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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

# KARYOLOGY AND EVOLUTION OF THE PLAINS POCKET GOPHER, *GEOMYS BURSARIUS*

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

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BY

EUGENE BLAKE HART

Norman, Oklahoma

1971

KARYOLOGY AND EVOLUTION OF THE PLAINS POCKET GOPHER,

GEOMYS BURSARIUS

APPROVED BY

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TABLE OF CONTENTS


| | Page |
|---|---|
| LIST OF TABLES. . . . . | vi |
| LIST OF FIGURES . . . . . | vii |
| INTRODUCTION. . . . . | 1 |
| MATERIALS AND METHODS . . . . . | 5 |
| RESULTS . . . . . | 7 |
| DISCUSSION. . . . . | 34 |
| CONCLUSIONS . . . . . | 72 |
| SUMMARY . . . . . | 76 |
| SPECIMENS EXAMINED. . . . . | 79 |
| APPENDIX I. . . . . | 84 |
| APPENDIX II . . . . . | 92 |
| APPENDIX III. . . . . | 97 |
| LITERATURE CITED. . . . . | 103 |

## LIST OF TABLES


| Table | | Page |
|---|---|---|
| I. | Somatic Chromosome Numbers and Morphologic Types of the Plains Pocket Gopher, *Geomys bursarius* | 8 |
| II. | Comparative Karyotypes of the Rodent Genus, *Geomys* | 60 |

LIST OF FIGURES


| Figure | | Page |
|---|---|---|
| 1. | Chromosomal races of the plains pocket gopher, Geomys bursarius. . . . . | 10 |
| 2. | Karyotype of a male Geomys bursarius major from Norman, Cleveland Co., Oklahoma. 2N = 72 FN = 72 . . . . . | 12 |
| 3. | Karyotype of a male Geomys bursarius major from Tillman Co., Oklahoma. 2N = 72 FN = 70. . . . . | 12 |
| 4. | Karyotype of a male Geomys bursarius illinoensis from near Collinsville, St. Clair Co., Illinois. 2N = 72 FN = 70. . . . | 13 |
| 5. | Karyotype of a male Geomys bursarius jugossicularis from Amistad, Union Co., New Mexico. 2N = 72 FN = 72 . . . . . | 14 |
| 6. | Karyotype of a male Geomys bursarius bursarius from Monona, Clayton Co., Iowa. 2N = 72 FN = 72 . . . . . | 14 |
| 7. | Karyotype of a male Geomys bursarius wisconsinensis from Gotham, Richland Co., Wisconsin. 2N = 72 FN = 72 . . . . . | 15 |
| 8. | Karyotype of a male Geomys bursarius industrius from Kinsley, Edwards Co., Kansas. 2N = 72 FN = 70 . . . . . | 15 |
| 9. | Karyotype of a male Geomys bursarius majusculus from Tilden, Antelope Co., Nebraska. 2N = 72 FN = 70 . . . . . | 16 |
| 10. | Karyotype of a male Geomys bursarius lutescens from Chadron, Dawes Co., Nebraska. 2N = 72 FN = 96 . . . . . | 16 |

Figure Page

11. Karyotype of a female Geomys bursarius lutescens from Clearwater, Antelope Co., Nebraska. 2N = 72 FN = 72. . . . . 17

12. Karyotype of a male Geomys bursarius lutescens from near Neligh, Antelope Co., Nebraska. 2N = 72 FN = 88 . . . . . 17

13. Karyotype of a male Geomys bursarius dutcheri from Wrightsville, Pulaski Co., Arkansas. 2N = 74 FN = 72 . . . . . 19

14. Karyotype of a male Geomys bursarius terricolus from Texas City, Galveston Co., Texas. 2N = 74 FN = 72. . . . . 19

15. Karyotype of a male Geomys bursarius brazensis from near College Station, Brazos Co., Texas. 2N = 74 FN = 72 . . . . 20

16. Karyotype of a male Geomys bursarius attwateri from Cuero, DeWitt Co., Texas. 2N = 70 FN = 72 . . . . . 20

17. Karyotype of a male Geomys bursarius llanensis from near Castell, Llano Co., Texas. 2N = 71 FN = 69 . . . . . 21

18. Karyotype of a female Geomys pinetis from near Tampa, Hillsborough Co., Florida. 2N = 42 FN = 72 . . . . . 21

19. Approximate distribution of the contemporary subspecies of the plains pocket gopher, Geomys bursarius (after Hall and Kelson, 1959). . . . . 23

20. Postulated mechanisms of chromosomal rearrangement from ancestral Geomys. . . . . 25

21. Karyotype of a male Geomys bursarius bursarius from Monona, Clayton Co., Iowa. 2N = 72 FN = 70. . . . . 37

22. Karyotype of a female Geomys bursarius wisconsinensis from Gotham, Richland Co., Wisconsin. 2N = 72 FN = 70. . . . . 37

Figure | Page


23. Karyotype of a male polymorphic Geomys bursarius major from Norman, Cleveland Co., Oklahoma. 2N = 72 FN = 72. . . . . 39

24. Karyotype of a male Geomys bursarius major from Ponca City, Kay Co., Oklahoma. 2N = 68 FN = 70 . . . . . 40

25. Karyotype of a female Geomys bursarius bursarius from near Scotland, Bon Homme Co., South Dakota. 2N = 70 FN = 68. . . . 40

26. Karyotype of a female Geomys bursarius majusculus from near Emporia, Chase Co., Kansas. 2N = 72 FN = 70. . . . . 41

27. Karyotype of a female Geomys bursarius lutescens from near Wakeeney, Trego Co., Kansas. 2N = 72 FN = 70. . . . . 41

28. Phylogenetic arrangement of species and subspecies of the Genus Geomys, depicting chromosomal relationships . . . . . 53

29. Conjectural distribution of Geomys during (Mankato or Valders Substages) late Wisconsin glaciation, 8,000 to 1,000 B.C. . . 56

30. Conjectural distribution of Geomys at the beginning of the Post-Pleistocene (Recent) period (Pre-Boreal) about 7,000 to 8,000 years ago . . . . . 57

31. Conjectural distribution of Geomys at the beginning of the Recent Xerothermic period (Sub-Boreal), about 3,000 B.C. . . . . 61

32. Conjectural distribution of Geomys at the close of the Recent Xerothermic period (Sub-Boreal), about 1,000 B.C. . . . . 62

33. The Diploid Numbers (2N) plotted against the Fundamental Numbers (FN) of some species, subspecies of Genus, Geomys. . . . 74

# KARYOLOGY AND EVOLUTION OF THE PLAINS POCKET GOPHER, *GEOMYS BURSARIUS*

## INTRODUCTION

The plains pocket gopher, *Geomys bursarius* (Shaw), occurs quite consistently throughout the American Great Plains, from Manitoba and Minnesota in the north to Texas and Louisiana in the south, and from Colorado, Wyoming, and New Mexico in the west to Illinois and Indiana in the east. Since the first forms were named in 1800, numerous modifications in taxonomy have been effected. There are currently 19 generally recognized subspecies (Baker and Glass, 1951; Jones, 1965). Considerable external morphological variation is present, especially among some of the northern populations. Indeed, several contemporary conspecific groups were at one time considered full species (Swenk, 1939; Blossom, 1938, as quoted by Glass, 1951), due to size and pigmentation of pelage.

Geomyid rodents possess a number of unique qualities which make them attractive animals for speciation studies. The pocket gopher is adapted to the subterranean habitat and possesses a multitude of unique traits. These have allowed

differentiation to flourish in response to local environmental factors to a degree not common among mammals. The pocket gopher is solitary (except during breeding season), herbivorous, and fossorial. Many authors have postulated further corrollaries of these fossorial rodents, i.e., restricted locomotor capacity, enforced dispersal of young, inbreeding, difficulty of mate finding, existence of small isolated or semi-isolated populations, local differentiation, etc. (Pearson, 1959; Kennerly, 1959; Vaughan, 1962).

In the past, Geomyid taxonomists have utilized principally skull and body measurement and pelage coloration as taxonomic criteria in differentiating subspecies. Selection of significant evolutionary characters in different geographic localities is usually difficult and very likely to be somewhat arbitrary.

Recently, however, provocative new insights have been drawn from a character approach relatively new to mammalian systematics--cytogenetic analysis. Chromosomal number and morphology (including arm ratio) are commonly accepted character criteria in cytotaxonomy.

In addition to their own qualities, chromosomes determine many other characteristics, including genetic interaction with other individuals. Chromosomes are an integral part of the genetic system, since they not only carry the character of the gene, but also affect the rate of gene

exchange between populations and determine the nature of genetic recombination and whether it occurs at all. Structural differentiation of the chromosomes results in immediate genetic discontinuity between the genotypes concerned, whether these genotypes are genetically differentiated or not (Lewis, 1969).

Inferences may be drawn from cytogenetics as to configuration of ancestral genomes, taking into consideration present day distribution, morphology, present and past ecological factors, and fossil records, where available. Lucid and logical deductions concerning speciation, historical biogeography, and phylogeny have been hypothesized, often clarifying the systematics of well-known mammals, and more especially those with unknown or doubtful affinities, i.e., Baker, Chiroptera, 1970; Egozcue, Primates, 1969; Patton, Perognathus, 1967, 1969; Zimmerman, Sigmodon, 1970.

There have been three published accounts on the chromosomes of Geomys bursarius. Cross (1931) listed a 2N of 84 for Geomys breviceps (equals G. b. dutcheri) in northeastern Texas. Matthey (1960) indicated a 2N of 70 or 72 (FN = 68 or 70) for G. b. majusculus near Lawrence, Kansas. Berry (1969) found a 2N of 70, 71, 72 (FN = 70) in Lubbock and Garza Counties in Texas, and a 2N of 70 (FN = 68) along the western range of G. b. major. Berry (op. cit.) observed a 2N of 74 (FN = 72) of G. b. dutcheri in Bradley County, Arkansas.

The present investigation was undertaken to study cytological intraspecific, intrapopulational relationships of the plains pocket gopher, Geomys bursarius. The specific objectives of this research were as follows:

1. To find which taxonomic category most closely corresponds with chromosomal number and morphology.
2. To examine the overall constancy and integrity of chromosomal subspecies within the species; to compare contemporary subspecific groupings based on conventional gross morphology.
3. To hypothesize probable center of origin and account for present day distribution of subspecies of Geomys bursarius.

## MATERIALS AND METHODS

Specimens of the plains pocket gopher, Geomys bursarius, were trapped primarily during June, July, October, November of 1969; in June and November of 1970; and May and July, 1971, from the states of Arkansas, Iowa, Illinois, Kansas, Louisiana, Missouri, New Mexico, Nebraska, Oklahoma, South Dakota, Texas, and Wisconsin. Traditional Macabee jaw traps were used the first summer and resulted in capture success of about 50% and a mortality of about one-half of those captured. Hardware cloth traps following Ingles (1939), modified by myself, were constructed for live capture. Subsequent capture success approximated 50%.

Bone marrow preparations of captured live animals were obtained and processed according to modified techniques of Patton (1967), Ford and Hammerton (1962), and Stock (personal communication). Hypotonic KCl was used the majority of the time. Cell suspensions were incubated at 37° C. for 11-12 minutes. Slides were soaked in a cold 20% methanol solution prior to flaming (Scherz, 1962). Fixative consisting of 3:1 solution of methanol-acetic acid proved effective as a preservative for cell suspensions refrigerated at 10° C.

A binocular Phase-Star (American Optical Co., Model 1043-A) microscope was used in finding, counting, and photographing cells. Some 10 or more spreads were counted from most animals, with an arbitrary minimum of 80% accuracy. Ideal chromosomal spreads were photographed with an American Optical 4 x 5 photographic cone, using Kodak 4 x 5 Ortho Contrast Process film. Individual chromosomes were cut out and arranged according to size and centromere location and glued to heavy weight (substance 32) white biology paper. A Pentax H3A single lens reflex camera and Kodak High Contrast Copy Film were used to rephotograph finished karyograms. I follow the terminology of Patton (1967) in the description of chromosomal morphology.

Designation of the Y chromosome was assumed in all cases to be a small acrocentric. Analysis of numerous meiotic preparations was attempted, but due to a very cyclic annual production of sperm, appropriate meiotic figures were not encountered. Also, the fluorchrome Y method of Pearson and Bobrow (1970) was unsuccessful.

# RESULTS

## Subspecies Characteristics

### Karyotypic Descriptions

Populations of all 19 currently recognized subspecies of Geomys bursarius (Shaw) were sampled in the present study. Two localities were intensively trapped to determine intrapopulation variation and to study zones of intergradation. Table I indicates chromosomal forms, localities of collection, numbers and sexes of animals sampled. A total of approximately 300 pocket gophers were captured; due to trap mortality and inadequate technique, about 200 were examined karyotypically.

Overall, 2N remains conservative within the group, varying only between 70 and 74 (FN = 69-72); chromosomal morphology varies somewhat among subspecies, with one exception (G. b. lutescens, FN = 72-100). Matthey (1949) designated FN (Fundamental Number) as the total number of autosomal arms. FN is used as an indicator of genetic mechanisms responsible for increase and decrease of biarmed chromosomes, i.e., Robertsonian fusion. The genetic mechanisms primarily responsible for chromosomal differentiation

Table I. Somatic Chromosome Numbers and Morphologic Types of Subspecies of Geomys bursarius.

| Geomys Subspecies | Locality | ♂ | ♀ | Total | 2N | FN | Autosome Morphology Acrocentric | Biarms | Sex Chromosomes X | Y |
|---|---|---|---|---|---|---|---|---|---|---|
| major | Claude, Ok. | 2 | 2 | 4 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | Hawley, Ok. | 1 | 2 | 3 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | Lexington, Ok. | 2 | 2 | 4 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | Norman, Ok. | 15 | 30 | 45 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | Ponca City, Ok. | 1 | 0 | 1 | 72 | 70 | 70 | 2 | L-Telo | Sm-Telo |
| illinoensis | Clinton, Ill. | 1 | 0 | 1 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | E. St. Louis, Ill. | 1 | 0 | 1 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| | Collinsville, Ill. | 3 | 6 | 9 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| bursarius | Monona, Ia. | 1 | 8 | 9 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Bankston, Ia. | 0 | 1 | 1 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Garbin, Ia. | 1 | 1 | 2 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Sullivan, Mo. | 0 | 1 | 1 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Scotland, S. D. | 0 | 1 | 1 | 72 | 72 | 68 | 0 | L-Meta | Sm-Telo |
| wisconsinensis | Gotham, Wisc. | 3 | 7 | 10 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| jugossicularis | Amistad, N.M. | 1 | 0 | 1 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Clayton, N.M. | 1 | 1 | 2 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Felt, Ok. | 0 | 1 | 1 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Liberal, Ks. | 0 | 3 | 3 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Sedan, N.M. | 0 | 1 | 1 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| | Tolar, N.M. | 0 | 2 | 2 | 72 | 72 | 70 | 2-Sm | L-Telo | Sm-Telo |
| majusculus | Emporia, Ks. | 0 | 1 | 1 | 72 | 70 | 72 | 0 | L-Telo | Sm-Telo |
| | Tilden, Neb. | 2 | 0 | 2 | 72 | 70 | 72 | 0 | L-Meta | Sm-Telo |
| industrius | Dodge City, Ks. | 1 | 2 | 3 | 72 | 70 | 72 | 0 | L-Meta | Sm-Telo |
| | Kinsley, Ks. | 2 | 1 | 3 | 72 | 70 | 72 | 0 | L-Meta | Sm-Telo |
| lutescens | Chadron, Neb. | 2 | 3 | 5 | 72 | 72-100 | 44-70 | 0-28 | L-Meta | Sm-Telo |
| | Neligh, Neb. | 3 | 11 | 14 | 72 | 72-100 | 44-70 | 0-28 | L-Meta | Sm-Telo |
| | Oakdale, Neb. | 4 | 2 | 6 | 72 | 72-100 | 44-70 | 0-28 | L-Meta | Sm-Telo |
| | Spencer, Neb. | 2 | 1 | 3 | 72 | 72-100 | 44-70 | 0-28 | L-Meta | Sm-Telo |
| | Wakeeney, Ks. | 0 | 1 | 1 | 72 | 70 | 70 | 0 | L-Telo | Sm-Telo |
| breviceps | Mer Rouge, La. | 1 | 4 | 5 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| brazensis | College Sta., Tx. | 2 | 2 | 4 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| dutcheri | Bowlegs, Ok. | 0 | 1 | 1 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| | Norman, Ok. | 5 | 4 | 9 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| | Wrightsville, Ark. | 5 | 2 | 7 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| ludemani | Double Bayou, Tx. | 1 | 4 | 5 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| pratincola | Glenmora, La. | 3 | 4 | 7 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| sagittalis | Alta Loma, Tx. | 1 | 1 | 2 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| terricolus | Texas City, Tx. | 2 | 1 | 3 | 74 | 72 | 72 | 0 | L-Meta | Sm-Telo |
| attwateri | Kenedy, Tx. | 2 | 1 | 3 | 70 | 72 | 64 | 4 | L-Meta | Sm-Telo |
| ammophilus | Cuero, Tx. | 1 | 1 | 2 | 70 | 72 | 64 | 4 | L-Meta | Sm-Telo |
| llanensis | Castell, Tx. | 1 | 1 | 2 | 71 | 69 | 69 | 0 | L-Telo | Sm-Telo |
| texensis | Mason, Tx. | 1 | 0 | 1 | 71 | 69 | 69 | 0 | L-Meta | Sm-Telo |

in the plains pocket gopher appear to be pericentric inversions. Robertsonian mechanisms are also significant, though to a lesser degree.

Chromosomal forms of G. bursarius seem to fall quite naturally into seven main groups, four in the north (2N = 72), three in the south (2N = 74, 71, 70) (Fig. 1). The northern group consists of G. b. major (whose distribution extends south into Texas), G. b. illinoensis; G. b. jugossicularis, G. b. bursarius, G. b. wisconsinensis; G. b. majusculus, G. b. industrius; and G. b. lutescens. The Gulf Coastal Plains group includes G. b. dutcheri (whose distribution extends well to the north), G. b. brazensis, G. b. breviceps, G. b. pratincola, G. b. ludemani, G. b. sagittalis, G. b. terricolus. This group will be referred to here as the "breviceps" assemblage. Prior to 1951 it was recognized as a full species and included the additional four subspecies referred to below.

The "attwateri" group, found near the southern Gulf Coast and in south central Texas, includes: G. b. attwateri and G. b. ammophilus.

The last group, G. b. texensis and G. b. llanensis, is found within a limited area near Mason and Castell, Texas, and will be referred to here as the "texensis" group. For convenience, these latter four subspecies will be considered herein as separate from the breviceps group in which they were formerly placed by Davis (1940).

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Four main chromosomal complements are evident within the northern subspecies; all have a 2N of 72. G. b. major (Figs. 2,3) and G. b. illinoensis (Fig. 4) both possess a chromosomal configuration of completely acrocentric elements. The X chromosome is a large acrocentric; the Y is presumed to be a small acrocentric. G. b. major was captured from various sites in Oklahoma. This subspecies has been designated (Hall and Kelson, 1959) as having a distribution of approximately 450 mi by 600 mi, and it may be that several chromosomal races are contained within these geographic limits.

G. b. jugossicularis (Fig. 5), G. b. bursarius (Fig. 6), and G. b. wisconsinensis (Fig. 7) all exhibit identical 2N number and morphology. Chromosomal complements consist of one small pair of biarmed chromosomes--the remainder of the complement is acrocentric. FN is therefore 72. The X chromosome is a large biarm, and the Y is thought to be a small acrocentric; acrocentrics account for the remainder of the chromosomal complement (2N = 72, FN = 70).

G. b. industrius (Fig. 8) and G. b. majusculus (Fig. 9) possess similar number and chromosome morphology. The X chromosome is a large biarm, and the Y is thought to be a small acrocentric; acrocentrics account for the remainder of the chromosomal complement.

