Peromyscus floridanus*), a Pleistocene relict. *J. Mammal.* 54:1-13.
- . 1974. Biochemical polymorphism and systematics in the genus *Peromyscus*. V. Variation in *P. gossypinus* and *P. leucopus*. (In prep.)
- STEBBINS, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, New York.
- . 1971. Chromosomal evolution in higher plants. Addison-Wesley, Reading, Mass.
- THAELER, C. S., JR. 1968. Karyotypes of sixteen populations of the *Thomomys talpoides* complex of pocket gophers (Rodentia-Geomyidae). *Chromosoma* 25:172-183.
- TODD, N. B. 1970. Karyotypic fissioning and canid phylogeny. *J. Theoret. Biol.* 26:445-480.
- WAHRMAN, J., R. GOITEIN, AND E. NEVO. 1969. Geographic variation of chromosome forms in *Spalax*, a subterranean mammal of restricted mobility, p. 30-48. In K. Benirschke (ed.), *Comparative mammalian cytogenetics*. Springer-Verlag, New York.
- WEBSTER, T. P., R. K. SELANDER, AND S. Y. YANG. 1973. Genetic variability and similarity in the *Anolis* lizards of Bimini. *Evolution* 26:523-535.
- WHITE, M. J. D. 1969. Chromosomal rearrangements and speciation. *Ann. Rev. Genet.* 3: 75-98.
- . 1973. *Animal cytology and evolution*. 3rd ed. Cambridge Univ. Press.
- ZAHAVI, A., AND J. WAHRMAN. 1957. The cytotaxonomy, ecology and evolution of the gerbils and jirds of Israel (Rodentia: Gerbillinae). *Mammalia* 21:341-380.
- ZIMMERMAN, E. G. 1970. Karyology, systematics and chromosomal evolution in the rodent genus, *Sigmodon*. *Michigan State Univ., Publ. Mus., Biol. Ser.* 4:385-454.