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CHROMOSOMAL AND MORPHOLOGICAL VARIATION IN THE PLAINS POCKET GOPHER, GEOMYS BURSARIUS, IN TEXAS AND ADJACENT STATES

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The plains pocket gopher, *Geomys bursarius*, has an extensive distribution in Texas, occurring throughout most of the state save for the southwestern region and South Texas south of the San Antonio River. This species demonstrates considerable geographic variation in Texas and its adjacent states as exemplified by the recognition of 13 subspecies (Hall and Kelson, 1959), eight of which occur in the eastern part of the state.

Most taxonomic and distributional studies of *G. bursarius* have been based on morphological and osteological characters (Baird, 1854; Merriam, 1890, 1895; Bailey, 1905; Davis, 1938, 1940; Villa and Hall, 1947; Baker, 1950; Baker and Glass, 1951). Although such studies have contributed to a better understanding of geographic variation, certain systematic problems have remained unsolved with respect to populations in Texas. As noted by Davis (1940), these problems concern the interpretation of the relationships, distribution, and differentiation of populations east of the Balcones Escarpment.

Several aspects of the biology of pocket gophers make systematic studies of this group (especially those based on conventional morphological characters) difficult. These rodents form small local populations isolated from one another by topography and indurate soils (Davis, 1940; Kennerly, 1954; Miller, 1964; Vaughan, 1967; Turner *et al.*, 1973). This pattern of distribution, defined by Wright (1943) as "island model" distribution, in com-

bination with the pocket gopher's low vagility greatly restricts migration and gene flow between populations. Where their ranges come in contact, different species and subspecies of pocket gophers do not occur sympatrically, but rather are distributed parapatrically with respect to one another (Miller, 1964; Vaughan, 1967; Thaeler, 1968*c*), making interpretation of the degree of reproductive isolation difficult. Soil is the major factor influencing the distribution of pocket gophers (Davis, 1938, 1940; Kennerly, 1954; Miller, 1964; Downhower and Hall, 1966), and certain external and cranial dimensions have been correlated with soil characteristics (Davis, 1938; Kennerly, 1954, 1959; Miller, 1964; Hendrickson, 1972). For these reasons it is difficult to determine whether morphological differences among populations are due to genetic factors or to environmentally related phenotypic responses.

A combination of isolation and phenetic adaptation to localized conditions, then, probably serves to promote divergence and explains in part the considerable degree of morphological variation recorded for *Geomys bursarius*. These factors also demonstrate the need to identify an index or population marker for the determination of genetically distinct populations. Morphological characters have not provided this index and in some cases have added to the already existing confusion.

Several authors (Patton and Dingman, 1968; Davis and Baker, 1974; Baker *et al.*, 1975) have noted the value of karyotypes as population markers in systematic studies. Karyotypic information has been used successfully to decipher systematic problems among other fossorial rodents, including *Spalax* (Wahrman *et al.*, 1969; Raicu *et al.*, 1968), *Ctenomys* (Reig and Kiblisky, 1969), *Thomomys* (Patton and Dingman, 1968, 1970; Thaeler, 1968*a*; Wentworth and Sutton, 1969; Berry and Baker, 1971; Patton, 1972), and *Pappogeomys* (Berry and Baker, 1972).

Like other fossorial mammals, *G. bursarius* shows considerable variation in chromosome number and morphology. Several authors (Hart, 1971; Kim, 1972; Baker *et al.*, 1973; Hart, 1978) have investigated karyotypic variation in the plains pocket gopher in Texas and have described eight karyotypically distinct populations (Fig. 1). These populations, referred to as chromosomal races (Baker *et al.*, 1973), can be arranged into three groups on the basis of similar karyotypic characteristics and geographic distribution. These are the *lutescens* group, chromosomal races A, B, C, D; the *attwateri* group, including chromosomal races F and G; and the *breviceps* group, consisting of chromosomal races E