The fourth and most aberrant northern subspecies is G. b. lutescens (Figs. 10, 11, 12). The 2N is 72, but the FN varies from 70 to more than 100. Geomys arenarius appears closely related (2N = 70, FN = 100, 102). G. b. lutescens has a large range (Hall and Kelson, 1959) and may have a

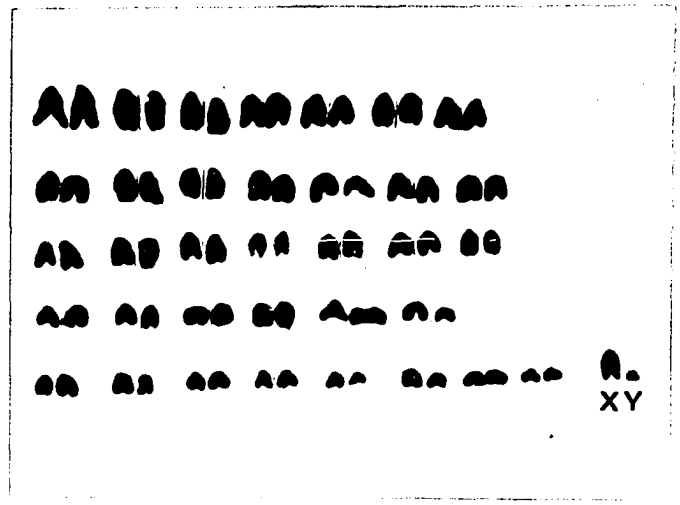



Figure 2. Karyotype of a male Geomys bursarius major from Norman, Cleveland Co., Oklahoma. 2N = 72 FN = 72.

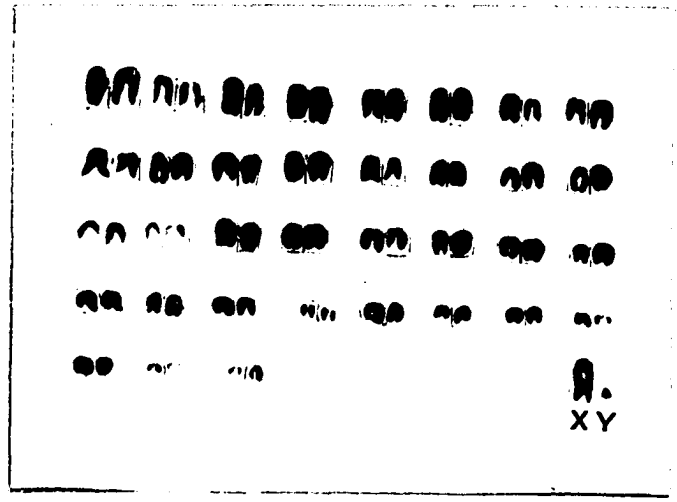



Figure 3. Karyotype of a male Geomys bursarius major from Tillman Co., Oklahoma. 2N = 72 FN = 70.

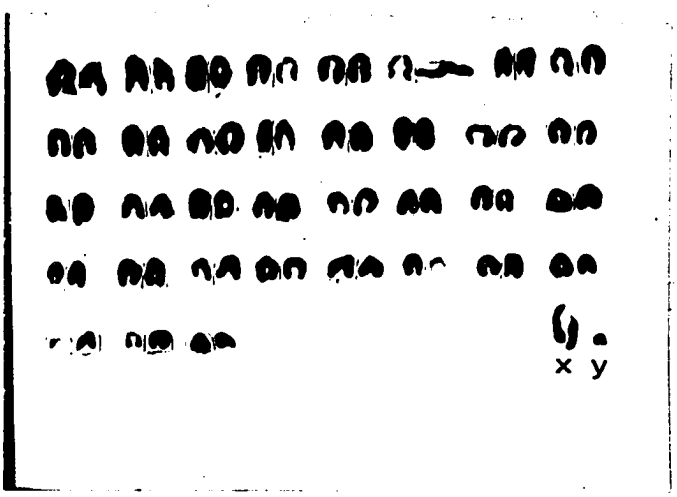



Figure 4. Karyotype of a male Geomys bursarius illinoensis from near Collinsville, St. Clair Co., Illinois. 2N = 72 FN = 70.

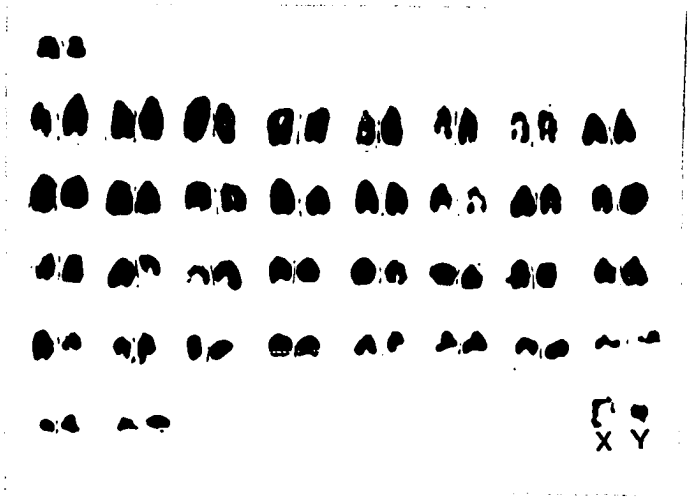



Figure 5. Karyotype of a male Geomys bursarius jugossicularis from Amistad, Union Co., New Mexico. 2N = 72 FN = 72.

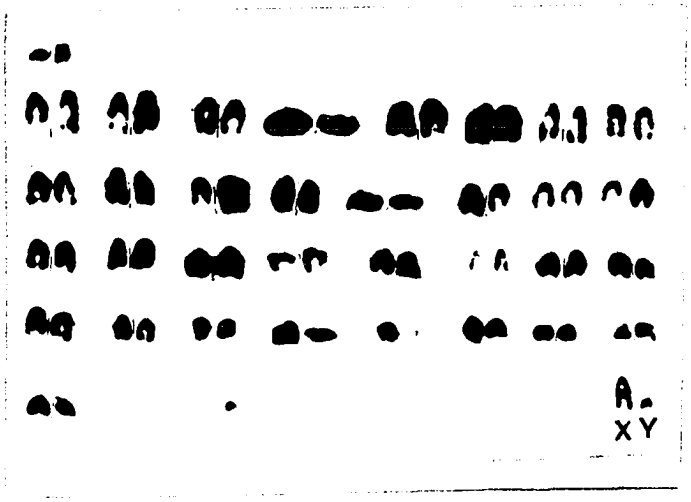



Figure 6. Karyotype of a male Geomys bursarius bursarius from Monona, Clayton Co., Iowa. 2N = 72 FN = 72.

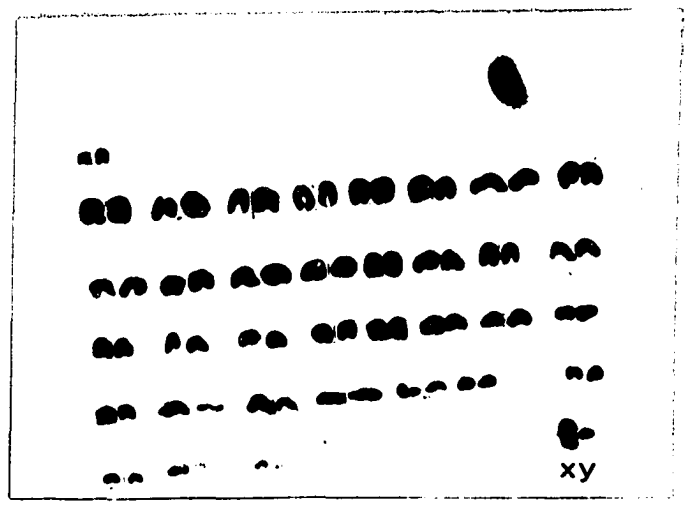



Figure 7. Karyotype of a male Geomys bursarius wisconsinensis from Gotham, Richland Co., Wisconsin. 2N = 72 FN = 72.

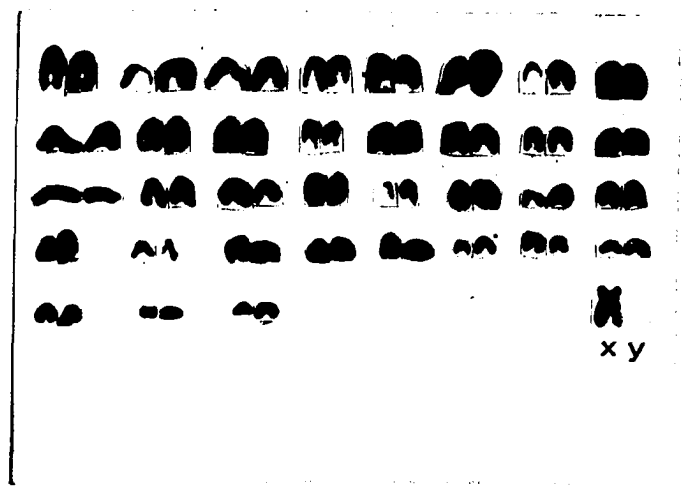



Figure 8. Karyotype of a male Geomys bursarius industrius from Kinsley, Edwards Co., Kansas. 2N = 72 FN = 70.

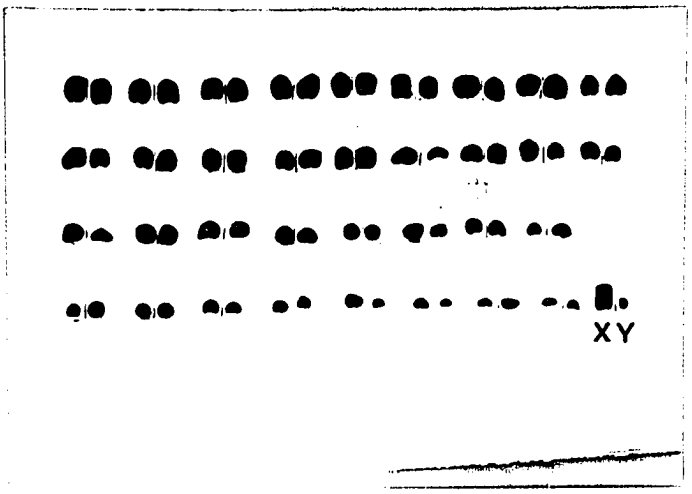



Figure 9. Karyotype of a male Geomys bursarius majusculus from Tilden, Antelope Co., Nebraska. 2N = 72 FN = 70.

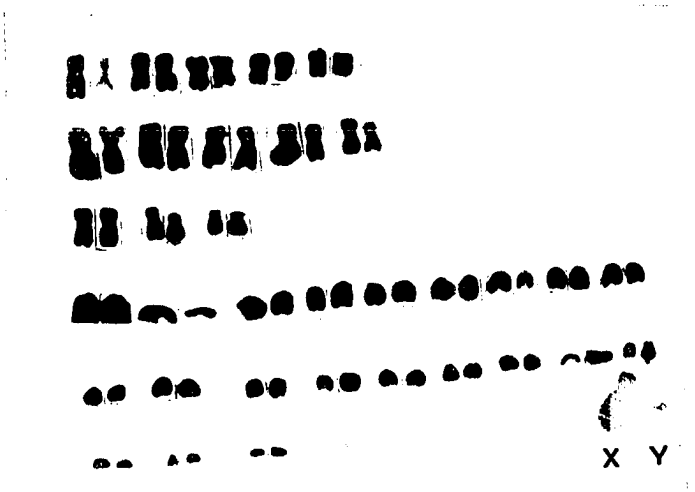



Figure 10. Karyotype of a male Geomys bursarius lutescens from Chadron, Dawes Co., Nebraska. 2N = 72 FN = 96.

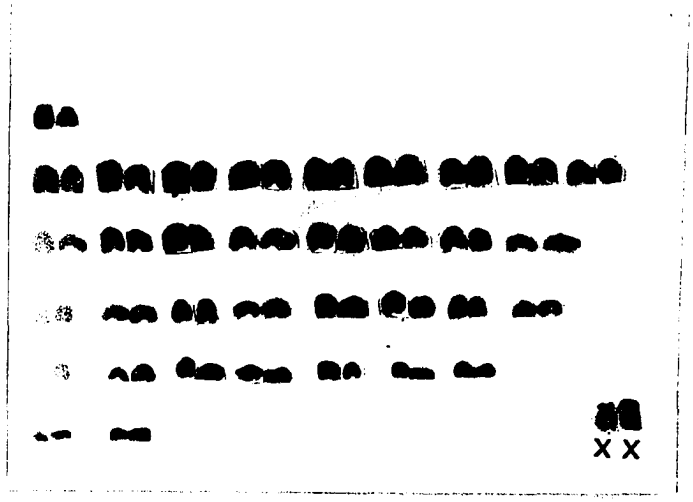



Figure 11. Karyotype of a female Geomys bursarius lutescens from Clearwater, Antelope Co., Nebraska. 2N = 72 FN = 72.

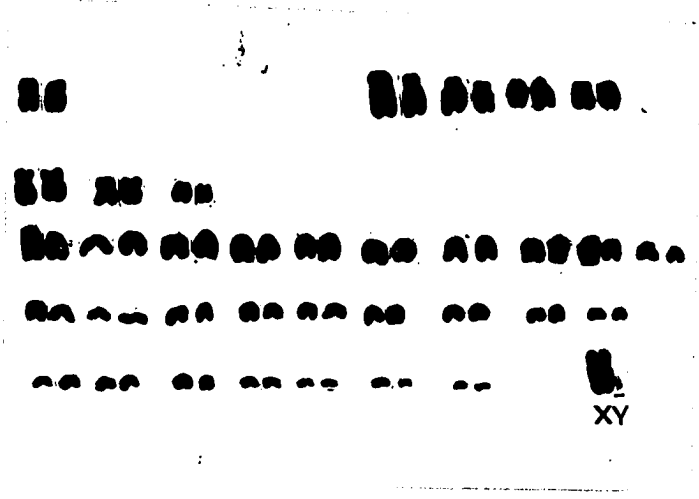



Figure 12. Karyotype of a male Geomys bursarius lutescens from near Neligh, Antelope Co., Nebraska. 2N = 72 FN = 88.

number of isolated forms. Its distribution centers in the extremely variable environment of Nebraska's Sand Hills. This area may well be the most marginal xeric habitat occupied by any subspecies of Geomys bursarius. Neotoma (Baker and Mascarello, 1969) has been found to be similarly polymorphic.

The most widely distributed of the southern groups, the breviceps group, includes G. b. dutcheri (Fig. 13), G. b. breviceps, G. b. pratincola, G. b. ludemani, G. b. terricolus (Fig. 14), G. b. sagittalis, and G. b. brazensis (Fig. 15). All have a 2N of 74, with an FN of 72. The X is a large metacentric; the Y is presumed to be a small acrocentric.

The second southern element, G. b. attwateri and G. b. ammophilus, reside in the extreme southernmost (Texas) distribution of Geomys bursarius (Fig. 16). I found these to have only 70 chromosomes but with an FN of 74, due to the presence of a large and small biarmed pair and a biarmed X; the Y was assumed to be a small acrocentric.

The third southern group, G. b. texensis and G. b. llanensis, possess a 2N of 71, FN of 69. The X is assumed to be a large telocentric and the Y a small telocentric (Fig. 17).

Two specimens of Geomys pinetis from near Tampa, Florida, were karyotyped. These possess a 2N of 42 with 36 biarmed autosomes, FN = 72 (Fig. 18).

As many as 12 supernumary chromosomes were found in G. b.

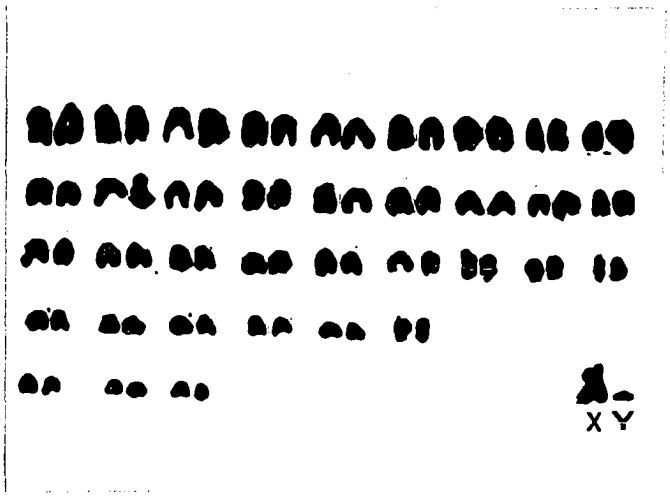



Figure 13. Karyotype of a male Geomys bursarius dutcheri from Wrightsville, Pulaski Co., Arkansas. 2N = 74 FN = 72.

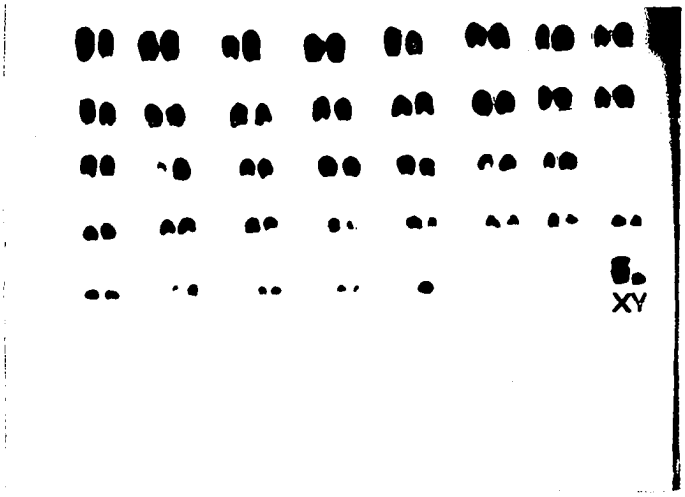



Figure 14. Karyotype of a male Geomys bursarius terricolus from Texas City, Galveston Co., Texas. 2N = 74 FN = 72.

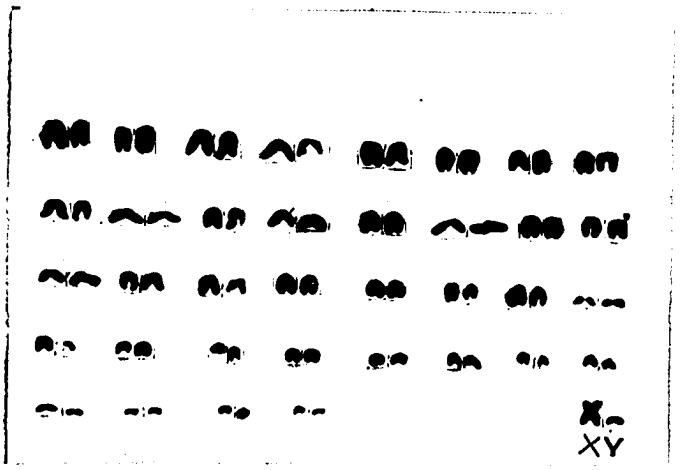



Figure 15. Karyotype of a male Geomys bursarius brazensis from near College Station, Brazos Co., Texas 2N = 74 FN = 72.

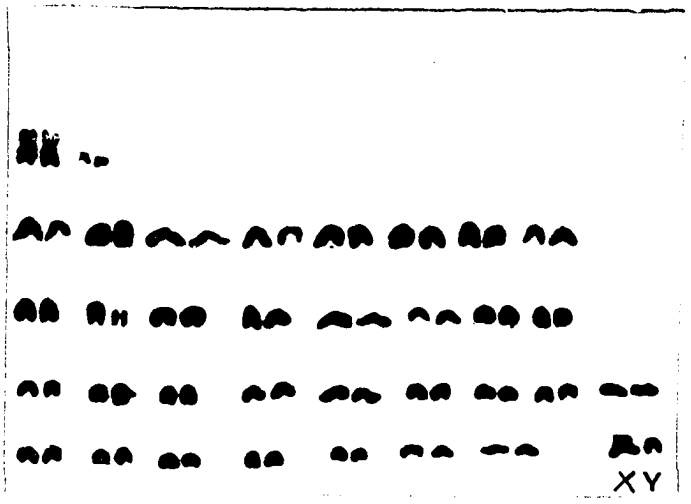



Figure 16. Karyotype of a male Geomys bursarius attwateri from Cuero, DeWitt Co., Texas. 2N = 70 FN = 72.

