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Apparent convergence of karyotypes in two species of pocket gophers of the genus *Thomomys* (Mammalia, Rodentia)[1]

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Abstract

Intraspecific variation in chromosome morphology is greater in two species of pocket gophers than within any other presently studied mammalian species. Diploid number varies only from 76 to 78. Therefore, the majority of the differences appear to be the results of pericentric inversions. These geographical chromosomal differences in *Thomomys bottae* and *T. umbrinus* are best explained as adaptations to habitat characteristics. Within both species, populations occurring in arid or shallow soil habitats have karyotypes characterized by a high number of acrocentrics, whereas populations in more favorable conditions have karyotypes composed entirely of metacentrics or submetacentric elements. These parallel trends suggest that the symmetry of the karyotype as a whole may have functional significance.

The chromosomal features of fossorial rodents have been studied in several different genera (*Thomomys, Spalax,* and *Ctenomys*) and from different ecological situations, and each study has revealed a relatively large degree of geographical chromosomal variation (SOLDATOVIC et al., 1967; PATTON and DINGMAN, 1968, 1970; RAICU et al., 1968; REIG and KIBLISKY, 1968, 1969; THAELER, 1968; WAHRMAN et al., 1969; WENTWORTH and SUTTON, 1969). Reviews of the nature of this variation are presented by PATTON and DINGMAN (1970) and REIG and KIBLISKY (1970).

The geographic area of our study complements that of PATTON and DINGMAN (1970). The variation found in *Thomomys bottae* chromosomes by PATTON and DINGMAN (1968, 1970) was in the number of biarmed

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versus uniarmed elements, with infrequent minor variations in the diploid number. Their study also revealed no intrapopulational variation.

Variation in osteology and pelage between populations of *T. bottae* and *T. umbrinus* has been a source of continuing taxonomic controversies. Several distinct species were recognized by BAILEY (1915). HALL and KELSON (1959) included all populations sampled by us within the single species *umbrinus*. On the basis of more recent collections and re-analysis of available museum specimens, ANDERSON (1966), whose classification is followed here, recognizes two species, *T. bottae* and *T. umbrinus*. Both species occur in a wide range of habitats, from desert to high montane meadows.

Karyotype samples presented in this paper are from specimens from the habitat extremes as well as from intermediate habitats. Possible explanations are proposed for the similarity of karyotypes in widely separated populations living in similar habitats.

Materials and methods

A total of 56 wild caught specimens of *Thomomys* were karyotyped by the techniques described by BAKER (1970). The only tissue used was bone marrow. A total of 10 to 50 spreads were counted per specimen, with an average of 25 per animal. For most specimens, the diploid number and number of acrocentrics were determined independently by each author, and data were compared. In one specimen our conclusions were different concerning diploid number; our determinations of the number of acrocentrics never differed by more than four and were usually in agreement. The source of inaccurate counts of the number of acrocentrics was the small elements with indistinct arms in the spreads in early prophase.

Chromosomal characteristics, sample size, locality data, and generalized habitat characteristics are listed in the table. We agree with PATTON and DINGMAN (1968, 1970) that the only natural classification of these karyotypes is into biarmed and uniarmed categories, and it is on this basis that our data were analyzed. As they pointed out, such a simple classification does not show many morphological differences between karyotypic variants.

In the following list of specimen localities, the numbers in parentheses are the locality numbers shown in table I. Two specimens are deposited at the American Museum of Natural History (AMNH). All others are deposited in the mammal collection of Texas Tech University. Museum numbers follow the locality data.

Thomomys bottae (EYDOUX and GERVAIS)