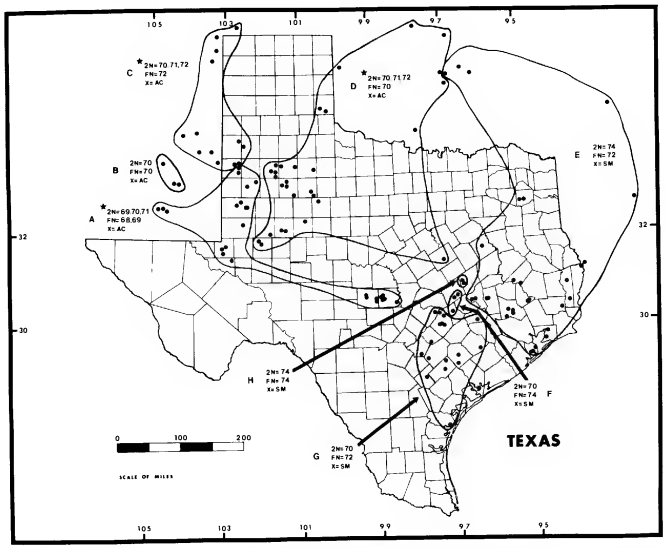

FIG. 1.—Distribution of chromosomal races A through H of *Geomys bursarius* in Texas and adjacent states. The diploid number is represented by 2N and the fundamental number by FN; morphology of the X-chromosome is represented by SM, submetacentric, and Ac, acrocentric. Stars indicate those races exhibiting chromosomal polymorphism. The *lutescens* chromosomal group is represented by chromosomal races A, B, C, and D; the *attwateri* group by chromosomal races F and G; and the *breviceps* group by chromosomal races E and H.

and H. The karyotypic characteristics separating these groups involve differences in diploid number (2N), fundamental number (FN), morphology of the X-chromosome, and degree of chromosomal polymorphism found within each region.

The *lutescens* complex is distributed in northwestern Texas, eastern New Mexico, and western Oklahoma. It includes four recognized subspecies, *G. b. llanensis* (race A), *G. b. texensis* (race A), *G. b. knoxjonesi* (races A and B), and *G. b. major* (races A, B, C, and D). Chromosomal variation in this complex involves differences in diploid and fundamental numbers, the former varying from 69 to 72 and the latter from 68 to 72. These differences result primarily from presence or absence of biarmed elements in the autosomal complement. Races A, C, and D exhibit chromosomal polymorphisms, but the sex chromosomes in all four races are constant and consist of an acrocentric X and Y.

Races F and G of the *attwateri* group are present west of the Brazos River in central and southern Texas, have a diploid number of 70, and possess a fundamental number of either 74 (race F) or 72 (race G). The X-chromosome is always a submetacentric and the Y a small acrocentric. Chromosomal polymorphism has not been found within either race. The distribution of this group coincides with that of three recognized subspecies, *G. b. brazensis* (races F and G), *G. b. ammophilus* (race G), and *G. b. attwateri* (race G).

The *breviceps* assemblage appears east of the Brazos River throughout central and eastern Texas, western Louisiana, eastern Oklahoma, and western Arkansas. A diploid number of 74 and a fundamental number of either 72 (race E) or 74 (race H) characterize this group. Chromosomal polymorphism is unknown within either race; the sex chromosomes are a large submetacentric X and an acrocentric Y. Race H, described by Kim (1972), is limited to two localities in central Texas. Race E, on the other hand, has an extensive distribution that encompasses the range of seven currently recognized subspecies, *G. b. brazensis* (races E and H), *G. b. sagittalis*, *G. b. pratincolus*, *G. b. terricolus*, *G. b. ludemani*, *G. b. dutcheri*, and *G. b. breviceps*.

The designation of three major groups has an historic basis. Davis (1940), in his revision of the genus *Geomys*, considered populations of the plains pocket gopher as representing two distinct species. These were *G. lutescens* in northwestern Texas, eastern New Mexico, and western Oklahoma, and *G. breviceps* from central and eastern Texas, eastern Oklahoma, Arkansas, and Louisiana. These remained as full species until Villa and Hall (1947) and Baker and Glass (1951) relegated them to subspecies of *G. bursarius* on the basis of morphological intergradation at zones of contact. Pocket gophers of the *lutescens* chromosomal group (including chromosome races A, B, C, and D) in this study correspond to *G. lutescens* in Texas as defined by Davis (1940). Pocket gophers of the *breviceps* group (including chromosome races E and H) occur east of the Brazos River in eastern Texas and were referred to the species *G. breviceps* by Davis (1940); those occurring west of the Brazos River in central and southern Texas (including chromosome races F and G) were not regarded as a separate species by Davis (1940), but rather as distinct subspecies of *G. breviceps*. However, because of the karyotypic distinctions between chromosome races F and G and races E and H, the former two have been arranged in a separate chromosomal group (designated the *attwateri* group) in this study.

In order to investigate the relationships, distribution, and amount of differentiation within and among the three chromosomal groups, a restricted study area consisting of 11 counties in eastern Texas was selected. Four chromosomal races are present in these counties; three (races E, F, and G) represent the *attwateri* and *breviceps* groups and the fourth (race D) represents one of the western Texas races of the *lutescens* group.

Specifically, the objectives of this study are as follows: 1) to determine the extent of chromosomal variation within and among populations of *G. bursarius* in an 11-county study area of eastern Texas; 2) to document the distribution of the chromosome races in the study area; 3) to examine factors important to the distribution of chromosomally distinct populations and to pocket gophers in general; and 4) to relate chromosomal variation to morphological variation in understanding the systematics of this species in Texas and adjacent states.