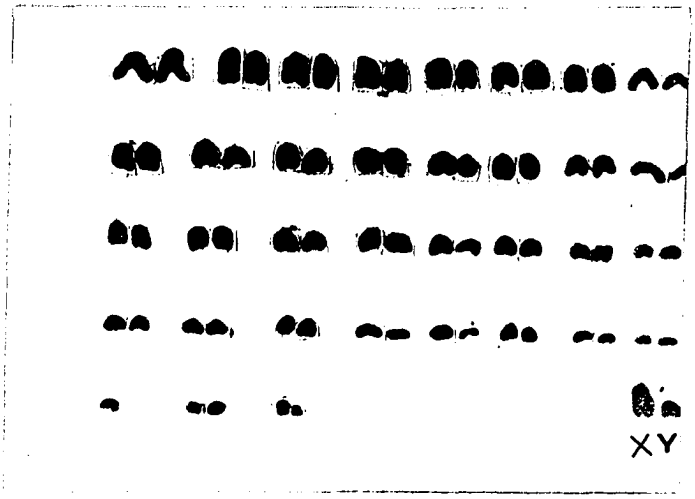



Figure 17. Karyotype of a male Geomys bursarius llanensis from near Castell, Llano Co., Texas. 2N = 71 FN = 69.

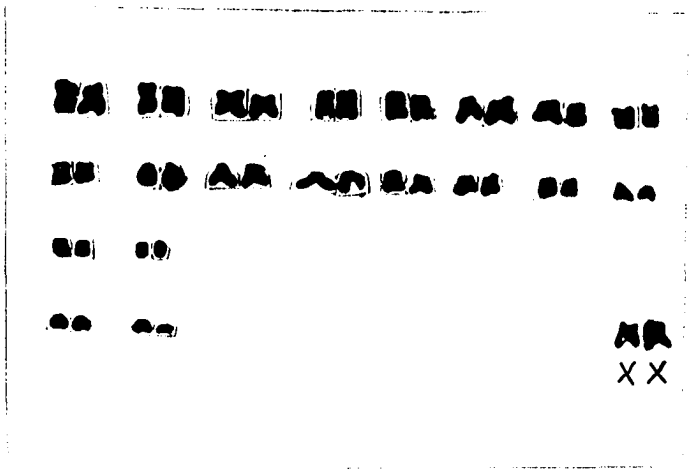


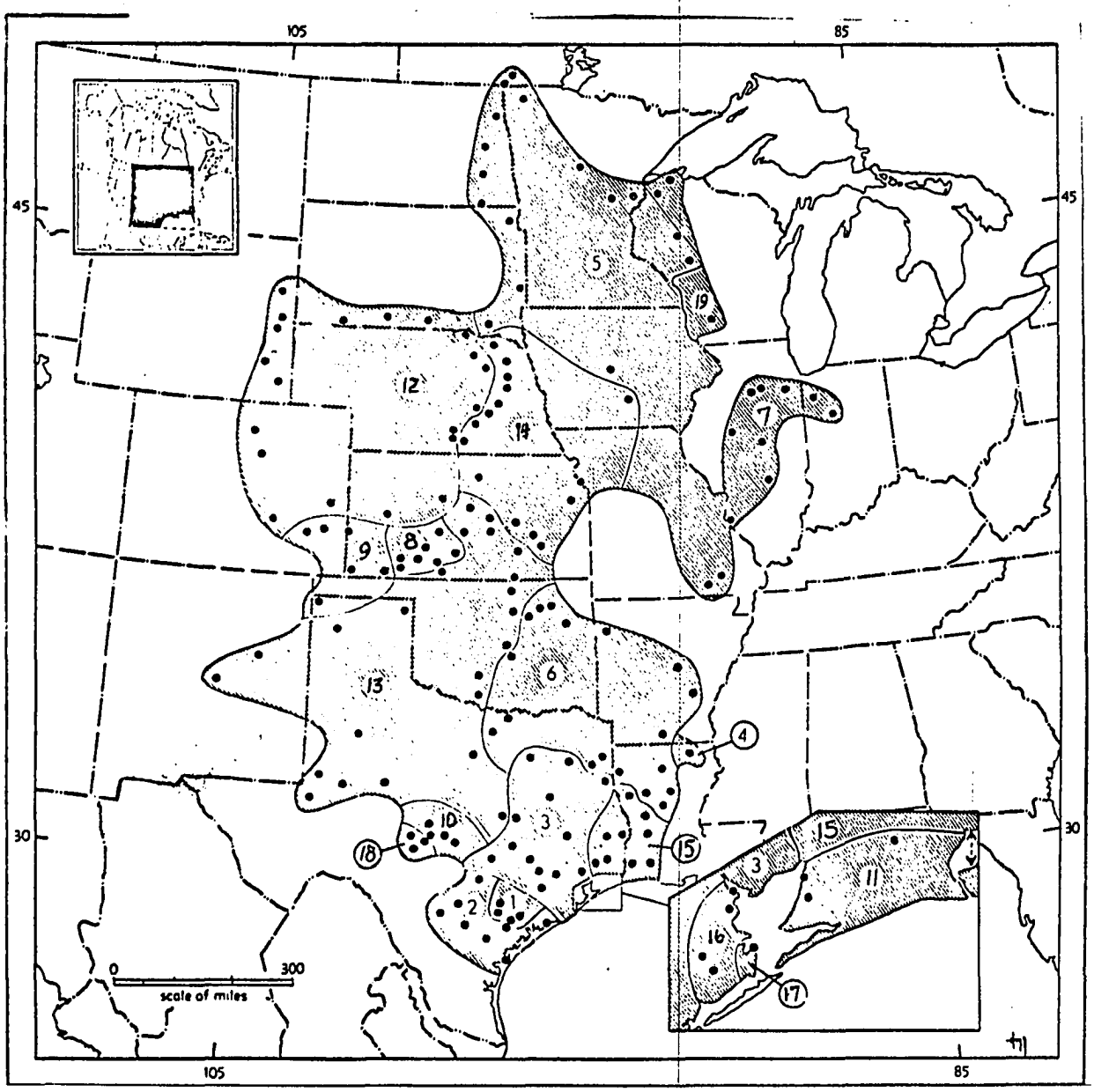

Figure 18. Karyotype of a female Geomys pinetis from near Tampa, Hillsborough Co., Florida. 2N = 42 FN = 72.

wisconsinensis. Most animals possessed some secondary constrictions, usually 2-4.

## Geographic Distribution

Geographic subspecies of Geomys bursarius are mostly, if not in every case, contiguously allopatric or parapatric (Fig. 19). Large rivers appear to delimit geographic forms; G. b. illinoensis apparently is confined east of the Mississippi River, and G. b. wisconsinensis may not occur on the south of the Wisconsin River, nor west of the Mississippi River. G. b. attwateri is known to occur on the north side only of the San Antonio River for 50 miles (Kennerly, 1959). Best and Hart (unpub. data) have amplified Kennerly's (1963) conclusions that small rivers probably exert few distributional barriers and little overall influence in delimitation of pocket gopher dispersal over long periods of time.

The inherent nature of the fossorial, sedentary pocket gopher should be taken into consideration, since gene pools of these act quite unlike that of other mobile, easily dispersable rodent populations. Pocket gopher populations seem to exist under a loose type of locally isolated conditions. They are not found indiscriminately within theoretical distribution boundaries, but rather in a patchwork pattern, apparently directly or indirectly influenced by optimal soils.




Legend:

1 - G.b. ammophilus
2 - G.b. attwateri
3 - G.b. brazensis
4 - G.b. breviceps
5 - G.b. bursarius
6 - G.b. dutcheri
7 - G.b. illinoensis
8 - G.b. industrius
9 - G.b. jugossicularis
10 - G.b. llanensis
11 - G.b. ludemani
12 - G.b. lutescens
13 - G.b. major
14 - G.b. majusculus
15 - G.b. pratincola
16 - G.b. sagittalis
17 - G.b. terricolus
18 - G.b. texensis
19 - G.b. wisconsinensis

Figure 19. Approximate Distribution of the Contemporary Subspecies of the Plains Pocket Gopher, Geomys bursarius (after Hall and Kelson, 1959).

In general, subspecies of pocket gophers do not appear to be limited to specific ecological areas nor are they always separated by rivers or streams as Patton (1969) reported for Perognathus.

## Ecological Distribution

The plains pocket gopher is well adapted to a diet high in grass (Vaughan, 1965); hence its occupation of the grasslands and prairie region of the American Great Plains. It is well adapted to the highly fertile Chernozemic soils of much of the region, as well as to the characteristic continental climate of typical middle continental grasslands (e.g.: 10-30 in. precipitation, cold winters, hot summers; Carpenter, 1940). Thornthwaite (1948) classified the American grassland as subhumid, mesothermal or microthermal, depending on locality. Appendix I outlines a more detailed discussion regarding ecology of distributional areas of Geomys bursarius.

## Chromosome Phylogeny

Sequences of chromosomal rearrangement of Geomys bursarius may have progressed along one of several avenues. It is hypothesized that ancestral forms possess higher diploid numbers, and completely telocentric complements, for reasons to be cited later. I favor mechanisms which are most direct in formation of these taxa (Fig. 20).

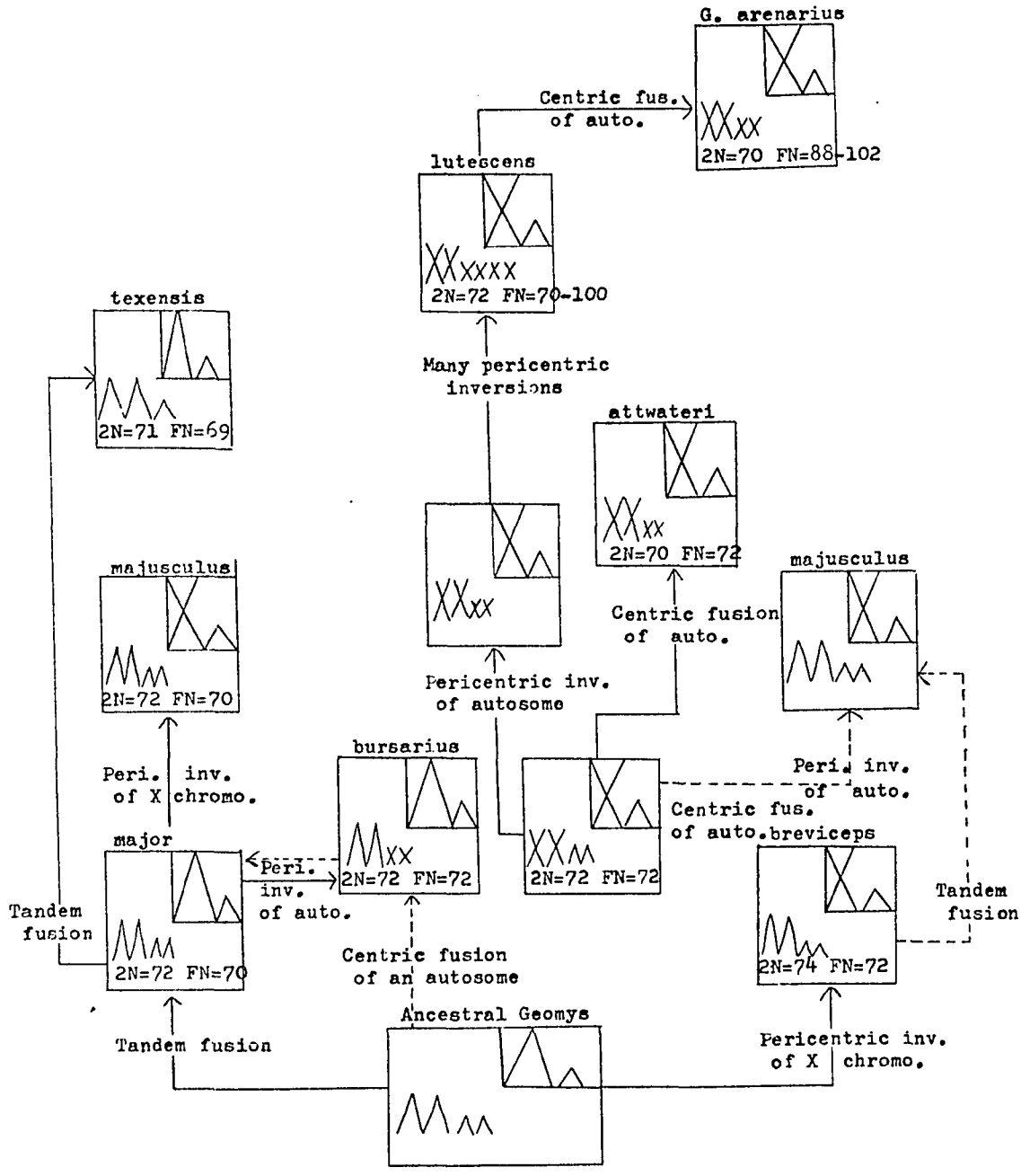



Figure 20. Postulated mechanisms of chromosomal rearrangement from ancestral Geomys.

Extant chromosomal subspecies suggest two main entities which arose from ancestral animals possessing a 2N of 74, FN = 72, telocentric X, sometime during late Pleistocene, probably during the Wisconsin.

The first entity, which is represented by the breviceps group, was formed by a pericentric inversion of the X chromosome. This population in turn may have undergone a process of tandem fusion which would have given rise to the G. b. majusculus, G. b. industrius karyotype, although the majusculus group is hypothesized here as having arisen via the other (G. b. major) basic entity. A centric fusion of an autosome from the same breviceps configuration gave rise to an intermediate group with 2N = 72, FN = 72, biarmed X. This intermediate group can be logically hypothesized to have undergone rearrangements (centric fusion of an autosome) to produce the attwateri group and eventually the lutescens (several successive pericentric inversions) configuration. It is logical that a centric fusion from G. b. lutescens produced the G. arenarius karyotype. The intermediate group spoken of above may have given rise to the majusculus group via a pericentric inversion of an autosome (broken line, Fig. 20). Interestingly, this intermediate group has chromosomes identical to G. personatus streckeri (2N = 72, FN = 72).

The second entity, primarily northern in distribution,

was derived from the same basic ancestral (2N = 74, FN = 72, telocentric X) group, probably during the Wisconsin. It is represented by extant G. b. major, G. b. illinoensis which may have arisen via a tandem fusion of an autosome either to another autosome or to the telocentric X chromosome. It is suggested that the bursarius group arose via a pericentric inversion of an autosome from the major group. An alternate pathway of rearrangement, in the event a tandem fusion did not occur, is the formation of the bursarius group via a centric fusion of an autosome (broken line, Fig. 20). Present distribution suggests that possibly the bursarius group (which occupies northern extremes of G. bursarius distribution) pre-dated the major group. I prefer to postulate G. b. major as ancestral to G. bursarius, as it requires fewer cytologic rearrangements to explain derivation of majusculus and texensis. The major group may then have arisen by way of pericentric inversion of one small biarmed chromosome to form an acrocentric. It is postulated here that formation of the majusculus group was by a pericentric inversion of the telocentric X of major to a biarmed element. The texensis group is hypothesized here as originating from west Texas G. b. major. The original telocentric X is preserved in this phylogeny (aside from majusculus group).

## Distributional Patterns

Based on karyotypes, I have postulated that the G. b. breviceps group is most similar karyotypically to ancestral progenitors of modern races. Members of breviceps have a 2N of 74, FN of 72. G. b. brazensis, G. b. dutcheri, and G. b. pratincola occupy large areas of eastern Texas and Oklahoma, western Arkansas and Louisiana. The remaining subspecies of the breviceps group, G. b. breviceps, G. b. ludemani, G. b. texensis, G. b. sagittalis, occupy restricted geographic areas in central Louisiana and around Galveston Bay (Fig. 19). The occupation of extensive areas of the Gulf Coastal Plains by the breviceps group is significant.

In the south, the breviceps group and G. b. major border the southern subspecies of G. b. ammophilus, G. b. attwateri, and G. b. llanensis; the former are separated slightly from G. b. texensis.

In the north, the derived G. b. majusculus, G. b. industrius occupy a central area and are parapatric with four of the other six morphological subspecies, representatives of all of the northern chromosomal forms. Spatially, G. b. majusculus and G. b. industrius, G. b. wisconsinensis and G. b. illinoensis are all separated.

G. b. major arose independently of the breviceps group, and, similar to contemporary G. b. bursarius, has one of the largest geographical distributions of all subspecies of

Geomyidae. In the south, major borders all subspecies but G. b. texensis, and it maintains borders with G. b. brazensis and G. b. dutcheri of the breviceps group. It also is contiguous with G. b. jugossicularis, G. b. industrius, and G. b. majusculus. The northern west-east sequence of subspecies includes G. b. lutescens, G. b. majusculus, G. b. bursarius, G. b. wisconsinensis, and G. b. illinoensis. G. b. bursarius and G. b. lutescens are widely distributed over several states. G. b. majusculus, G. b. illinoensis, and G. b. wisconsinensis are more restricted in distribution than other northern subspecies groups (Hall and Kelson, 1959).

## Ecology of Contact Zone

Superficially, the ecology of contact zones between subspecies of Geomys bursarius varies little with the surrounding countryside in all areas of contact in the plains. I have compared sites of capture of animals in a zone of contact between the G. b. majusculus to the east and G. b. lutescens in Antelope County, Nebraska.

Jones (1965) wrote that typical G. b. lutescens were taken near Neligh (elevation 1746 feet), while G. b. majusculus were taken only 5 miles southeast near Oakdale (elevation 1710 feet). Since limits to distribution of pocket gophers often appear to be influenced either directly

or indirectly by the nature of soils (Davis, 1940; Miller, 1964), it was useful to compare soil types from each location of capture with the U. S. Department of Agriculture's Bureau of Soils (1921) soil survey of Antelope County, Nebraska.

Antelope County lies on the western border of the hill area of northeastern Nebraska, and includes parts of the sand-hill and high-plains regions. Agents primarily responsible for the formation of the present topographic features are stream erosion and wind action. The region was originally covered with a thick mantle of plains loess. Erosion and wind action have removed most of the loessial material, lowering the surface substantially below original conformation.

The influence of climate (i.e., precipitation, wind) has directly influenced the development of soils in this belt, perhaps as nowhere else in the U. S. Annual precipitation between immediately adjacent counties to the east and west both receive 22.5 in per year. The soils on both sides of the zone are western Pedocals, broadly classified as subhumid, and whose horizons contain greater amounts of carbonate of lime than is present in parental geological material beneath (Carter, 1931).

Although the parental materials underlying parts of the county differ widely, the precipitation has been influential

in the process of soil formation. The upland soils to the east have accumulated carbonates in the lower subsoil due to inadequate moisture, which fails to leach the soil to very great depths. The Marshall and Holt series are typical examples. These dark and fertile soils contain substantial organic materials and are loessial in origin. The upper two horizons contain dark, friable soils, while the third distinct horizon contains concentrations of carbonates. This soil occurs primarily in the southeast portion of the county and is highly fertile and mostly cultivated. The range of G. b. majusculus falls mainly within these soils.

The other soils in this area from which I took pocket gophers can be roughly classified as readily leached soils; Valentine, Dunesand, Waukesha, Sioux, and Sarpy are all different types of sandy loams with poorly developed horizons, yet with good leaching properties and lowered concentrations of carbonates. Land to the west of Oakdale broadly belongs to this latter series and is almost all sandy pastureland, especially at the sites of gopher capture. Intergrades and animals closely resembling G. b. lutescens all were taken from uncultivated soils (pastureland) except at an alfalfa field 4 mi. north of Neligh. All soils were of sandy texture. Due to the disturbed nature of the overgrazed countryside, it was most difficult to postulate probable distributions on the original prairie. To the east of Oakdale,

pastureland has been overgrazed and to the west much arable land is under cultivation.