Texas: Crockett County: (1) 27 miles by road N.W. Ozona, one female, 6896; (2) 25 miles by road N.W. Ozona, one female, 6781; (3) 17 miles N.W. Ozona on Texas 137, two males, 6994, 6703; (4) 8 miles S. Ozona, one female, 6700; (5) 15 miles N., 11 miles W. Ozona, one male, 6701; (6) 11 miles N.W. Ozona on Texas 137, one female, 6702; (7) 7 miles E. Ozona, one female, 8322. Irion County: (8) 4 miles N. Barnhart, one male, one female, 6765, 6875. Jeff Davis County: (9) 9 miles N.E. Fort Davis, one male, 7746; (10) 9.5 miles N.E. Fort Davis, two males, 7792, 7793; (11) 11 miles N.E. Fort Davis, one male, four females, 7898, 7899, 7900, 7901, 7787; (12) 11.7 miles N.E. Fort Davis, one male, 7796; (13) 12 miles N.E. Fort Davis, one female, 7784; (14) 0.5 miles N. Wildrose Pass on Texas 17, one female, 7785; (15) 1.7 miles N.E. Wildrose Pass on Texas 17, one female, 7786; (16) Sawtooth Mountain, one female, 8909. Presidio County: (17) Clay Miller Ranch, Sierra Vieja, two females, 8462, 8583. Reagan County: (18) 6 miles S.E. Stiles, one male, 6885; (19) 3 miles S.E. Stiles, one male, 6238; (20) 4 miles W., 4 miles S. Big Lake, one female, 6779. Sutton County: (21) 2 miles S. Sonora, one female, 6402; (22) 1.9 miles S. Sonora, one male, 6401; (23) 20 miles W. Sonora, one male, 8319; (24) 5 miles W. Jct. U.S. 277, FM 189, one female, 8320; (25) 1 mile W. Jct. U.S. 277, FM 189, one female, 8321. *New Mexico:* Bernalillo County: (26) S. suburbs of Albuquerque, one female, 6400. Eddy County: (27) Guadalupe Mountains, N 32° 6′, W 104° 45′, one male, one female, 8323, 8324. Otero County: (28) Sacramento Mountains, Lightning Lake, 14 miles S. Cloudcroft, two males, three females, 6884, 6891, 6892, 6893, 7417; (29) Sacramento Mountains, 3 miles S. Jct. New Mexico 24 and New Mexico 130, one male, 10288; (30) Tularosa, two males, three females, 8463, 8464, 10289, 10290, 10291. *Mexico:* State of Coahuila: (31) Rancho Del Chupadero N 29° 24′, W 101° 51′, one female, 7406. State of Zacatecas: (32) 3½ miles road E. Mazapil, one female, 9718.

Thomomys umbrinus (RICHARDSON)

Arizona: Santa Cruz County: (33) Patagonia Mountains, 10.5 miles by Washington Camp Road E. Jct. Ariz. 82, one male, 9368. *Mexico:* State of Durango: (34) Highway 40, kilometer marker 1113, 2 km. E. Buenos Aires, two males, one female, 8482, AMNH 215276, AMNH 215277. State of Zacatecas: (35) 4 miles W. Trancoso on Mex. 45, one female, 8707; (36) 10 miles S.E. Fresnillo, one female, one male, 9706, 10287.

Results

Thomomys bottae (EYDOUX and GERVAIS)

Diploid numbers from *T. bottae* captured in western Texas, New Mexico, and Coahuila were 76, 77, and 78. The number of acrocentric chromosomes ranged from none (fig. 1) to 38 (fig. 2), with many intermediate numbers. The morphology of the sex chromosomes was constant throughout the area studied. The X is a large metacentric, and the Y is minute.

Highest numbers of acrocentric chromosomes appear to be associated with the most arid environments (table I). The frequency of acrocentric chromosomes increases from east to west on the Edwards Plateau, Texas, and correlates with an increase in xerophytic vegetation. Further

Table I. Numbers of acrocentric (A) chromosomes and diploid numbers (2N) in *T. bottae* and *T. umbrinus* from various habitats.

A	2N	♂	♀	Locality Nos.[1]	Habitat description
T. bottae					
0	76		1	26	river valley, deep silt
2	76	2	3	28	high montane meadow, dark organic soil
2	76	1		29	ponderosa pine forest, deep porous soil
22	76		1	32	mountain slope cornfields, clay-loam
22	76	1	2	21, 22, 25	oak-juniper open woodland, clay-loam
23	77		1	24	oak-juniper open woodland, clay-loam
26	76	1	2	4, 7, 23	mesquite-juniper open woodland, clay-loam
26	76		1	31	lechuguilla on plain in fine sand
28	76	1	1	27	ponderosa pine-oak, banks of intermittant stream
30	76		1	20	mesquite-juniper, shallow clay-loam
30	78	1	1	8	mesquite, shallow clay-loam
32	76	5	8	9–15	cottonwood, banks of intermittant streams
32	76	2	2	1, 2, 3	mesquite-juniper shrubs, shallow clay-loam
34	76		1	16	steep mountain slope, shallow soil
34	78	1	1	5, 6	mesquite-juniper shrubs, shallow clay-loam
36	78	2		18, 19	mesquite-juniper shrubs, shallow clay-loam
36	76	2	2	30	irrigated alfalfa field, sandy soil
38	76		1	30	irrigated alfalfa field, sandy soil
38	76		2	17	lechuguilla on hills, shallow rocky soil
T. umbrinus					
2	76	2	1	34	montane meadow, dark organic soil
10	78		1	35	cornfield on high plateau, deep loam
10	78	1	1	36	high plateau grassland, deep loam
56	78	1		33	hillside oak woodland, shallow soil