Study Area

The area chosen for intensive study represents 11 counties located in eastern Texas (Fig. 2) and was selected because the ranges of the three major chromosomal groups (*lutescens*, *attwateri*, and *breviceps*) converge in this region.

Soils in the study area can be divided into three types (alluvial, clay, and sandy soil). Alluvial soils are located along river channels and two major associations occur along the Brazos River, the Miller-Norwood-Yahola and Miller-Norwood associations, which contain soils consisting of clay to fine sandy loam (Templin *et al.*, 1958). Clay soil associations, ranging in texture from clay to clay loam, occupy large portions of Falls and McLennan counties and half of Milam County. Sandy soil associations are characterized by textures ranging from sandy to sandy loam.

Four rivers (Colorado, Brazos, Navasota, and San Jacinto), which represent potential barriers to pocket gopher dispersal, flow transversely across the study area. The Brazos, located in the center of the area, is the most extensive of these and has no less than 12 oxbows along its course. These oxbows represent localized areas where the river has changed course, as a result of shifting channels, and has transferred land from one bank to another. The entrance to an abandoned oxbow becomes separated from the new river channel by deposits of silt and, over time, the entire lake is replaced with sedimentation. Larger tracts of land also can be shifted from one bank to the other by the meandering of a

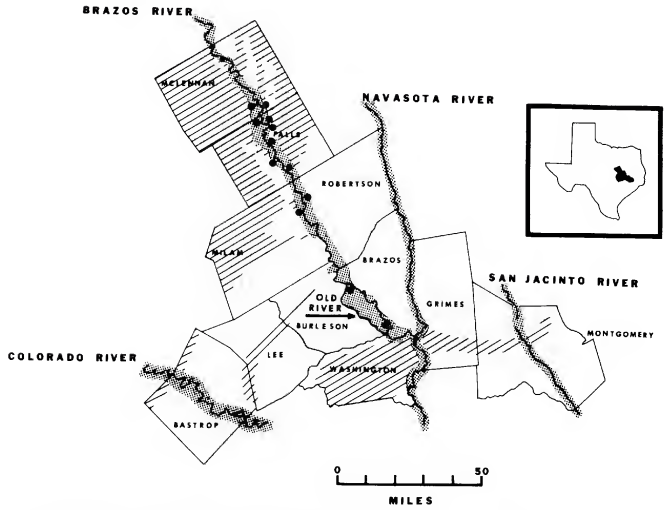

FIG. 2.—Map showing the 11-county study area in eastern Texas. Stippled areas represent alluvial soil associations; diagonal lines, clay soil associations; and unshaded areas, sandy soil associations. Dots along the Brazos River identify the location of the 12 oxbows. The Old River in Burleson County represents a meander scar of the Brazos.

river, a common occurrence in the flood plain of larger rivers (Cleland, 1929). Old River in Burleson County represents just such a meander scar (old river channel) of the Brazos. In this area, a considerable amount of land was transferred from what is now Brazos County to Burleson County when the river altered course.

METHODS AND MATERIALS

A total of 464 specimens (386 for morphological analysis and 200 for karyotypic analysis) from Texas and Louisiana were utilized in this study. All were prepared as conventional museum study skins (skin with skull or skeleton only) and deposited in either the Texas Cooperative Wildlife Collection, Texas A&M University (TCWC) or The Museum, Texas Tech University (TTU).

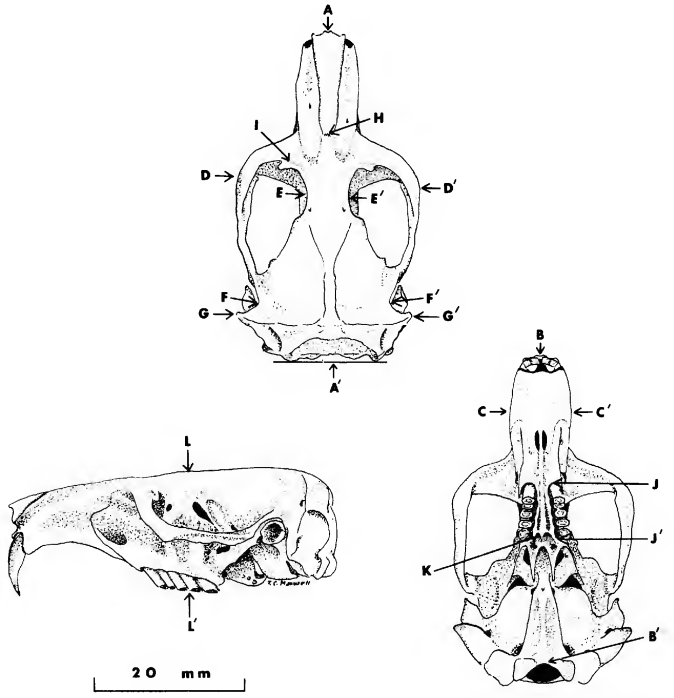

FIG. 3.—Skull of *Geomys bursarius* showing cranial measurements used in statistical studies. Measurements are as follows: greatest length of skull (GLS), A-A′; basal length (BL), B-B′; breadth of rostrum (BR), C-C′; zygomatic breadth (ZB), D-D′; interorbital breadth (IB), E-E′; breadth of braincase (BB), F-F′; mastoidal breadth (MB), G-G′; length of nasals (LN), A-H; length of rostrum (LR), A-I; length of maxillary toothrow (LTR), J-J′; palatal length (PL), B-K; and palatofrontal depth (PFD), L-L′.