## Intergradation

A zone of secondary intergradation between G. b. lutescens to the west and G. b. majusculus to the east near Oakdale and Neligh, Nebraska, was studied. Although cytologic results are incomplete, it appears that there is some limited interbreeding between the two subspecies. In an alfalfa field on the western edge of Oakdale, morphological forms similar to both parental forms were encountered. Animals taken exhibited from 4 to 26 biarmed chromosomes. Within a distance of 3 to 4 mi west of Oakdale, a grayish, intermediate form was encountered with chromosomes similar to G. b. lutescens, with 10 to 26 biarms. In the vicinity of Neligh (5 mi west), all animals externally appeared as lutescens, and biarm numbers ranged from 4 (in Clearwater, 10 mi west of Neligh) to 26 (4 mi south of Neligh). Incidentally, two females trapped within 100 yards of each other in Clearwater, exhibited 4 and 24 biarmed chromosomes, respectively.

Baker and Glass (1951) determined that a narrow zone of intergradation existed between 2 to 3.5 mi east of Norman, Cleveland Co., Oklahoma. Parental morphological forms, G. b. dutcheri and G. b. major, were found east and west,

respectively, of this zone. On the basis of intergrading morphological types between Norman and Shawnee (50 mi east), Baker and Glass assumed interbreeding and reduced G. b. dutcheri (breviceps group) to subspecific status.

In this study, 16 animals were captured from 1 mi to 5 mi east of Norman, most linearly along New Highway 9. One male from 1 mi east exhibited a 2N of 73, although cells with 72 and 74 were counted within the same animal, no biarms. Some 2.8-3 mi east of Norman, I found animals with 70 and 74 diploid numbers, both males and females with two large biarms. Three animals were captured 5 mi east, 1 mi south which all possessed standard G. b. dutcheri complements, 2N = 74, FN = 72. Over 50 animals were trapped in Norman, approximately 2 mi west of the 73 chromosome male mentioned. Only two unique males with atypical G. b. major chromosomes (2N = 72, FN = 72) were found. Sufficient time has not yet been available to completely work out the dynamics of this zone. However, it is fairly obvious that there is at least some reproductive exchange between the two forms. Lewis (1969) stated that genetic continuity between populations can be maintained by extremely low rates of gene exchange.

Analysis of both the Nebraska and Oklahoma zones is continuing.

# DISCUSSION

The validity of chromosomal analyses, as with other taxonomic characters, varies at different levels of taxa. Nadler (1969) stated that the utility and significance of chromosomal characters are useful taxonomic characters to distinguish subgeneric and subspecific population levels, with significance increasing proportionately from the former to the latter.

Genetic mechanisms most often invoked to explain rearrangement among closely related groups are usually of two very different types: 1) Robertsonian mechanisms, which lowers 2N and raises FN; and 2) pericentric inversions, which may raise or lower FN but do not influence 2N. In other words, Robertsonian fusion simply combines existing telocentrics to form biarmed chromosomes; and pericentric inversions involve a centromeric shift, forming one biarmed chromosome from a single, preexisting telocentric chromosome.

## Heterozygosity and Polymorphism

Patton (1969) stated that in allopatric races of mammals where intraspecific variation is present, each race

has been found to be monomorphic (i.e., one homozygous for the original arrangement, one homozygous for the derived arrangement); populations with individuals of intermediate condition are not known. However, Berry (1969) reported a heteromorphic pair (excluding sex chromosomes) in 11 of 13 pocket gophers having 2N of 71 near Lubbock, Texas. Davis, Williams, and Lopez (1971) reported polymorphic systems which produced hetermorphic pairs among subspecies of Geomys personatus. Apparently, either heterozygotes are not selected against or these animals are in a stage of chromosomal rearrangement.

During normal mechanisms of chromosomal rearrangement, heterozygotes are a necessary prerequisite to formation of derived homozygotes. It is thought that normally heterozygotes are somewhat rapidly eliminated, especially when the breeding systems permit inbreeding and compression through small population sizes (Carson, 1967).

However, Carson (1967) indicated that another effect of inbreeding may be to permit establishment of fixed heterozygosity, due to the great and obvious benefits. When areas of the genome are shut off from recombinations by inversions, chiasma localization, or differential segments in translocations, obligatory heterozygosity may accumulate, rendering a return to the homozygous state increasingly difficult.

Among animals which are speciating, one should expect to encounter intermediate diploid numbers, especially in cases of Robertsonian fusion, which lowers diploid numbers. Or, perhaps each parental population possesses different diploid numbers in areas of intergrading populations.

Nadler (1969) maintained that heterozygote formation is a rather brief event, characterized by presence of originally homozygous animals, and derived homozygous animals. He stated that this kind of chromosomal polymorphism is the forerunner of karyotype evolution accompanying speciation. Patton (1969) believed that balanced or transitional polymorphisms within the species range are not compatible with allopatrically distributed races. White (1969) gave an interpretation which does not assume an ancestral widespread condition of balanced polymorphism.

I observed the occurrence of several polymorphisms among pocket gophers as follows: Of 7 animals analyzed from one population in northeastern Iowa, one female, OU10089, (Fig. 21) possessed no biarmed chromosomes as compared with the general occurrence of two small biarmed chromosomes in the remainder of animals examined.

Of 11 G. b. wisconsinensis examined, one female (Fig. 22) possessed no small biarms.

In Norman, Oklahoma, of 35 animals examined from one breeding population, two adult males, OU9331 and EBH552, possessed two small autosomes and one large biarmed (X)

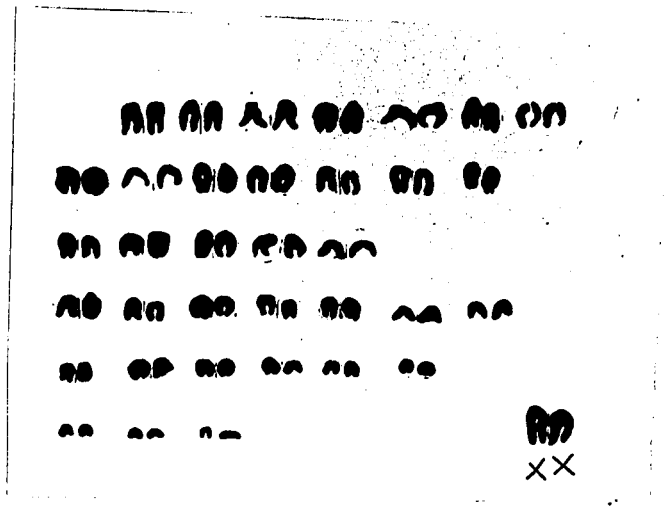


Figure 21. Karyotype of a male Geomys bursarius bursarius from Monona, Clayton Co., Iowa. 2N = 72 FN = 70.

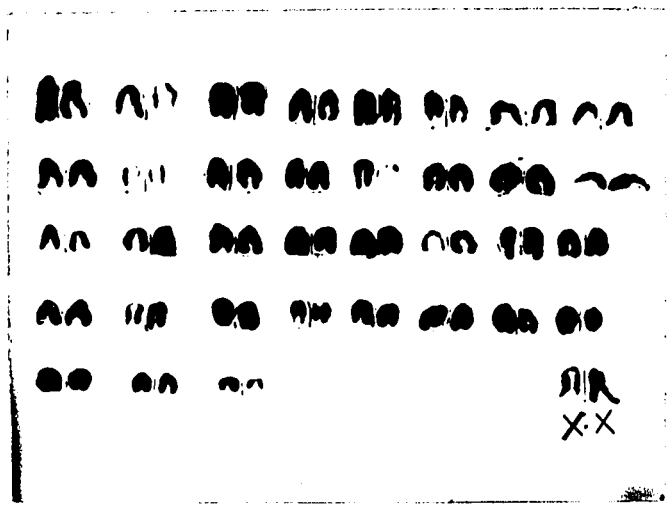


Figure 22. Karyotype of a female Geomys bursarius wisconsinensis from Gotham, Richland Co., Wisconsin. 2N = 72 FN = 70.

sex chromosome (Fig. 23), as compared with completely acrocentric complements for the remaining animals. This particular karyotype is doubly interesting because it represents the necessary intermediate step in the proposed phylogeny of southern breviceps and is the only example encountered so far. Especially intriguing is the fact that it was found within 1-3 miles of a secondary zone of contact between major and breviceps, which probably accounts for the presence of the polymorphisms.

In the overall investigation, several other animals were found to have discrepant chromosomal morphology, but these representative variances were attributed to the possible occurrence of other chromosomal races within subspecies distributions:

One male (EBH512) from Ponca City, Oklahoma, (Fig. 24), supposedly well within the range of the G. b. major subspecies, exhibited two large biarmed chromosomes and a 2N of 72 (perhaps due to one pericentric inversion). A female (EBH307) taken from near Scotland, South Dakota (Fig. 25), had two large biarmed chromosomes, 2N = 70, unlike the two small biarms possessed by other members, 2N = 72, of G. b. bursarius. A female G. b. majusculus (Fig. 26) taken near Emporia, Kansas, exhibited a completely acrocentric complement as compared to possession of a biarmed X among other G. b. majusculus. A female G. b. lutescens captured near (Fig. 27)

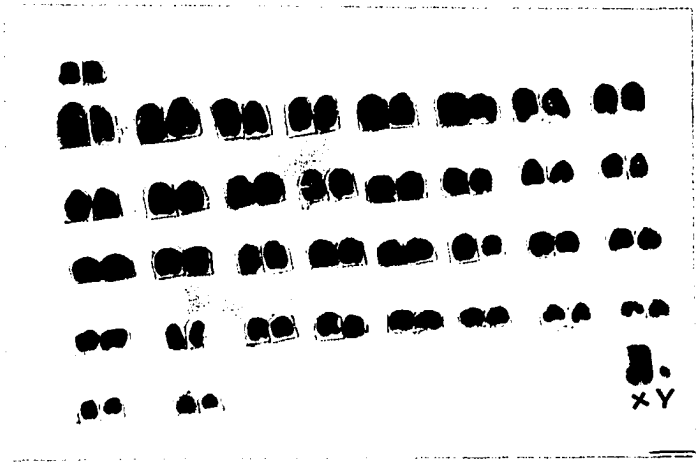



Figure 23. Karyotype of a male polymorphic Geomys bursarius major from Norman, Cleveland Co., Oklahoma. 2N = 72 FN = 72.

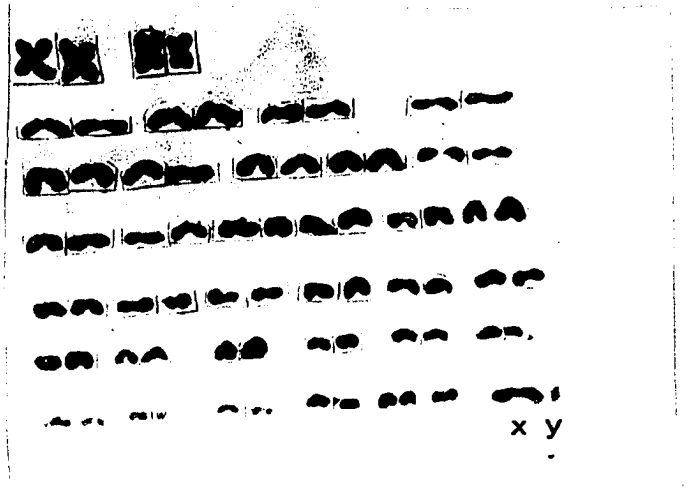



Figure 24. Karyotype of a male Geomys bursarius major from Ponca City, Kay Co., Oklahoma. 2N = 68 FN = 70.

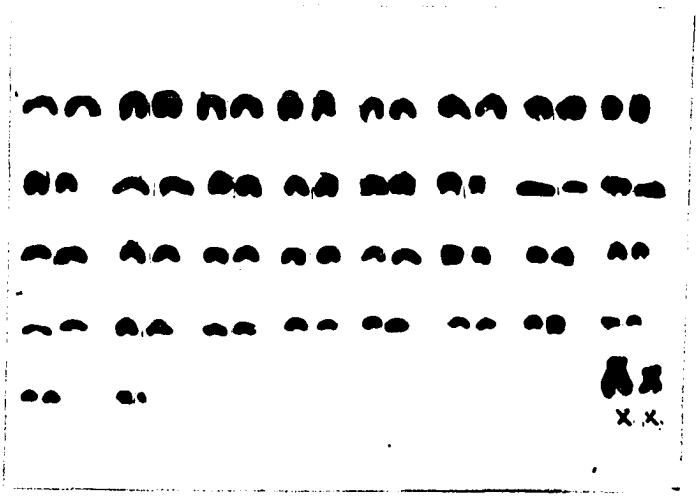



Figure 25. Karyotype of a female Geomys bursarius bursarius from near Scotland, Bon Homme Co., South Dakota. 2N = 70 FN = 68.

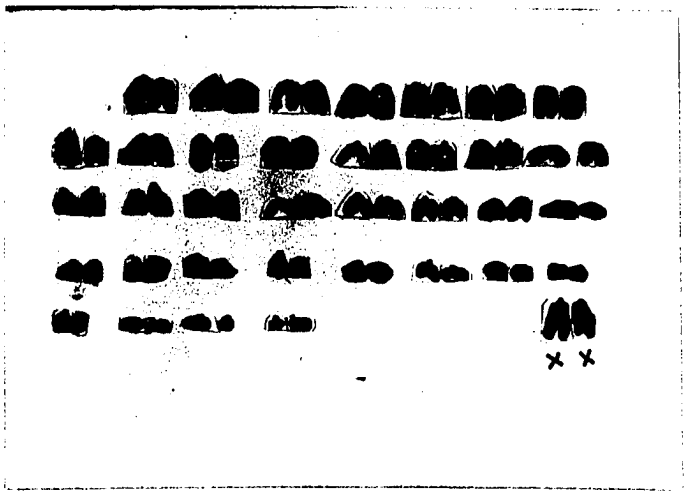



Figure 26. Karyotype of a female Geomys bursarius majusculus from near Emporia, Chase Co., Kansas. 2N = 72 FN = 70.

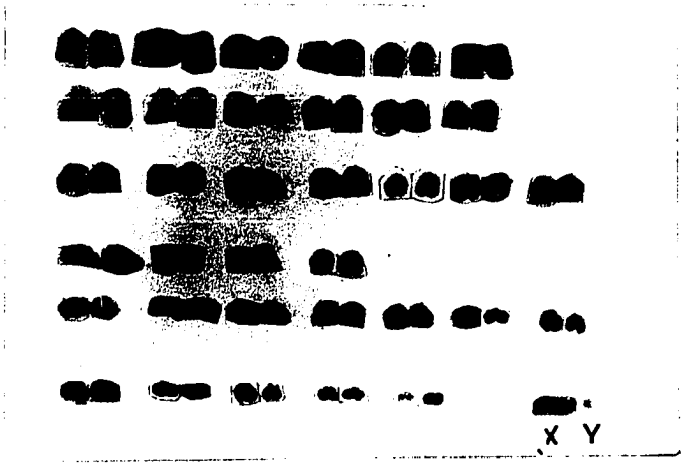



Figure 27. Karyotype of a female Geomys bursarius lutescens from near Wakeeney, Trego Co., Kansas. 2N = 72 FN = 70.

Wakeeney, Kansas, had all acrocentrics. Externally, both of the former two animals appeared typical of their respective subspecies. These individuals listed may be typical members of their own populations, perhaps cryptic chromosomal races, although they may be polymorphically rare animals. Additional collecting is needed, especially from Kansas and South Dakota and northern Oklahoma.

It may be that these relatively rare polymorphic animals are selectively advantageous, or neutral, allowing them to be carried within the population.

The occurrence of chromosomal polymorphs in Wisconsin, Iowa and Oklahoma, representing 14%, 9%, and 6% of all animals examined, may point up existence of exceptionally high heterozygosity. In small populations, these individuals stand an excellent chance of becoming the predominant chromosome type, due to unusual opportunity afforded individual animals as a result of genetic drift. In pocket gophers, the tendency for selfing, inbreeding and polygamous mating (especially in polymorphic males) may greatly enhance the probability of conservation of new rearrangements.

Da Cunha, et. al., (1959) suggested that in Brazilian Drosophila, population distributions in central geographic areas are more polymorphic; populations which occupy rich and diversified environments are more polymorphic than are those of submarginal environments; populations which face

the competition of closely related species are more monomorphic than those enjoying near-monopolistic status.

Generally, these same observations may be true of pocket gophers. But, near zones of secondary contact between chromosomally different subspecies, results indicate greater variety of polymorphisms than expected under normal conditions. The dynamics of zones of secondary contact offer much fertile ground for additional research.

There has been some question as to the origin of genetic isolating mechanisms, however. Mayr (1963) insisted that geographical isolation (allopatric model of speciation) is essential to the process of speciation, via formation of reproductive barriers/genetic discontinuity. This model is generally accepted by vertebrate biologists, as opposed to the sympatric model of speciation (Test, 1946; Thorpe, 1945; Emerson, 1949).

However, White (1968) recently proposed a stasipatric model of speciation of continuous populations of morabine grasshoppers in Australia to explain their apparent direct conversion into parapatric races.

Due to the present alignment of subspecies and presumed sequences of chromosomal rearrangement, with the most derived populations occupying distal expansions of the total range, it appears that the allopatric model satisfies the present subspecies alignments. Isolates, which have fragmented and

become separated from peripheral areas differentiated, then spread outwardly into unoccupied areas. Patton (1969) ascribed allopatric speciation to present day Perognathus goldmani distributions in Mexico.

## Fossil History

Russell's (1968) monograph concerning the evolution and classification of pocket gophers of subfamily Geomyinae has been a useful guide to this present study. Russell's conclusions concerning the original distribution of Geomys are as follows:

Probably four separate lineages differentiated around Plio-Pleistocene time--Geomys, Zygogeomys, Pappogeomys, and Orthogeomys on the central Mexican Plateau presumably from the same ancestral stock. Progeitors of Geomys and Zygogeomys radiated northward. Zygogeomys may have extended as far north as extreme southern Colorado and Texas Panhandle in early Pleistocene; it is unknown north of southeastern Arizona in Middle Pleistocene age. The apparent northward dispersal of Pappogeomys is comparatively recent, i.e., during late Pleistocene and Recent times. Ancestral Geomys are common in Pleistocene deposits throughout North America especially in the Great Plains.

The Great Plains area was the center of distribution and differentiation of Thomomys and Geomys according to

Russell. Records of closely related Geomyid ancestors are relatively common in the Pliocene of the Great Plains, and the earliest Pleistocene records of the genera also are from the Great Plains. Probably the rarity of Thomomys as contrasted to the abundance of Geomys, during early and middle Pleistocene, was due to allopatric distribution of the two genera; yet, Geomys and Thomomys both were taken from Oklahoma during the Illinoian, and G. pinetis and Thomomys were taken from the Sangamon cave fauna in Florida. Perhaps reduced preferred habitat of Thomomys was instrumental. Hibbard (1960, 1964) stated that inferred climatic sequence explains a wide variety of data, such as former close association of species that are presently allopatric and living in widely separated areas.

Probable ancestral forms of Geomys are abundant in the Illinoian of Kansas and Oklahoma. Excavated Geomys, mostly referrable to the living species, are common from the Sangamon Interglacial of Kansas, Nebraska, Texas. Geomys bursarius is known from the Wisconsin of Kansas, Texas, Illinois, Wisconsin, and Nebraska.

Probably G. pinetis was derived from Geomys of the Illinoian, and by the following interglacial (Sangamon), was differentiated. G. pinetis fossils from Florida are referrable to the Sangamon (Russell, 1968).

## Post Pleistocene Events

Probable environmental changes since Wisconsin are thought to have had decisive influence on present animal distribution. However, I attribute formation of the majority of modern plains pocket gopher subspecies to late Post Pleistocene, Recent events.

Smith (1965) summarized evidence of biota changes in distribution during the Post Pleistocene, Recent period. He took the modified view that fauna near periglacial borders consisted of admixtures of both boreal and austral elements.

Significantly, plains pocket gophers withstood cold glacial climates in northern areas. Fossils referrable to pluvial periods have been found in several central and north central states (summarized by Russell, 1968); these pocket gophers apparently ranged near glaciated regions.