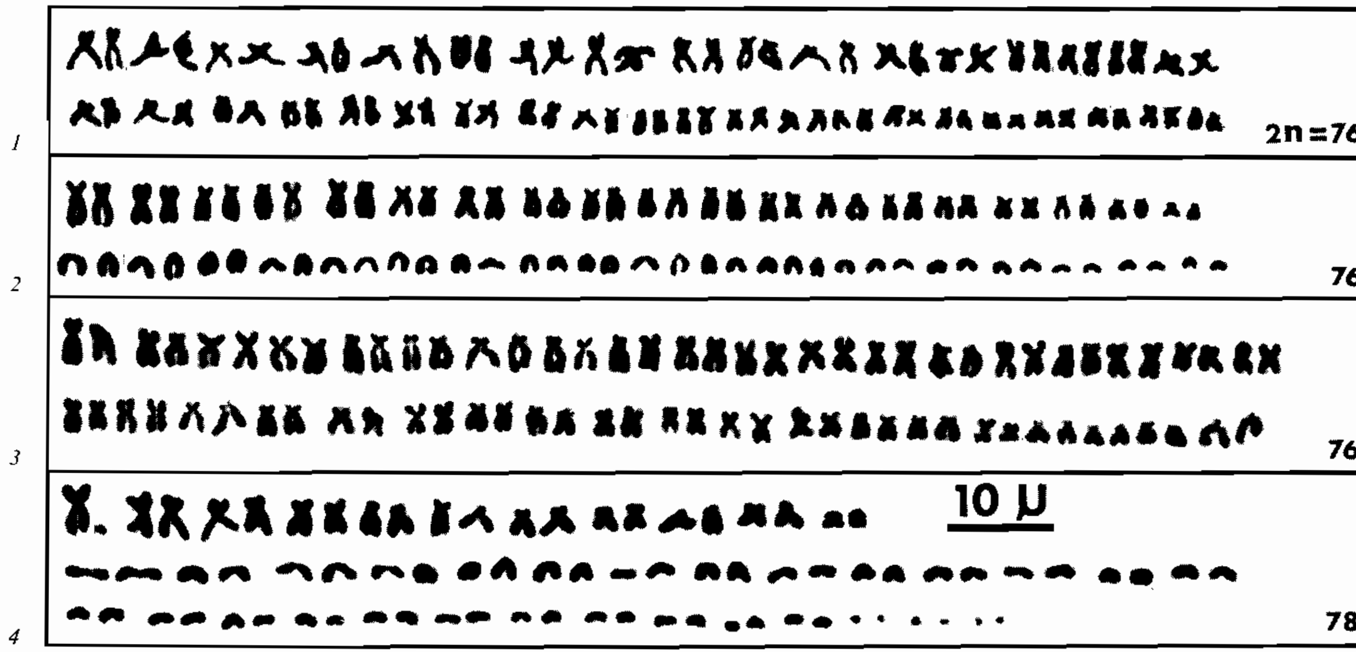
[1] See materials and methods section for specific localities.

Fig. 1. Karyotype of a *Thomomys bottae* from Bernalillo Co., New Mexico. Note that all chromosomes are biarmed.

Fig. 2. Karyotype of a *Thomomys bottae* from Tularosa, Otero Co., New Mexico. Note the 38 acrocentric elements.

Fig. 3. Karyotype of a *Thomomys umbrinus* from near La Ciudad, Durango, Mexico. Note that nearly all elements are biarmed.

Fig. 4. Karyotype of *Thomomys umbrinus* from Patagonia Mts., Santa Cruz Co., Arizona. Note the 56 acrocentric elements. The first three specimens were from females. Number four is from a male. In each case the first pair of chromosomes are the sex chromosomes.



1
2n=76
2
76
3
76
4
78
10 μ

west, corresponding to generally increasing aridity and greater annual variation in precipitation, the karyotype of *T. bottae* from the canyon bottom of Limpia Creek in the Davis Mountains, Jeff Davis County, is very similar to those from the western Edwards Plateau, whereas a specimen from steep slopes on the western side of the range had an additional pair of acrocentrics. In the less arid pine-oak zone at 1850 m in the Guadalupe Mountains, Eddy County, New Mexico, the number of acrocentrics approaches that found in more eastern samples from the Edwards Plateau. The lowest numbers of acrocentrics found in *T. bottae* in this study were in populations from near 2700 m in moist montane meadows in the Sacramento Mountains, Otero County, New Mexico, and from farther north in the Rio Grande Valley in Bernalillo County, New Mexico. The highest numbers of acrocentrics in *T. bottae* were found in specimens from irrigated alfalfa fields at Tularosa, Otero County, New Mexico, and in patches of lechuguilla (*Agave lechuguilla)* and prickly pear (*Opuntia* sp.) in the Sierra Vieja, Presidio County, Texas, both areas of extremely low precipitation relative to adjacent high mountains and areas to the east.