Kendeigh (1961) suggested that late glacial and post-glacial chronology was as follows (modified from Deevey, 1949; Deevey and Flint, 1957; Flint, 1957): Sub-arctic climates prevailed during and following deglaciation 14,000 to 11,000 B.C. From 10,000 to 8,000 B.C., the climate was cool and moist (pre-boreal). Spruce and fir occurred in northern central United States. The hypsithermal (thermal maximum, 7,000 to 1,000 B.C.) consisted of three main climates: the warm, dry boreal (8,000 to 7,000 B.C.),

typified by pine in north central U.S.; the warm, moist climatic optimum (Atlantic--6,000 to 3,000 B.C.) during which deciduous forests of oak, beech, and hemlock extended far north; the warm, dry xerothermic (Sub-boreal--3,000 to 1,000 B.C.) which allowed extension of the grasslands and prairies far to the east and north. Grassland animals penetrated far to the north and east, presumably including pocket gophers.

From approximately 1,000 B.C. to A.D. 1,000, cooler, moister climates (Sub-atlantic) prevailed, similar to today's climate (Smith, 1957). Transeau (1935) cited substantial evidence to support his contention that extensive prairies developed in areas formerly occupied by deciduous forest which extended as far east as Pennsylvania and New York. The prairie peninsula receded, leaving populations of biota far behind where they are relict today. Beech and hemlock deciduous forests moved west from the East, and spruce moved southward from the North. Lakes of the Great Basin were refilled with water. Somewhat harsh climatic conditions have prevailed since this general period.

Fauna which moved eastward with the prairie was soon excluded by gradual return of deciduous forests. Present evidence of former western forms in the east is offered by relict populations of one amphibian, eight reptiles, and three small mammals. Additional evidence is suggested by remains of pocket gophers from Randolph

County, Illinois, somewhat to the south of present G. b. illinoensis distribution.

Kendeigh (1961) suggested that the amelioration of the climate recently has permitted the northward dispersal of fauna. Northern communities are not presently saturated with the variety of species they could support. Other workers (Smith, 1964, 1957; Borchert, 1950; Gleason, 1922; Transeau, 1935) generally agree with this summary.

Remington (1968) coined the term "suture-zones" for localized areas of significant gene exchange between allopatric pairs of species and subspecies. Careful investigation into biogeographic history of North America has suggested that biotic and physical barriers to dispersal of biota have largely disappeared or been modified during the past 2,000-3,000 years, hence, the existence of extensive areas of hybridization.

The modern arrangement of pocket gopher subspecies is indicative of a relaxation of recent barriers to distribution. The dearth of tangible barriers demarcates limits of distribution, with the exception of physiographic factors, where they exist. The relatively homogeneous Great Plains has only few physiographic boundaries.

## Phylogeny

Considering the emergent patterns of chromosomal races and the historical biogeography (Appendix II), it becomes

necessary to fit these data together in view of contemporary scientific theory.

Russell (1968) stated that original differentiation of modern genera of Geomyidae occurred on or near the Central Plateau of Mexico. Zygogeomys has subsequently been found only as far north as southeastern Arizona (Middle Pleistocene). Fossils of Geomys have been excavated in many parts of North America, principally in the central Great Plains, where Russell postulated speciation occurred; Geomys is thought to be one of the most primitive of living genera based on dentition and skull qualities.

Some authors have correlated specialization of animals with low diploid number and possession of a predominance of biarmed chromosomes (Bender and Chu, 1963). However, Egozcue (1969) has shown that very specialized primates, such as the Tarsiers, have some of the highest diploid numbers in the order and many acrocentrics. He felt that the "primitiveness" of the species has no correlation with the morphology of its chromosomes.

In my study of the plains pocket gopher chromosomal systems, it appears that chromosomal rearrangement has proceeded from higher to lower diploid numbers. Postulation of the reverse, lower to higher numbers, is possible only in the event of fission or dissociation as reviewed by White (1957), and Nadler (1969). Some examples of fission have

been hypothesized, but these are rare exceptions to mammalian chromosomal evolution. Patton (1969) hypothesized a diminution of diploid number in the closely related Heteromyid, Perognathus. Wahrman (1969), however, reported increasing diploid numbers among progressively derived populations in Spalax, the blind mole rat, in Israel.

In addition, forms of Geomys bursarius which possess the highest numbers of acrocentric chromosomes are found in areas such as currently occupied by the breviceps group which are to have been the most historically stable (Auffenberg and Milstead, 1965).

Ancestral karyotypes of Geomys are probably represented by an ancestral form similar to the breviceps group, except that the former possessed a 2N of 74, and an acrocentric X chromosome. Davis, Williams, and Lopez (1971) have postulated that the ancestral Geomys had a diploid number of "about 70" with all acrocentrics based on karyograms of Geomys personatus, G. arenarius, and G. tropicalis.

There are several lines of logic which support this chromosomal reduction hypothesis in Geomys. If the breviceps group (with a biarmed X) were postulated as ancestral, one would have to explain the subsequent derivation of a uniarmed X in several of the northern subspecies via a pericentric inversion. However, sex chromosomes appear to be more stable than are autosomes and do not dissociate as

readily. Also, if the ancestors were identical to the breviceps group, this presents some difficulties in explanation of present subspecies distribution. G. b. major (2N = 72, FN = 70) becomes a derived form, with G. b. bursarius group (2N = 72, FN = 72) an immediate ancestor. This arrangement is unwieldy in view of the current distribution, i.e., adjacent populations.

In order to explain a reduced diploid number, several mechanisms are possible. Tandem fusions or centric fusions followed by pericentric inversion of autosomes are both theoretically possible. Since the ancestral forms are postulated here to have a diploid number of 74, reduction probably occurred, utilizing one of these two mechanisms.

The tandem fusion mechanism appears to be the most logical method because if one of the ancestral forms (breviceps) possessed the biarmed X, it would be possible to postulate formation of basic majusculus-like (2N = 72, FN = 70) forms within several generations. White (1957), however, has stated that tandem fusions (in groups with monocentric chromosomes) between acrocentrics, will give rise mostly to extremely awkward meiotic figures when heterozygous. In addition, he stated that meiotic configurations which appear to have arisen by tandem fusions, in reality probably arose by centric fusion followed by pericentric inversion.

Animals which have acquired elaborate complexes of biarmed chromosomes via fusion to protect coadapted gene

complexes of high selective value for a specific "set" of habitat factors, show no tendency or ability to dissociate chromosomes already "locked" by fusions. These (as Dipodomys merriami, Geomys pinetis, and Geomys tropicalis) are apparently at an evolutionary dead end.

Undoubtedly "pre or postzygotic accidents" (Mayr, 1963) probably account for a high mortality among heterozygotes. However, only one animal requiring only one generation must pass through the "bottleneck of heterozygosity" before homozygotes can be produced. Genetic drift of small populations with substantial inbreeding may then fix the rearrangement in the gene pool with extreme rapidity.

A phylogeny of the breviceps group is proposed (Fig. 28) and apparently has remained in the relatively "secure" Gulf Coastal Plains since early Pleistocene, despite sea level fluctuations, as long as the environment continued to be inhabitable. This breviceps group extended its population borders extensively during interglacials and other optimal expansion periods, but always maintained the stable ancestral habitats when environmental extremes increasingly impinged on peripheral populations.

The majority of Geomyid fossils have been found mainly in the central Great Plains; few from the Gulf Coastal Plains. This is partially accountable due to more collections being obtained in the former area. It is possible

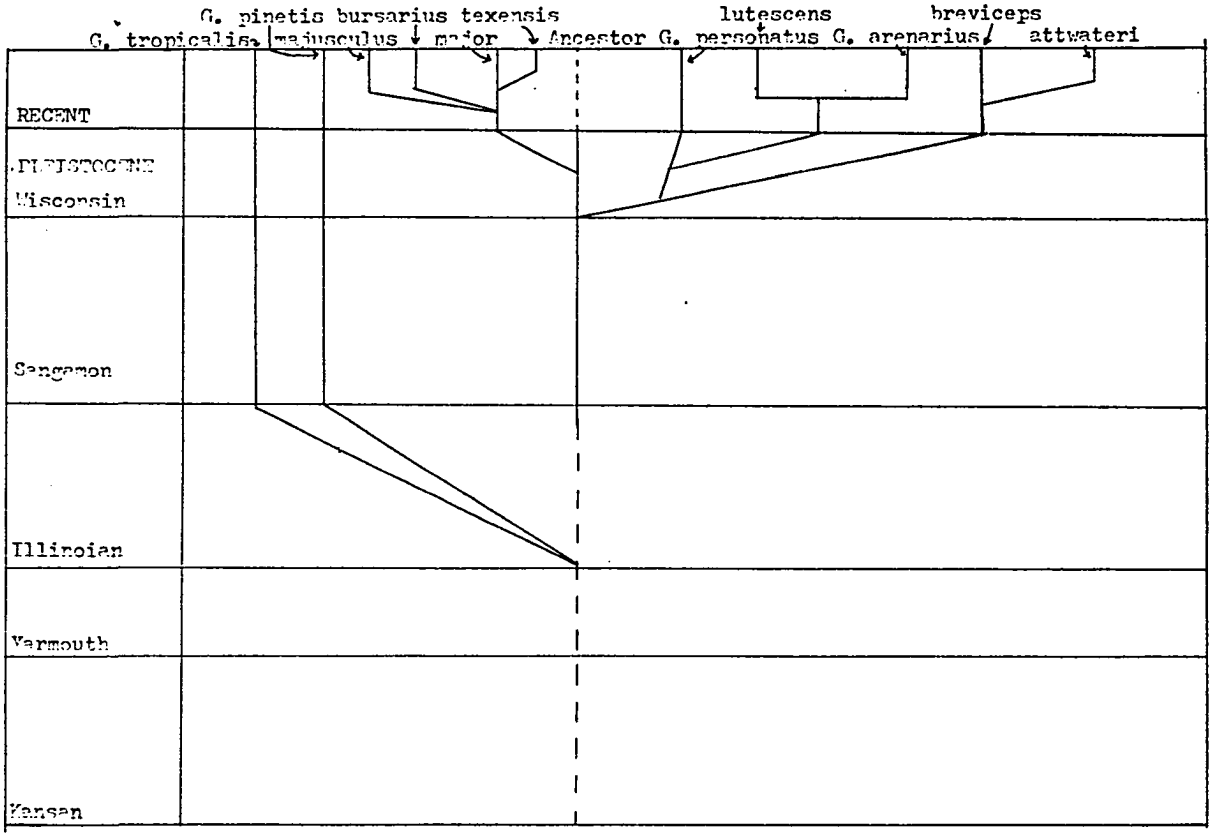



Figure 28. Proposed phylogenetic sequence of Geomys. Chromosomal rearrangement events as compared to geologic time is conjectural (modified from Russell, 1968, and others).

that these fossils represent the breviceps group which ranged far and wide during Pleistocene.

Dichotomy in the original ancestral karyotype (2N = 74, FN = 72, acrocentric X) during Wisconsin glaciation, resulted in two branches represented by G. b. major and the breviceps group. I found no animals actually possessing the ancestral karyotype, although it is possible that these exist somewhere, perhaps adjacent to the derived breviceps and G. b. major groups.

The ancestral or derived breviceps group is postulated to have been widespread during the Illinoian, extending far to the east and south. Resultant ameliorization of this pluvial (Sangamon Interglacial) left two disjunct populations as the major distribution receded, one in the region of Tamaulipas, Mexico, and the other in Florida, where both have remained isolated since. Configurations of the chromosomes of the two are quite similar today (Fig. 18), which may indicate similar elapsed time since isolation. Resultant centric fusion in both has formed 36 biarmed chromosomes in G. pinetis in Florida and 36, 34 biarmed chromosomes in G. tropicalis in Tamaulipas, Mexico (Berry, 1969; Williams, Davis, Lopez, 1971).

G. personatus probably represents a recent invasion from the south, perhaps as far south as Tamaulipas, where Alvarez (1963) listed populations of G. personatus as still extant. Kennerly (1959) stated that G. personatus and G.

bursarius are closely related species with few qualitative diagnostic character differences. Original bifurcation from ancestral breviceps may have occurred during early Wisconsin glaciation. Populations of early Geomys personatus (originating along the eastern Mexico Coast) radiated north into New Mexico during a Wisconsin interglacial and became isolated for a considerable period of time during which the postulated series of pericentric inversions occurred (Fig. 29). Following Pleistocene (Fig. 30), during the climatic optimum, populations radiated north to eastern Colorado, western Nebraska. Subsequent chromosomal realignments have varied within G. personatus. Davis, Williams, and Lopez (1971) reported diploid number to vary from 68 to 72 and FN to vary from 70 to 76 in this chromosomally plastic group. Several disjunct subspecies of G. personatus exist which are chromosomally unique. It is suggested that independent events resulted subsequent to original G. personatus disjunctions from breviceps ancestors, although homologous morphology is present among some populations of both groups. G. personatus appears to have been derived well before attwateri, probably residing far to the south for many years, only lately invading southern Texas. I suggest that G. personatus is probably the ancestral form of both G. b. lutescens, G. arenarius. Kennerly (1959) hypothesized ancestral G. bursarius occupied the region between the Nueces and San

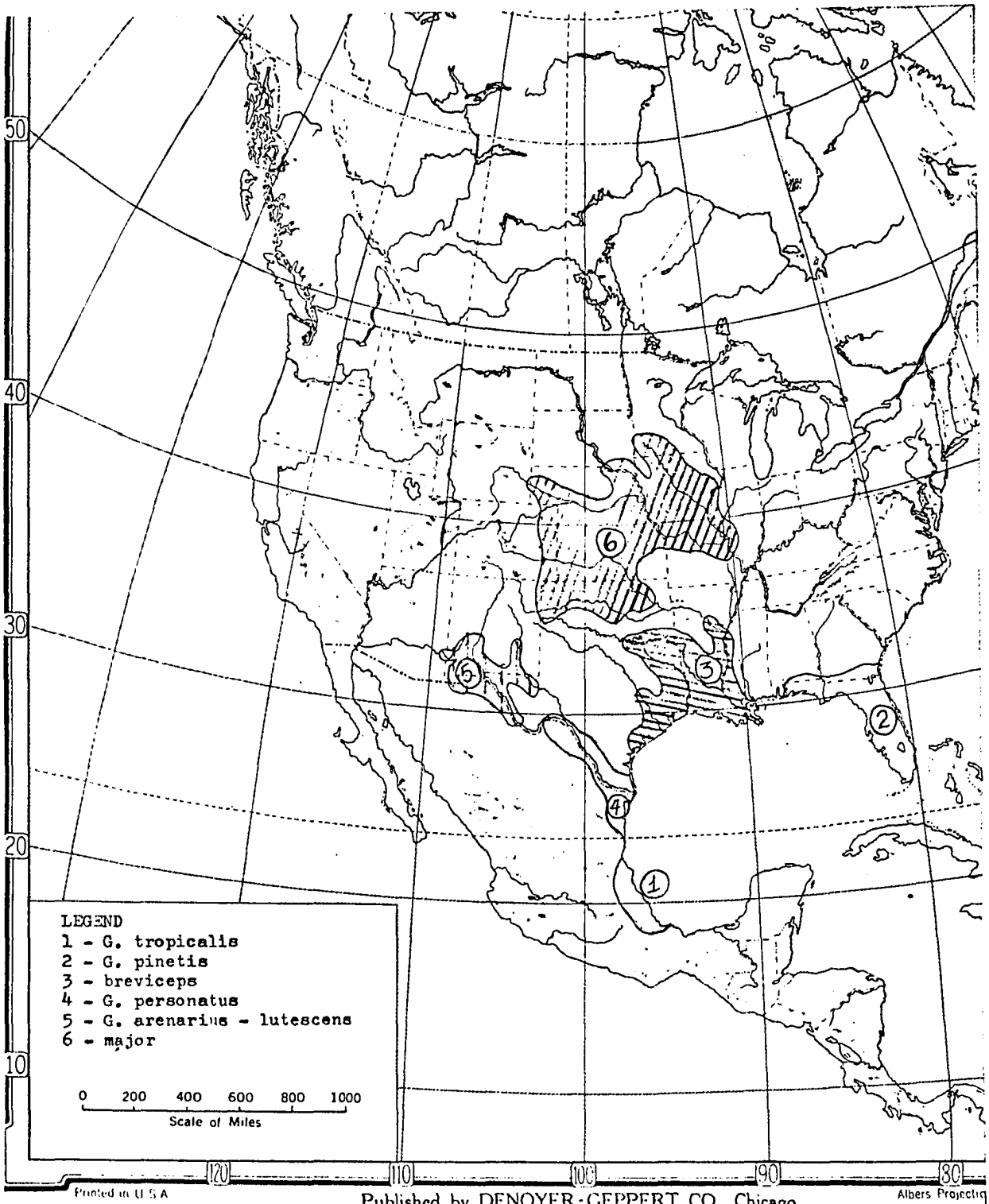



Figure 29. Conjectural distribution of Geomys during (Mankato or Valders Substages) late Wisconsin glaciation, 8,000 to 1,000 B.C.

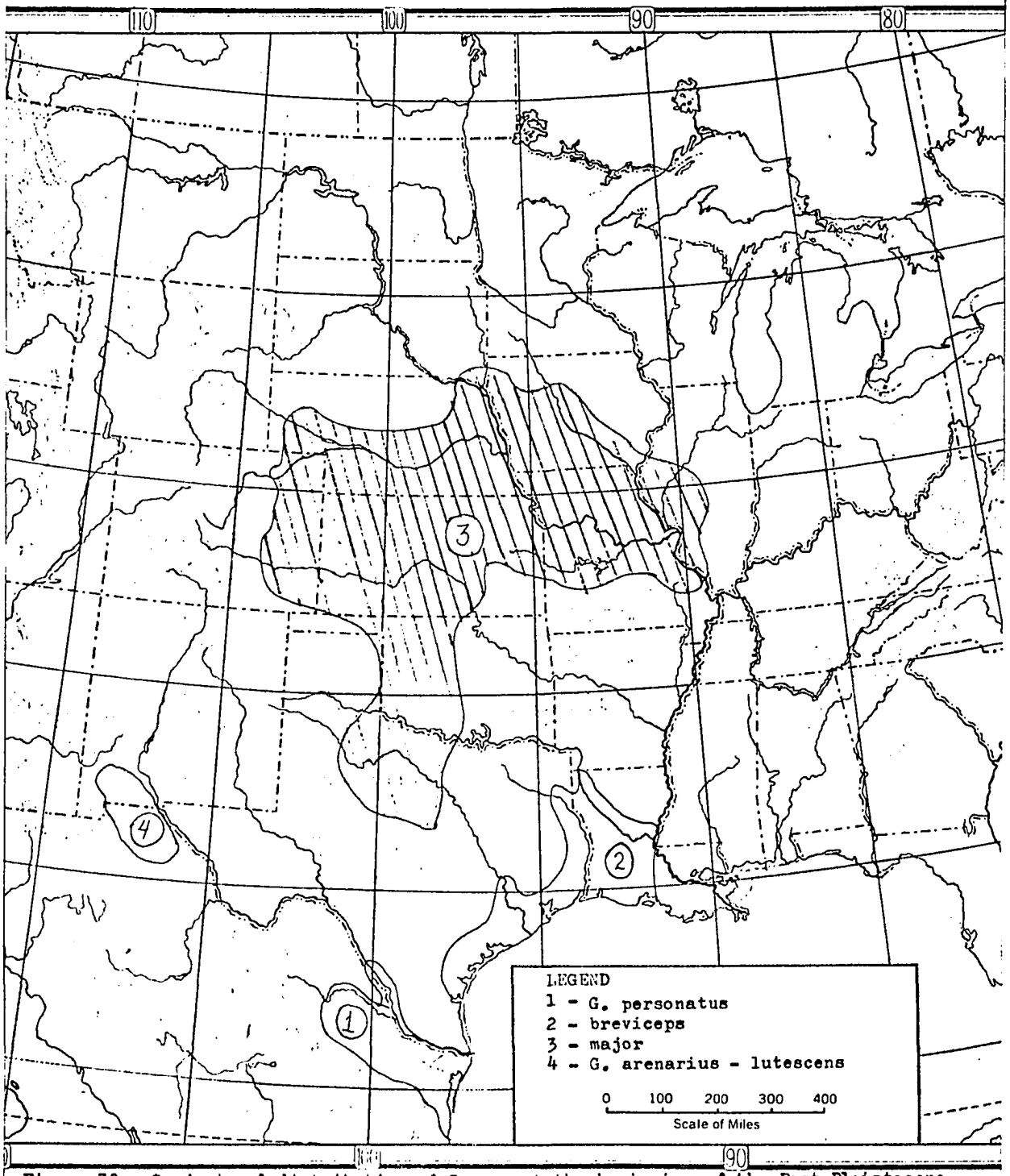



Figure 30. Conjectural distribution of Geomys at the beginning of the Post-Pleistocene (Recent) period (Pre-Boreal) about 7,000 to 8,000 years ago.

majusculus genotype radiated to the north and west. G. b. majusculus spread to the west and north. Populations of the bursarius group karyotype, after it became established as far south as Kansas, were bifurcated into two segments by encroaching lutescens populations from the xeric areas in the north to which G. b. lutescens appears superiorly adapted. G. b. majusculus either moved west and north from eastern Kansas into eastern Nebraska, western Iowa, and central Kansas, or it may have been present in part of this area since glaciation (Fig. 32). G. b. lutescens seemingly replaced some populations of bursarius and only recently came into contact with G. b. majusculus in eastern Nebraska and central Kansas. In recent years, G. b. major has made substantial inroads towards the north, spatially separating the majusculus karyotype into G. b. majusculus and closely related G. b. industrius.

According to Berry (1969), an extensive area in west Texas along the Pecos and Colorado River drainages showed a peculiar 2N = 70, FN = 68 form as being most common along the fringe of the species' southwestern range. This area may represent a transition from where a new rearrangement has dispersed to the south and possibly southeast. This lineage is separate from G. arenarius, since a uniarmed X, and no biarmed elements, are present. However, radiation of this basic type (2N = 70, FN = 68) probably gave rise to

Antonio Rivers prior to the recent arrival of ancestral stock of G. personatus from the south (Table II).

The attwateri group may have fragmented from the southern extreme of the breviceps distributional range during the Recent period. Two successive autosomal Robertsonian fusions are accountable for dervied changes.

Concomittantly, G. b. major populations (or bursarius already with two small biarm autosomes) radiated far to the north and east of the Mississippi River during Climatic Optimum (Fig. 31). Sometime following initial widespread dispersion, possibly during the Xerothermic period when populations diminished in size and became isolated, a pericentric inversion of a small autosome eventually resulted in widespread genetic rearrangement, probably via the allopatric model (possibly from refuges) over widespread occupied and unoccupied areas of northern U. S. This rearrangement was effectively separated by the Mississippi River, since contemporary remnant populations east of the Mississippi River (G. b. illinoensis) still retain chromosomes identical to G. b. major. Approximately the same time, in an area of eastern Kansas and central Missouri, an isolated population underwent a pericentric inversion of the X chromosome to form ancestral majusculus.

Following Xerothermic period (Fig. 32), when moist, humid conditions became prevalent, gophers of the Geomys bursarius

Table II. Comparative Karyotypes of the Genus Geomys.

| Geomys Species/Subspecies | 2N | FN | Autosomes No. Biarms | Autosomes No. Uniarms | Sex Chromosomes X | Sex Chromosomes Y | Author |
|---|---|---|---|---|---|---|---|
| Geomys arenarius | 70 | 88 | 20 | 48 | ? | ? | Berry, 1969. |
| G. a. arenarius | 70 | 102 | 34 | 34 | LMeta | SmTelo | Davis, 1971. |
| G. b. breviceps group | 74 | 72 | 0 | 72 | LMeta | SmTelo | Hart, 1971. |
| G. b. attwateri group | 70 | 72 | 4 | 64 | LMeta | SmTelo | Hart, 1971. |
| G. bursarius dutcheri (Ark.) | 74 | 72 | 0 | 72 | LMeta | SmTelo | Berry, 1969. |
| G. b. major, illinoensis | 72 | 70 | 0 | 70 | LTelo | SmTelo | Hart, 1971. |
| G. b. bursarius group | 72 | 72 | 2 | 68 | LTelo | SmTelo | Hart, 1971. |
| G. b. majusculus, industrius | 72 | 70 | 0 | 70 | LMeta | SmTelo | Hart, 1971. |
| G. b. lutescens | 72 | 70-100 | 0-28 | 52-70 | LMeta | SmTelo | Hart, 1971. |
| Geomys personatus fallax | 68, 70 | 70, 71 | 2-4 | 62,65, 66 | LMeta | SmTelo | Davis, 1971. |
| G. p. maritimus | 70 | 70 | 2 | 66 | LMeta | SmTelo | Davis, 1971. |
| G. p. megopotamus | 70 | 72-74, 76 | 4-6, 8 | 60, 62-64 | LMeta | SmTelo | Davis, 1971. |
| G. p. personatus | 70 | 71 | 3 | 65 | LMeta | SmTelo | Davis, 1971. |
| G. p. strecheri | 72 | 72 | 2 | 68 | LMeta | SmTelo | Davis, 1971. |
| Geomys pinetis | 42 | 72 | 36 | 4 | LMeta | SmTelo | Hart, 1971. |
| Geomys tropicalis | 38 | 70 | 34 | 2 | MMeta | SmAcro | Berry, 1969. |
| Geomys tropicalis | 38 | 72 | 36 | 0 | MMeta | SmTelo | Davis, et. al. 1971. |
| G. b. major | 70-72 | 68, 70 | 1,2 | 68-70 | LTelo | SmTelo | Berry, 1969. |

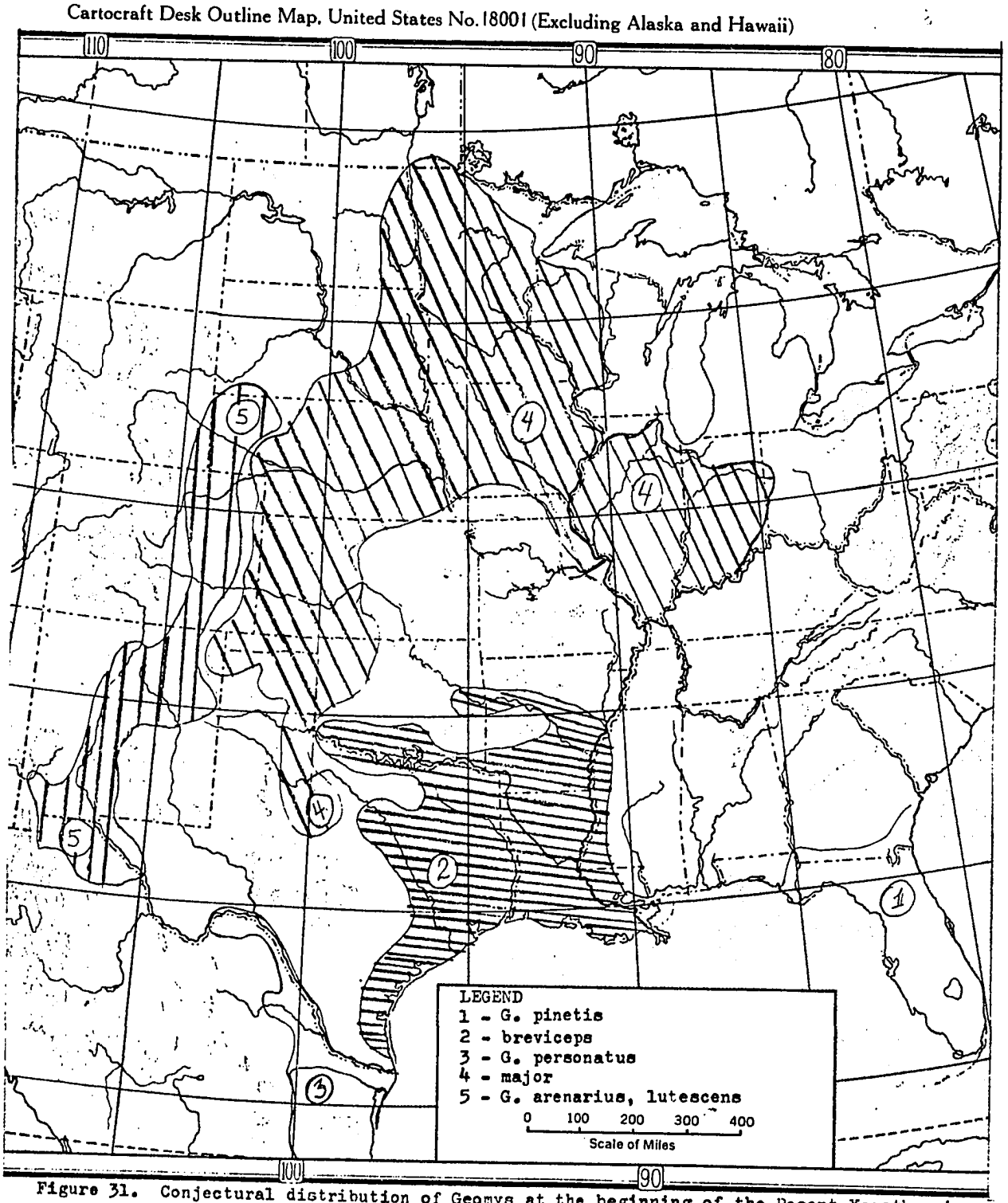



Figure 31. Conjectural distribution of Geomys at the beginning of the Recent Xerothermic period (Sub-Boreal) about 3,000 B.C.

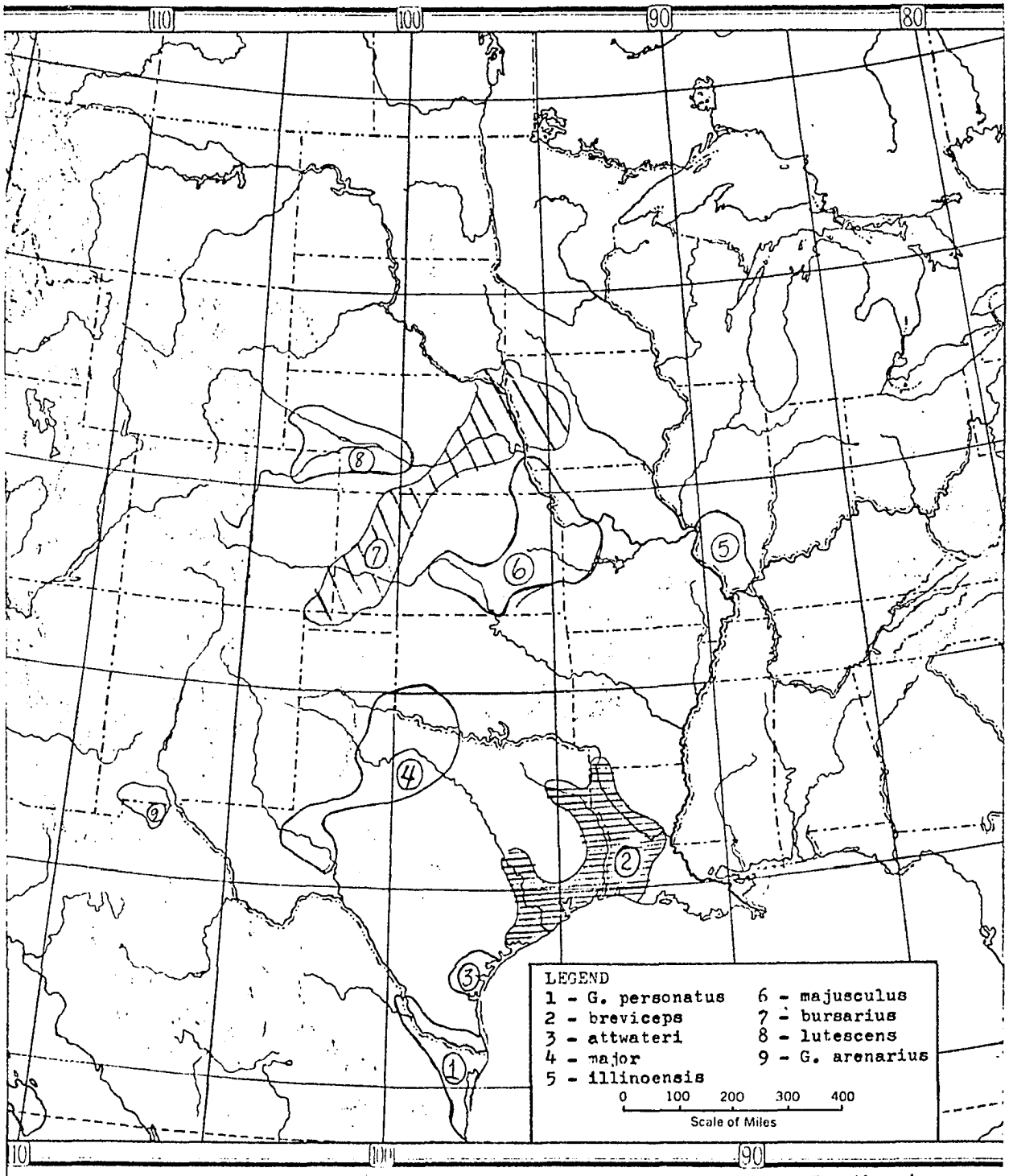



Figure 32. Conjectural distribution of Geomys at the close of the Recent Xerothermic period (Sub-Boreal) about 1,000 B.C.

the texensis. There exists an interesting 2N = 71 form in Lubbock which appears identical to texensis. Drainages of the Colorado River and the Llano River may have provided dendritic means of dispersal. This reasoning suggests texensis is more closely related to G. b. major and probably only recently occupied its present range. Berry's (1969) results may document configurations during a period of actual genetic rearrangement, i.e., a change from typical G. b. major to that of another chromosomal subspecies.

As mentioned, Geomys personatus may have arisen from ancestors which became disjunct from the breviceps group during the Wisconsin and became distributed further to the south, only recently moving north, and forming parapatric borders with attwateri. Russell (1968) suggested that G. personatus and G. arenarius both arose from G. bursarius, which may or may not coalesce with the proposed outline of dispersal.

Alvarez (1963) considered G. tropicalis as intermediate between G. personatus and G. arenarius. This assumption is interesting, since the former two are herein postulated to have been derived originally from breviceps stock, though at widely varying time periods. Davis, Williams, and Lopez (1971) suggested that G. tropicalis is more similar to G. personatus than to G. arenarius; that G. tropicalis was derived from G. personatus stock which became isolated on

the barrier beach in southern Tamaulipas. My model disagrees with the latter assertion.

The phylogeny of Alvarez (1963) supports the model presented here, that G. tropicalis and G. personatus were derived from breviceps ancestors, independently. However, chromosomally, it does not appear that G. tropicalis arose directly from G. personatus as proposed by Davis, Williams, and Lopez (19/1).

Berry (1969) hypothesized a disjunction of G. tropicalis from G. arenarius-G. personatus ancestry. He postulated that G. arenarius and G. b. major in New Mexico and western Texas may be related and that G. personatus may have moved east along the Rio Grande River drainage from populations formerly connected to G. arenarius. The present model precludes the former assumption though agrees with the latter. The G. tropicalis group is a separate offshoot of much earlier origin; there is no chromosomal evidence to support hypothesis of a close relationship between G. personatus and G. arenarius. Their geographic ranges which are in approximately adjacent locals is a function of superimposed glacial epochs; there is no chromosomal evidence to rationalize a close relationship between them. Although the diploid numbers are similar, the fundamental numbers vary too dramatically (G. personatus, FN = 70-76; G. arenarius, FN = 100-102) to hypothesize a close phylogenetic origin.

## Subspeciation

White (1969) suggested that chromosomal rearrangements are directly involved in speciation. The question arises, however, whether subspecies formation involves parallel genetic rearrangement (including chromosomes) and morphological changes, or whether this is a separate and distinct process.

Due to the propensity of pocket gophers to speciate rapidly (Patton, 1970), it becomes difficult to distinguish between these characters which are assumed to be expressions due to geography and environment and those which are truly characters significant in speciation.

Durrant (1959) stated that the species is as dynamic as a "pot of boiling water." If the surface were frozen at any instant, configuration of peaks would be totally different than if frozen at any other time, due to changing selection and chance. He said that the modern concept of mammalian species is that it is truly a multidimensional, dynamic entity.

It thus becomes a problem to recognize what really represents a species in pocket gophers. Kennerly recognized (1959) the quandry represented by geographically separate "types" of pocket gophers, though whose populations remain contiguously allopatric. He stated that perhaps, at one extreme, morphological features may be consistent throughout

a single species, masked by a large amount of geographic variation; at the other extreme, it is possible that species-specific criteria do not exist. Kennerly also stated that "morphologic distinctiveness is not a reliable indicator of the actuality of a species."

Dice and Blossom (1937) indicated that mammalian pelage color is in part dependent upon soil color, yet there is no direct evidence that natural selection is effectively producing races, since differences in climate and vegetation are wholly inadequate to explain coloration differences of local races, which have no definite physical or climatic barrier to free interbreeding in the southern Arizona desert. They concluded that most races are probably not to be regarded as incipient species. Durrant (1952) stated that for the most part, subspecific variation is non-adaptive.

In the distribution of Geomys bursarius near the extremes of their established ranges, conspicuous barriers are also mostly absent. Obvious physiographic and ecological barriers to distribution, which have so conspicuously affected reproductive isolation in the fauna and flora of other places, for example, in the Rocky Mountains, mostly are lacking here. However, considering the multiplicity of environmental changes within the Great Plains, I feel that there is little question but what the plains pocket gopher has undergone both non-adaptive and adaptive differentiation.

became fragmented or separated from larger populations and remained separated for a time during Pleistocene glaciation and post-Pleistocene. In some cases, these derived populations gave rise to sister populations, but which otherwise have remained unchanged to the present time. Dillon (1970) stated that speciation proceeds most rapidly under tropical conditions; that speciation is probably proceeding relatively slowly today.

I surmise that subspeciation in the pocket gopher has taken place to some degree during late Pleistocene, Recent events, although they may well be much older--Middle Pleistocene. Ecological and geographic factors have elicited change in pocket gophers, at times paralleling evolutionary change (of which chromosomal rearrangment appears to be a by-product); the latter processes have resulted in geographic forms which may or may not have little relation to speciation. Dice and Blossom (1937) concluded that subspecies formation usually is a function of environment.

Speciation (and chromosomal rearrangements) has occurred, as exemplified by the specific mechanism of multiple pericentric inversions to form the distinctive G. arenarius and G. b. lutescens. It is thought that other chromosomal rearrangements within the subspecies of G. bursarius are more or less directly linked with ultimate speciating processes.

Weaver and Fitzpatrick (1932) observed that perhaps the intermediate character of the Great Plains makes this an area of transition, where environmental conditions are not apparently intensive enough or extensive enough to mould forms into peculiar fauna.

Kennerly (1959) noted that no abrupt ecological changes coincided with areas of contiguous borders of Geomys bursarius and Geomys personatus. However, he found ecological factors responsible for separation of all but two subspecies of Geomys personatus in southern Texas.

There is some correlation between Geomys bursarius distribution and such edaphic factors as sandy soils and rocky escarpments; Geomys bursarius subspecies apparently have few, if any, ecological or physiographical factors which separate subspecies boundaries. Intraspecific competition is thought to be the factor primarily responsible for separation of subspecies. Kennerly (1959) attributed interspecific competition as responsible for present separation between Geomys bursarius and Geomys personatus. Probably a combination of Grinnell's (1943) intangible barriers to distribution are operative.

Whatever causes are producing subspecies remains somewhat of an enigma; the logical explanation is that similar interbreeding populations originally inhabited the central Great Plains. Individuals and/or small populations

Rate of subspeciation is open to some conjecture. Durrant (1952) cited seven distinct subspecies as an example of rate of subspeciation. These are thought to have occupied an island in the Great Salt Lake for only about 2,000 years. In other instances, perhaps the "patchwork" distribution of pocket gophers is much more conducive for imposition of complete or partial barriers for varying lengths of time under varying conditions.