Thomomys umbrinus (RICHARDSON)

Samples of *T. umbrinus* are from widely separated localities from Arizona to Zacatecas. Diploid numbers were 76 and 78. The number of acrocentric chromosomes ranged from 2 (fig. 3) to 56 (fig. 4), with few intermediates. The X is a large metacentric or submetacentric, and the Y is minute. The highest number of acrocentrics is found in the most arid habitat, as in *T. bottae* (table I). Specimens from moist, friable soil near the continental divide in the Sierra Madre Occidental, Mexico, had a karyotype with two acrocentrics. Specimens from the drier plateau in Zacatecas had a karyotype with 10 acrocentrics. The specimen from Arizona with 56 acrocentrics was captured on sloping terrain with very shallow soil. Valley populations in deeper soils of the area are *T. bottae* with low numbers of acrocentrics (PATTON and DINGMAN, 1968).

Discussion

Studies of western areas of contact strongly confirm the distinctness of *T. bottae* and *T. umbrinus* (ANDERSON, 1966; DUNNIGAN, 1967; PATTON and DINGMAN, 1968; HOFFMEISTER, 1969). The precise delimitation of species separation in the eastern areas of possible contact is still uncertain (HOFFMEISTER, 1969). The occurrence of a mosaic distribution and apparent intergrades between local karyotype forms in *T. bottae* in Texas supports the conclusion of PATTON and DINGMAN (1970) that the chromosomal differences result in little genetic isolation. Consequently, the difference in karyotype between northern Coahuila and northeastern Zacatecas (fig. 5) is not suggestive of reproductive isolation. Nor are the differences between northeastern Zacatecas and southern Zacatecas or Durango significant considering the wide range of variation found in both *T. bottae* and *T. umbrinus*.

Limited dispersibility and a resultant high rate of inbreeding may facilitate development of karyotypic differences in the genus *Thomomys*, as suggested by PATTON and DINGMAN (1970). Given the potential for changing chromosomal structures at a high rate, it is not surprising that general patterns appear to be convergent in similar habitats for closely

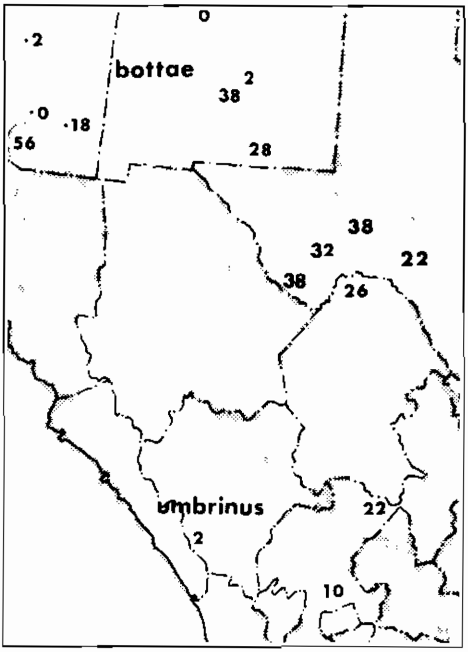


Fig. 5. Generalized geographic distribution of *Thomomys bottae* and *T. umbrinus* in the southwestern United States and northwestern Mexico. Values represent the total number of acrocentrics characteristic of the respective geographic populations. Intermediate numbers are omitted in western Texas. Asterisks indicate data from PATTON and DINGMAN (1968).

related species. STEBBINS (1950) noted that in many groups of plants the forms with asymmetric karyotypes (i.e., with centromeres displaced from the midpoints of the chromosomes and large differences in size between largest and smallest chromosomes) are more specialized than relatives with more symmetrical karyotypes. The asymmetry of the karyotype in *T. bottae* and *T. umbrinus* seems to increase with increasing aridity of the habitat. The functional significance of the symmetry of karyotypes is open to speculation. STAIGER (1954) related chromosomal types in *Thais* (a prosobranch mollusc) with ecologically distinct tidal zones; however, the chromosomal variation involved centric fusion, not pericentric inversions.

Chromosome morphology as well as chromosome number may influence the rate of expression of genetic variability. Thus the karyotype might be considered as an aspect of the "adaptive strategy" of an organism with predictable relationship to the heterogeneity of the environment, as theoretically analyzed by LEVINS (1968). TURNER (1967) suggested some conditions which may increase selection for higher recombination frequency between pairs of interacting genes on the same chromosome. These include migration and mutation, random effects, and changing environment. Thus differences in migration rates, population sizes, and environmental stability may be found to correlate with the kind of karyotypic variation found in *T. bottae* and *T. umbrinus*.

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