Patton (1970) found two types of variation in Thomomys, mountain pocket gophers. The "heavy rostrum" group (T. bottae, T. umbrinus, T. townsendi) are characterized by high diploid numbers (2N = 74-78), but extensive variation in chromosome morphology (non-Robertsonian rearrangements). The "slender rostrum" group (T. talpoides) is characterized by relatively low diploid numbers, (2N = 40-60), as well as change in morphology (Robertsonian variation).

In northern Geomys, karyotypic evolution most closely resembles Patton's "heavy rostrum" group which is distributed in the southwest, with little variation in diploid numbers, but some variation in chromosomal morphology. The marked possession by southern animals (G. tropicalis and G. pinetis) of low diploid numbers coalesces more with karyotypic variation in populations of Thomomys talpoides, which is mostly northern in distribution. These data correlate northern Geomys (G. b. lutescens) and southern Thomomys with propensities

for non-Robertsonian changes--pericentric inversions. Southernmost genera of Geomys (G. tropicalis and G. pinetis) appear to have undergone Robertsonian fusions to a marked degree, as did northern T. bottae.

Since there is no latitudinal correlation between types of chromosomal evolution in Thomomys and Geomys, perhaps a correlation between extremity of environments present both in the Nebraska area (G. b. lutescens) and Arizona, Mexico (T. umbrinus, T. bottae, T. townsendi). Here, similarity of relative precipitation (aridity) has resulted in a plastic pericentric inversion system.

G. pinetis and G. tropicalis chromosomal rearrangements resemble those of T. talpoides, which is often completely isolated by Rocky Mountain geography. In addition, correlation with isolated southern Geomys forms may be made since both primarily utilized Robertsonian fusion.

It appears that in Geomys at least, Robertsonian mechanisms occur in instances where it is important to conserve vital gene sequences. Robertsonian fusions appear to "lock up" genes which determine vital functions, so that these co-adapted gene sequences cannot be lost by subsequent genetic rearrangement.

Non-Robertsonian rearrangement mechanisms seemingly function in the opposite manner and appear to insure that genetic variability is maintained. The widest degree of

variation has been noted in animals from the least stable environments (Durrant, 1952, 1959). Established sequences of genes are readily rearranged via pericentric inversions, as though the animal were consciously experimenting with all possible rearrangements to enable it to remain at a maximum of flexibility to cope with changing exigency in a capricious environment.

As stated, Durrant felt that subspecific variation is for the most part non-adaptive. The effects of non-Robertsonian chromosomal rearrangement, i.e., pericentric inversions, appear in Geomys bursarius lutescens to produce a less distinct, adaptive variation. Moreover, within the entire species where pericentric inversions have been postulated to be operative, generally only fairly closely related subspecies exist. However, in instances of Geomys tropicalis and G. pinetis, Robertsonian fusions produced conditions where adaptive variations were paramount to have elicited evolvement of separate species.

The plains pocket gopher has shown a remarkable capacity for chromosomal change and subsequent fixation, as have other completely fossorials in various parts of the world (Wahrman, 1969; Reig and Kiblisky, 1968; Patton, 1970; Thaeler, 1968). As Patton (1970) has reiterated, it is not presently understood exactly what in the basic biology of fossorials augments speciating capacity to such extremes.

# CONCLUSIONS

Chromosomes of the plains pocket gopher were found to be indicative of evolutionary status at the subspecies level. Remarkable stability of 2N and FN was noted throughout the ranges of chromosomally distinct races. Occasional polymorphic forms were encountered, though in most cases these were found near distributional border, and may have been due to introgressing, different chromosomal arrangements from adjacent populations. However, it is hoped that future studies will be oriented towards assessment of variation at the population level. Many gaps remain to be investigated thoroughly.

Subspecies formation within the plains pocket gopher has resulted in morphological forms which, for the most part, have paralleled actual actual evolutionary processes to which chromosomal rearrangement is directly related. The value of chromosomal phylogenetic implications appear obvious that it is in some way directly linked to reorganization of the genome; however, it should be noted that significant evolutionary events may occur which are not easily detectable (as by paracentric inversions or by gene rearrangement) by gross chromosomal number and morphology.

Phylogenetic interpretations favor the view that two basic stocks were derived from ancestral Geomys.

It appears logical that ancestral forms inhabiting the central Great Plains (including the Gulf Coastal Plains) gave rise to G. tropicalis and G. pinetis during Early Pleistocene. Figure 33 indicates evolutionary divergence of Genus members by comparison of both diploid number (2N) and fundamental number (FN).

Breviceps stock eventually gave rise to G. personatus (which gave rise to G. b. lutescens and G. arenarius).

The discrepant diploid number of 70 (FN = 72, 4 biarmed members) of the two attwateri subspecies, indicates there is little chance of successful intergradation with parental breviceps (2N = 74, FN = 72, all acrocentrics). Likewise, I suggest further study be centered in the contact zone with breviceps members; it is probable that this study will warrant recognition of a separate species of G. b. attwateri and G. b. ammophilus. G. b. texensis and G. b. llanensis were derived from G. b. major of west Texas.

At the moment, it appears that breviceps and major intergrade to a very limited degree. Sixteen animals were trapped and slides are currently being examined to illucidate the nature of the zone of secondary intergradation. Intergradation appears to take place between G. b. lutescens and G. b. majusculus in Nebraska.

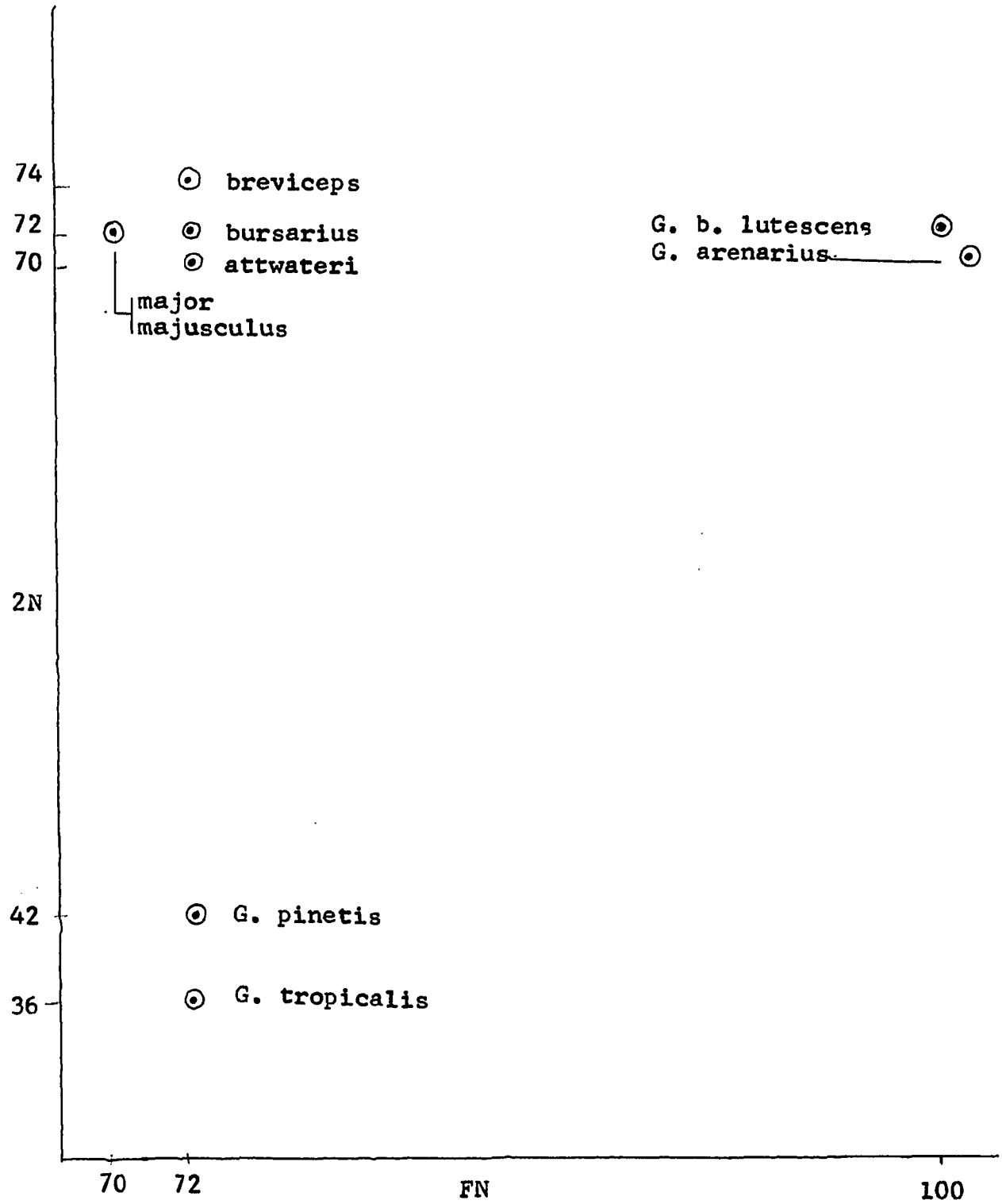



Figure 33. The diploid numbers (2N) plotted against the fundamental numbers (FN) of some species, subspecies of Genus, Geomys.

It is hoped that future studies will sample large numbers from numerous localities. Many gaps remain to be filled; knowledge is by no means complete within this group. Undoubtedly, careful study will yield additional chromosomal forms which will enhance understanding of speciation of fossorial mammals.

## SUMMARY

Representatives of all 19 contemporary subspecies of the plains pocket gopher, Geomys bursarius, were sampled. It was found that 2N and morphology of chromosomes are diagnostic at the subspecies level, and that these chromosomal races agree remarkably with taxonomy based on morphology.

Geomys bursarius subspecies fall into seven overall entities, four in the north (2N = 72) and three in the south (2N = 74). It is surmised that ancestral forms possessed a 2N of 74, FN of 72, acrocentric X. During the Wisconsin, two basic stock were formed: the major group (2N - 72, FN = 70, acrocentric X) via a tandem fusion, and the breviceps group (2N = 74, FN = 72, biarmed X) via a pericentric inversion of the X chromosome.

The northern group consists of G. b. major and G. b. illinoensis which have completely acrocentric complements. G. b. bursarius, G. b. wisconsinensis, and G. b. jugossicularis all have a 2N = 72, FN = 72, two small biarmed elements and arose from G. b. major by an autosomal pericentric inversion. G. b. lutescens (2N = 72, FN = 70-100) is closely related to G. arenarius and probably arose from G. personatus

during Wisconsin via a number of pericentric inversions. G. b. majusculus and G. b. industrius (2N = 72, FN = 70) are completely acrocentric, except for possession of a biarmed X chromosome. This group probably arose from G. b. major stock via a pericentric inversion of the X chromosome. G. b. texensis and G. b. llanensis (2N = 71, FN = 69) are thought to have descended from G. b. major from west Texas.

The southern entities include the breviceps group, consisting of G. b. breviceps, G. b. dutcheri, G. b. pratincola, G. b. ludemani, G. b. brazensis, G. b. terricolus, saggitalis. All have identical chromosomal complements (2N = 74, FN = 72), including presence of a biarmed X chromosome. This group represents most closely the ancestral karyotype of the Genus, Geomys. It gave rise to G. b. personatus during the Wisconsin which subsequently was ancestral to G. b. lutescens (2N = 72, FN = 70-100) and G. arenarius. During the Recent period, it is postulated that two centric fusions of this parental stock gave rise to the G. b. attwateri, G. b. ammophilus (2N = 70, FN = 72, biarmed X).

A phylogeny is proposed to account for the existence of Geomys tropicalis and G. pinetis, as well as a Wisconsin offshoot, Geomys personatus.

Fossil history, events of the Pleistocene and Recent periods thought to influence present distribution, and a summary of limiting factors are included.

This study indicates cryptic chromosomal subspecies. Also, it indicates G. b. attwateri and G. b. ammophilus should probably be recognized as a distinct species, depending upon future demonstration of a lack of interbreeding with G. b. brazensis.

## SPECIMENS EXAMINED

Most voucher specimens are deposited in the Collection of Recent Mammals, Stoval Museum of Science and History at the University of Oklahoma, Norman. Numbers with no prefix are Museum catalog numbers; specimens with a prefix of EBH (E. B. Hart) and TLB (T. L. Best) are also available in the Museum. Asterisks (*) refer to specimens with fewer than 8 (4-7) chromosomal spreads counted.

Geomys bursarius ammophilus: (Total 2.) 1♀ (TLB3799*), 1♂ (EBH571*), 1 mi. SE Cuero, DeWitt Co., Texas.

Geomys bursarius attwateri: (Total 3.) 1♀ (TLB3809), 2♂ (TLB3806, TLB3807), 8 mi. NE Kenedy, Karnes Co., Texas.

Geomys bursarius brazensis: (Total 3.) 1♀ (EBH567), 0.5 mi. W College Station, Brazos Co., Texas; 1♂ (EBH569), 2.5 mi. W College Station, Brazos Co., Texas; 1♀ (EBH570), 4 mi. W College Station, Brazos Co., Texas.

Geomys bursarius breviceps: (Total 5.) 1♂ (7698), 2 mi. W

Mer Rouge, Morehouse Parish, Louisiana; 4♀ (7707, 7708, 7710, 7711), 2 mi. NW Mer Rouge, Morehouse Parish, Louisiana.

Geomys bursarius bursarius: (Total 13.) 1♀ (7543), 4 mi. NE Bankston, Dubuque Co., Iowa; 1♀ (7535), 1♂ (7536), 4 mi. NE Garbin, Dubuque Co., Iowa; 1♀ (7538), 4 mi. E Monona, Clayton Co., Iowa; 6♀ (10085*, 10086, 10087, 10088, 10089, 10091), 1♂ (10082), Monona, Clayton Co., Iowa; 1♀ (7533), 4.5 mi. E Scotland, Bon Homme Co., South Dakota; 1♀ (7727), 2.5 mi. E Sullivan, Franklin Co., Missouri.

Geomys bursarius dutcheri: (Total 18.) 4♂ (7696, TLB3748, EBH562, EBH563), 2♀ (7694, TLB3749), 3 mi. E P.O. Wrightsville, Pulaski Co., Arkansas; 1♀ (TLB3765), 1.6 mi. N Pollock, Grant Parish, Louisiana; 1♀ (EBH206), near Bowlegs, Seminole Co., Oklahoma; 1♀ (EBH635), 1 mi. W Tecumseh, Pottawatomie Co., Oklahoma; 4♀ (EBH658, EBH661, EBH666, EBH669), 5♂ (EBH657, EBH662, EBH663, EBH664, EBH665) near Norman, Cleveland Co., Oklahoma.

Geomys bursarius illinoensis: (Total 7.) 1♂ (7552), 1 mi. S Clinton, DeWitt Co., Illinois; 4♀ (7719*, 10065, 10066, 10067), 1♂ (7724), 4.5 mi. S P.O. (O'Fallon Rd.), Collinsville, Madison Co., Illinois; 1♂ (7718), East St. Louis, Missouri.

Geomys bursarius industrius: (Total 5.) 1♂ (7477), 1♀ (7479), 4 mi. S P.O. Dodge City, Ford Co., Kansas; 1♀ (7474), 5 mi. W Kinsley, Edwards Co., Kansas; 2♂ (7475*, 10116), Kinsley, Edwards Co., Kansas.

Geomys bursarius jugossicularis: (Total 9.) 1♂ (EBH544), 2.4 mi. W, 3.2 mi. N Amistad, Union Co., New Mexico; 1♂ (EBH541), 13.5 mi. S Clayton, Union Co., New Mexico; 1♀ (EBH545), 10.1 mi. S Clayton, Union Co., New Mexico; 1♀ (EBH540), Felt, Cimarron Co., Oklahoma; 3♀ (7480, 7485, 7486), 10.5 mi. S Liberal, Seward Co., Oklahoma; 1♀ (EBH542), 3 mi. W, 1.6 mi. N Sedan, Union Co., New Mexico; 1♀ (EBH543), 9 mi. S, 1 mi. W Tolar, Roosevelt Co., New Mexico.

Geomys bursarius llanensis: (Total 2.) 1♂ (EBH575), 6 mi. E Castell, Llano Co., Texas; 1♀ (TLB3815*), 5.8 mi. E Castell, Llano Co., Texas.

Geomys bursarius ludemani: (Total 5.) 1♂ (TLB3786), 4♀ (TLB3771, TLB3772, TLB3775, TLB3785), 7 mi. S Anahuac, Chamber Co., Texas.

Geomys bursarius lutescens: (Total 27.) 1♂ (7507), 20 mi. S Chadron, Ford Co., Nebraska; 2♀ (7495, 7498*), 11 mi. S Chadron, Ford Co., Nebraska; 1♀ (7504), 2 mi. SW P.O.

Chadron, Ford Co., Nebraska; 1♀ (7473), 20 mi. S Wakeeney, Ford Co., Kansas; 1♀ (7528), Spencer, Boyd Co., Nebraska; 1♂ (7531), 4.5 mi. SE Spencer, Boyd Co., Nebraska; (intergrades) 4♂ (7509, 7512, 7513, 10103), 2♀ (7516, EBH396) near Oakdale, Antelope Co., Nebraska; 3♂ (7517, 10107, EBH398), 11♀ (7518, 10100, 10101, 10102*, 10105, 10106, 10108, 10110, 10111*, 10112, EBH399) near Neligh, Antelope Co., Nebraska.

Geomys bursarius major: (Total 39.) 1♀ (9095), 1♂ (9096), 0.25 mi. E Claude, Stephens Co., Oklahoma; 2♀ (9097, 9320), 0.25 mi E, 0.75 mi. S Claude, Stephens Co., Oklahoma; 2♀ (9108, 9116), 1♂ (9115), 1.4 mi. W, 1 mi. N Hawley, Grant Co., Oklahoma; 1♂ (EBH512), Ponca City, Kay Co., Oklahoma; 2♀ (9001, EBH513), 3 mi. N P.O. Lexington, Cleveland Co., Oklahoma; 19♀ (9002, 9003, 9004, 9007, 9009, 9093, 10060, 10062, EBH202, EBH503, EBH516, EBH554*, EBH644, EBH645, EBH646, EBH647, EBH648, EBH659, EBH660), 10♂ (9005, 9006, 9008, 9331, EBH515, EBH536, EBH552, EBH649, EBH652, EBH670), Norman, Cleveland Co., Oklahoma.

Geomys bursarius majusculus: (Total 3.) 1♀ (EBH547), 1.3 mi. N, 13 mi. W Emporia, Chase Co., Kansas; 2♂ (10114, 10115), 1 mi. W Tilden, Antelope Co., Nebraska.

Geomys bursarius pratincola: (Total 8.) 6♀ (EBH566, TLB3763,

TLB3764, TLB3765, TLB3768, TLB3769), 2♂ (TLB3762, TLB3767), 2.3 mi. N, 8.8 mi. W Glenmora, Rapides Parish, Louisiana.

Geomys bursarius sagittalis: (Total 3.) 1♂ (TLB3794), 2♀ (TLB3795, TLB3796), Alta Loma, Galveston Co., Texas.

Geomys bursarius terricolus: (Total 3.) 2♂ (TLB3791, TLB3793*), 1♀ (TLB3792), 1 mi. N Texas City, Galveston Co., Texas.

Geomys bursarius texensis: (Total 3.) 2♀ (TLB3811*, TLB3813*), 1♂ (TLB3814*), Mason, Mason Co., Texas.

Geomys bursarius wisconsinensis: (Total 11.) 5♀ (7540, 7544, 7547, 7548, 7549), 2♂ (7541, 7542), 0.5 mi. E Gotham, Richland Co., Wisconsin; 2♀ (10072, EBH601), 2♂ (10073, EBH605), Gotham, Richland Co., Wisconsin.

Geomys pinetis: (Total 2*.) 1♀ (EBH654), 1♂ (EBH655*), near Tampa, Hillsborough Co., Florida.

## APPENDIX I

### Detailed Ecological Distribution of Geomys bursarius Subspecies

Geomys bursarius bursarius, G. b. wisconsinensis, G. b. illinoensis, and G. b. majusculus occur largely in Clements and Shelford's (1939) true prairie. Originally, tall perennial grasses occupied this area, but due to settlement, it is now regarded as a disclimax with ponds and marshes as the most important seral stage. It receives an average precipitation of 29 in. Valley woodland is the most important postclimax within the area. Dice's (1943) Illinoian biotic province extends over much the same area. Soils are chiefly of glacial origin or loess material, high in organic material, and fertile. Sandy soils with low soil moisture holding capacity are fairly extensive, however. G. b. illinoensis inhabits a silt loam where the loess blankets the glacial till.

Fenneman (1938) has recalled that the northern parts of the Central Lowland, including Minnesota, the Dakotas, northern Iowa, were glaciated, resulting in strong terminal morraines leaving morainic lakes, swamps and boulder fields. Gravelly, sandy, or swampy plains of glacial outwash are

extensive and common. Drainages are young. However, the ground moraine or till plains occupies much of the area. In Iowa, drift sheets from all of the major Pleistocene glaciations are present. The Dissected Till Plains of southern Iowa, Missouri, eastern Kansas, and eastern Nebraska compose a nearly flat till plain, sub-mature to mature in its erosion cycle and covered by loess.

G. b. lutescens, G. b. jugossicularis, and G. b. industrius reside within Clements and Shelford's (1939) mixed-grass prairie, named for its mixture of middle-short bunch grasses and diverse assemblage of dominants from very widely separated origins. Carpenter (1940) separated the mixed- and short-grass prairies; he suggested that the mixed-grass prairie is a narrow ecotone between the more expansive short-grass prairies in the west and the tall-grass eastern true prairie. Carpenter (op. cit.) called the short-grass plains the most xerophytic climax of the grassland biome. Weaver and Clements (1938) regarded the short-grass prairie as a modified form of mixed-grass prairie and a distinct disclimax due to overgrazing. Clements and Shelford (1939) suggested that postclimaxes within this plant association are floodplain, woodland and tall grass, and short-grass plains. The climate is semiarid to arid; rainfall varies from 27 in in the south to 10 in in the north. Sandy soils of this general area are extensively spread, often in bottomlands; clay content is low.

One of the most desolate areas of the Great Plains is Nebraska's Sand Hills. These are dry-subhumid, steeply sloping areas of windblown sands in rounded or choppy hills, with irregular ridges, intervening draws and broad land bottoms. Rainfall is deficient. It is notable that the chromosomally polymorphic subspecies, G. b. lutescens, inhabits this xeric portion of Nebraska where environment fluctuates to summer and winter extremes.

Topographically, G. b. lutescens distribution consists primarily of the High Plains of western Kansas and eastern Colorado. The High Plains are bordered on the north by the Sand Hills and Pine Ridge Escarpment of Nebraska. The eastern border is described by Fenneman (1931) as an erroded, encroaching segment of the High Plains. The High Plains extend south as far as the Llano Estacado, almost reaching the Rio Grande of Texas.

G. b. ludemani, G. b. terricolus, and G. b. sagittalis all occupy restricted habitats on elevated prairied fragments all near the sea, located in Clement and Shelford's Coastal Plains province and Blair's Austroriparian biotic province. This limited area is circumferential to much of the Gulf of Mexico, beginning at the western edge of pine subclimax in eastern Texas, continuing around Galveston Bay. Seral stages include gulf bayou, mud flats, and sandy areas lying within approximately 10 mi of the sea. Mosaics of elevated prairie fragments often contain populations of pocket gophers. The

coastal plains have a higher precipitation than any other grassland plant formation. Winters are warm, and the area is richer in perennial forbs than even the True Prairie.

The pocket gopher has Austroriparian affinities, but ranges westward into Texas on the deep sands of Kansan and Tamaulipan biotic provinces. Pocket gophers appear to be closely restricted to sandy soils; their distribution follows the pattern of soil distribution (Davis, 1940). They fail to extend westward on the thin clay soils of Edwards Plateau.

G. b. dutcheri occupies portions of Clements and Shelford's (1939) True Prairie in central and eastern Oklahoma and northern Texas. As its range extends into Arkansas, the vegetation forms change to a savanna-woodland, with dense vegetation growth. Blair's (1938) Osage Savanna biotic district continues into the Ozarks of Arkansas. G. b. dutcheri occupies the Arkansas Valley Region located between the Boston and Ouachita Mountains to the Mississippi Lowlands embayment in central Arkansas. The Arkansas Valley is a rolling lowland, homologous with the Cherokee and low strips in the Osage section. Pocket gophers were abundant and were taken (in the present study) from an alluvial terrace of the Arkansas River.

G. b. breviceps and G. b. pratincola both exist near deciduous forest and mixtures of pine subclimax in northern and central Louisiana and eastern Texas. G. b. breviceps

is apparently isolated on the sandy soil of the old Mississippi fell, former Mississippi flood plain. Savannas are present containing scattered groves where the forest biome gives way to the prairie. The well-formed shrub and herb stratum have a rich variety of flowering plants (Kendeigh, 1961). This area is included in Blair's (1950) Austroriparian biotic province. Simonson (1957) defined this area as having forest and savanna-covered soils of humid wet-dry tropical and sub-tropical climates, with Latsolic soils. Soils are fine, sandy loam and light brown silt loam; they are fine textured, slightly permeable with dark-gray loam to clay surface soils. Also present is a heavy dense clay, dark gray to black, very sticky when wet (U. S. Agric. Yearbook, 1957). Specific collecting sites within this area were cultivated lands in savanna and flood plains area.

The remaining group of plains pocket gophers, G. b. ammophilus, G. b. attwateri, G. b. llanensis, G. b. texensis, and G. b. major, occupy portions of Clements and Shelford's (1939) Desert Plain in the relatively limited areas of central and southeastern Texas. This portion of the Desert Plains resembles a savanna, due to the general presence of shrubs. The western and southern portions possess large numbers of dwarf and half shrubs. A disclimax is formed by annual grasses replacing perennials, especially in the drier areas. This region may appear to be of desert climate with

low humidity and corresponding high evaporation. However, an annual rainfall is typical of this xeric grassland; 18 in of rainfall is average but is reduced to about 6 in at the desert margin in the west. The Desert Plains possess a greater array of dominants than any other unit of the grassland and includes the true short grass or steppe community. The Desert Plains form a wide ecotone with the coastal prairie in west-central Texas and meets the mixed prairie near the southern areas of the Texas Panhandle.

G. b. attwateri and G. b. ammophilus occupy Blair's (1950) Tamaulipan biotic province, which is composed chiefly of thorny brush on sandy soils. There is supposedly a corridor of interchange with fauna of Austroriparian via Coastal Prairie Province, since the proximity of coast favors more gradual change in ecology from east to west than further inland. It is reasonable to expect original migrations of progenitors west from the Gulf Coast Plains via this corridor. It has a logical break from the Texan province as eastern pedalfers give way to western pedocals and due to the presence of the Balcone fault. The climate is semiarid and megothermal (Thornthwaite, 1948).

G. b. texensis and G. b. llanensis occupy the Balconian biotic province on the Llano Uplift (Blair, 1950); this physiographically discrete unit is characterized principally by intermixture of faunal elements of other major provinces

with the oak-hickory-mesquite flora. Most of the province lies on Comanchean Cretaceous Limestone, but igneous intrusives and sediment as old as pre-Cambrian are exposed. Comanchean sediment of Balconian province has been much dissected, particularly in the south and east, where several rivers (including the Llano River) drain the area. Topography of the east and south parts are due to rugged dissection of limestone by these rivers and tributaries. Drainage is poor, broad uplands exist between canyons of the streams. Sandy soils predominate and contrast with the clays and clay loams of Edwards Plateau. The eastern half is classified by Thornthwaite as dry subhumid, mesothermal with average annual potential evaporation. The stream valleys have probably been important avenues of dispersal of most of these Austroriparian species across the prairies of the Texas province to the Balconian province.

G. b. brazensis occupies an area that corresponds roughly to the Texan biotic province of Blair (1950). The Texan is mainly a broad ecotone between the deciduous forest to the east and the grasslands to the west. Climate is subhumid (Thornthwaite, 1958). Sandy soils support an oak-hickory forest in which originally clay soils supported a tall grass prairie. The drainage of the Texan Biotic Province has important biographic implications and is considered a transitional area by Blair (1955).

G. b. major occupies Dice's (1943) Kansan Biotic Province in Texas. This mixed grass distribution (described by Blair and Hubbell, 1939) also includes much of the range of three biotic districts, which occupies a broad strip in western Oklahoma and the Texas Panhandle; this is the short grass country known as Llano Estacado. Carter (1931) classifies this area as High Plains, characterized by mainly clay derived soils in the north and sandy loam soils in the south.

## APPENDIX II

### Factors Influencing Distribution

Factors reported to restrict distribution of Geomyids and other strictly fossorials from immigrating may include the quality of soils; its composition, texture, depth, cultivation; physiography including topography, edaphic factors, lava flows, climate, temperature, precipitation, streams, desert and/or permanent bodies of water, and competition (Blair, 1954; Davis, 1940; Davis, Ramsey, and Arendale, 1938; Downhower and Hall, 1966; Durrant, 1952; Grinnell, 1926; Howard and Childs, 1959; Ingles and Biglione, 1952; Miller, 1964; Thaeler, 1968; Vaughan, 1967; Wahrman, 1969). All of these probably have merit, especially as they interact with one another in natural local situations.

Soils are apparently of at least passive importance in pocket gopher distribution. They are the product of both climate and vegetation (Odum, 1959). Davis (1940) stated that the G. breviceps group (southern subspecies groups) occurred exclusively in sandy soils; that "rarely, if ever, is it found in alluvial silts, clays, or stoney soils." He cited examples of populations that are isolated on islands

of sandy soils in "seas" of clay or silt deposits, especially in the Coastal Plains of Texas and Louisiana.

Davis, Ramsey and Arendale (1938) reported that pocket gophers occurred in Lufkin and Ochlockonee series soils, both of which have relatively deep, sandy surfaces. They found that gophers were absent from the Wilson clay and usually from Ochlockonee silt loam.

Others have agreed that soil composition is important; that Geomys prefers friable, sand-derived soils and rarely, if ever, is found in areas of indurate soils (Miller, 1964; Kennerly, 1959).

Physiography (including edaphic factors, topography, etc.) undoubtedly has been instrumental in the distribution of Geomyids during historical times. Durrant (1952) has shown that especially in mountain pocket gophers (Thomomys talpoides, T. bottae) topography was instrumental in subspeciation of Great Basin forms.

Glass (1951) indicated that subspecies of Geomys bursarius largely occupy broadly distinct physiographic regions in Oklahoma: G. b. major inhabits the red soils of the Permian region of western Oklahoma, and G. b. dutcheri inhabits the parts of eastern Oklahoma where soils are formed from decomposed sandstone and the Coastal Plain. Glass felt that types of vegetational climaxes affect occurrence but apparently not speciation in Oklahoma.

Durrant (1952) and Kennerly (1959) agreed that a lack of moisture, aridity, is probably not critical, since considerable evidence has accumulated that pocket gopher ranges expanded during post-Pleistocene climates which are thought to have been considerably more arid than at present.

McNab (1966) suggested that high temperatures are probably more limiting than lower temperatures. Pocket gophers may either adjust smaller body size and/or increase length of tail to increased temperatures. He showed that in Florida, the distribution of G. pinetis is correlated to the presence of soils with low water holding capacity (sandy soils). He suggested that correlation of pocket gopher body size exists compared to soil depth--a reflection of an inverse correlation of body size and mean burrow temperature.

Davis stated (1940) that rivers may be important in range expansion of Geomys, that where river bottoms are wide and the soils heavy clay silts, gophers are prevented from crossing. Conversely, where the bottom is narrow or where it is wide and the soils sandy, pocket gophers can, and apparently do, cross. Davis (1940) mentioned that a number of rivers cut transversely the pocket gopher ranges in the Coastal Plains, but in most cases, flow is intermittant. In the case of larger streams, as the Red River, channels change often, permitting an interrupted exchange between populations.

Grinnell (1926) cited the importance of the Colorado River in separating two very different forms of Thomomys. Durrant (1952) cited the upper Colorado River as exerting differential barrier effects--whether the river paralleled the ranges of animals with north-south distribution and caused little impedance, or whether it cut at right angles across animals with the same north-south distribution and exerted barrier effects. In respect to mobility of the pocket gopher across water, Jackson (1961) described the pocket gopher as unable to swim, while Kennerly (1963) demonstrated that two animals were able to sustain themselves in deep water for 2 minutes and 40 seconds each. New data (Best and Hart, manuscript in preparation) have amplified these experiments and found that Geomys bursarius and G. pinetis have considerable swimming ability, especially the young.

Competition is probably the most important factor restricting current range expansion of subspecies of G. bursarius. As stated, the plains pocket gopher is an exceedingly pugnacious, solitary animal (except in breeding season). Fragmentation and resulting isolation of progenitors presumably climaxed in some genetic separation; differentiated populations arose during and following extreme fluctuation of climate during and following Wisconsin glaciation. Resultant expansion of ranges via suitable substrate (soils, physiography) was eventually curtailed by

mutual exclusion as borders of ranges coincided. The forthcoming competition (mutual exclusion) was probably no more drastic than among members of the same population, as shown by Vaughan (1967) among closely interdigitated populations of Thomomys bottae and T. talpoides in Colorado. Maintenance of distinct territories by the pugnacious pocket gophers (Howard and Childs, 1959) probably is a real factor in the dynamics of present-day distributions.

Grinnell (1943) classified distribution barriers as tangible or intangible. Intangible barriers consist of zonal (temperature), faunal (atmospheric humidity) and associational (food supply, breeding places, refuges). Tangible barriers include land (to aquatic species) and bodies or streams of water (to terrestrial species). In the absence of tangible barriers, a combination of intangible factors exert limits on the species, not necessarily the individual.

## APPENDIX III

### Historical Background

Prior to the Wisconsin glaciation, all of early Pleistocene climates were broadly similar; they were more maritime than the modern climates at sites where fossils have subsequently been collected. Few of the pre-Wisconsin faunas known could live in the present combination of hot summers and extremely cold winters. Dry seasonal climates of today appear to be a Wisconsin or post-Wisconsin development (Taylor, 1964). Gleason (1922) postulated that during Sangamon, most or all of the Middle West was occupied by deciduous forest. Pocket gophers are said (Russell, 1968) to have been widespread in both the East and Midwest during this interglacial.

Wisconsin glacial epochs followed by warmer interludes (interglacials) proved to be disastrous for many of the ungulates. There is no doubt that these glacial periods drastically altered the biota of most of North America. Many animals simply were not equipped to adapt to the more or less suddenly changing environmental conditions and became extinct. Martin (1958) suggested that survival was

enhanced by small size, large range, and forest habitat. It is feasible that pocket gophers survived in the more southern extremes of their ranges and that widely distributed northern forms were killed off.

Hibbard (1964) suggested that probably all Recent mammalian species originated during the Quaternary. He documents faunal shifts of Great Plains animals, the first of which was the Cudahy fauna of the late Kansan. Some living mammal species extended their Boreal Subregion south during Illinoian and/or Wisconsin. There are many examples of south and southwestern retractions and western migrations.

Blair (1965) and some others (Deevey, 1949; Blair, 1958) have argued strongly for drastic southern latitudinal displacement of fauna during pluvials. Fragmentation of warmth-adapted species occurred as they retreated to refuges in Florida and Mexico. Sufficient opportunity existed for fragmentation of populations in the many north to south, then south to north, expansions following advant of successive glacials, warmer interglacials.

Blair (1954) stated that the Wisconsin alone probably accounts for up to eight north-south, south-north migrations. Most of the speciation in grassland forms can be attributed to this shifting of ranges to the south. Fragmentation of various east-west species pairs of Anurans in North America is attributed to southern splitting from previous ranges via

shifting climatic zones during warmer interglacial stages. Urodeles (adapted to cold and moisture) dispersed during glacial stages (in unglaciated regions), with disjunction occurring during interglacials. This interpretation of glacial events during the Wisconsin readily lends itself to postulated movements of plains pocket gophers which ultimately resulted in fragmentations from whence chromosomal forms arose.

Martin and Mehringer (1965) calculated that pine and spruce invaded the Southwest previous to and during maximum Wisconsin glaciation. From 17,000 to 23,000 years ago, the Mohave Desert was a woodland, as was west Texas. High pollen frequencies of grass-Artemesia (some oak) were typical of a climate slightly cooler, more moist than now, 22,000-32,000 years ago.

Braun (1955) and others believed that biota shifted only locally during glacial epochs and that only xero-mesophytes dispersed widely. Martin and Harrell (1957) stated that the presence of similar extant flora in the eastern United States and Mexico can best be explained by mid-Cenozoic disjunction. They suggested that a cool savanna or open woodland corridor permitted few temperate forest animals to cross the arid Texan barrier during the Pleistocene. I consider the pocket gopher to qualify as "xeric" adapted, able to cross this "arid" Texan barrier,

as Pleistocene fossils (Russell, 1968) from Texas attest.

The tundra zone associated with glaciation probably was narrow, maybe stretching only a few kilometers from the glacier (Frye and Williams, 1958). The climate was cooler than at present and extended considerably south of glacial lobes. During interglacial times a northern shift in ecological belts repopulated the areas exposed by melting ice. A late interglacial fauna and flora near Toronta, Canada, indicates a climate of 2-3° C. warmer than at present (Flint, 1957; Dorf, 1959). Other instances are cited to show that interglacials were considerably warmer than at present. It is likely that differences in distribution of precipitation between different Pleistocene substages existed also (Ross, 1964). This alone would have allowed for differential selection of ancestral stocks of pocket gophers.

Others (Auffenberg and Milstead, 1964) characterized the Pleistocene by its dynamic temperatures, humidity and sea level changes. They maintained that each succeeding glacial moved further south, retreated less far to the north, becoming progressively more severe. Each interglacial likewise was cooler than the previous. Also, Auffenberg and Milstead felt that the level of the sea fell and rose with pluvials and subsequent interglacials, respectively. High sea levels provided a physical mechanism for isolation, while low sea levels made available dispersal routes. The

humidity factor is very important in the east-west distribution of reptiles. Humidity changes were significant in opening and closing east-west dispersal routes, as well as in providing a physical mechanism for isolation and speciation. Suwanee Strait in the Florida Archipelago was flooded during each Pleistocene interglacial with salt water. It connected the Gulf and Atlantic during high sea levels and thus limited the southward or northward dispersion of some terrestrial species. These observations appear to logically substantiate environmental conditions resulting in isolation of G. pinetis in Florida during Early, Middle Pleistocene.

There were three important dispersal routes--Gulf, north-south Great Plains, and Rocky Mountains in southern Arizona and New Mexico. Most important was the Gulf corridor; it was open during all of the Pleistocene. Temperature probably decreased markedly in eastern USA following or during Wisconsin. A shift to xeric conditions allowed xeric-adapted species to migrate to the east (Auffenberg and Milstead, 1964). G. pinetis and G. tropicalis are both assumed to have migrated via this Gulf corridor, later becoming disjunct. The permanency of the Gulf corridor was important as a refuge for the breviceps group, from whence periodic migrations or extending populations became isolated subsequently to give rise to G. personatus, attwateri groups.

Carpenter (1940) suggested that the Pleistocene Epoch of advance and retreat of glaciers apparently had a profound effect on vegetation regions through changes of the continental climate. The prairies were driven by successive vegetation changes south and west, back and forth, during retreat and advances, corresponding to glacial periods and interglacials.

Gleason (1922) stated that, in general, there were two regions which served as retreats for the biota during glacial advance, the southeast and the southwest. The Ozarks are considered an area important in post-glacial dispersion. He believed that post-glacial invasions of deciduous forests followed river courses almost exclusively. Drainages appear significant in pocket gopher dispersal, also.

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