Karyotypic Analysis

Pocket gophers used in the karyotypic analysis were live-trapped by means of a technique described by Baker and Williams (1972). The *in vivo* colchicine—hypotonic citrate sequence described by Patton (1967) and modified by Lee (1969) was used to prepare the karyotypes of metaphase chromosomes from bone marrow cells. The diploid number (2N) was determined by counting at least 10 spreads per slide. A representative spread was pho-

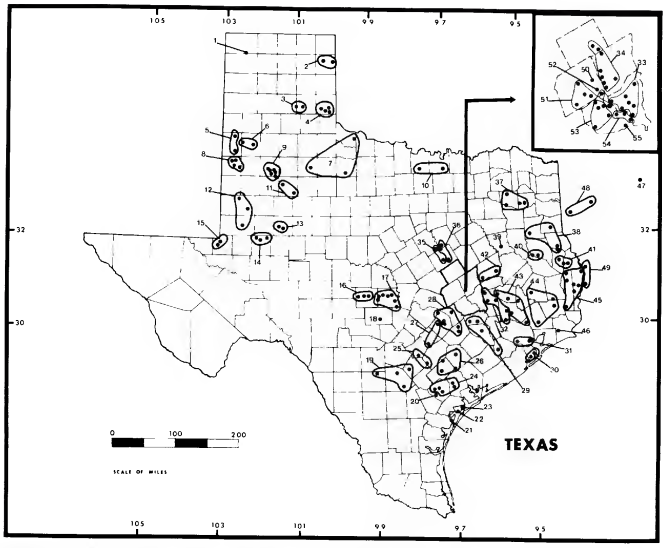

FIG. 4.—Map showing the geographic location of 55 samples of *Geomys bursarius* used for statistical analysis of morphological variation. The enlarged area represents the location of samples from four counties (Robertson, Brazos, Milam, and Burleson) in the center of the 11-county study area in eastern Texas.

tographed and a karyotype constructed on the basis of the number of biarmed and uniarmed autosomes and the morphology of sex chromosomes (Patton and Dingman, 1968). Metacentric, submetacentric, subtelocentric, and acrocentric chromosomes were described using the terminology of Patton (1967). The fundamental number (FN) was defined as the number of major chromosome arms in the autosomal complement.

Morphological Analysis

Twelve cranial measurements were taken, as illustrated in Fig. 3, by means of dial calipers and recorded in millimeters (mm.). Only adult animals were used in the morphological analysis. Animals were considered adults if the basioccipital—basisphenoid suture was completely ossified. Males and females were treated separately due to marked sexual dimorphism (Kennerly, 1958; Baker and Genoways, 1975).

Specimens from approximately 218 localities were grouped into 55 units (Fig. 4) to obtain larger samples for statistical analysis of morphological variation. Care was taken to group localities according to geographic and physiographic regions, known taxonomic boundaries, major waterways, and known karyotypes. Due to small sample sizes in males, only adult females were used in the analysis of morphological variation. Samples with only one individual were eliminated to mitigate errors resulting from improperly-sexed individuals.

Various univariate and multivariate statistical techniques were employed to elucidate patterns of morphological variation among chromosomally distinct samples. Standard statistics (mean, range, standard deviation, standard error of the mean, variance, coefficient of variation) were computed for each of the 55 samples with a program of the Statistical Analysis Systems (SAS) designed and implemented by Barr and Goodnight (Service, 1972). Several geographic transects were constructed for selected characters from these statistics and displayed in the form of Dice-Leraas diagrams to illustrate the degree of clinal variation in size.

Multivariate techniques were used to cluster samples according to phenetic similarity. These were performed with NT-SYS computer programs (Rohlf and Kishpaugh, 1972). Each sample was considered an operational taxonomic unit and means of cranial measurements were used as characters. Matrices of Pearson's product—moment correlation and phenetic distance coefficients were generated from standardized character values. Cluster analyses were conducted by means of UPGMA (unweighted pair-group method using arithmetic averages) on both the correlation and distance matrices, and a phenogram was generated for each. Only the distance phenogram is illustrated here because it had a higher cophenetic correlation value.

In order to assess the degree of divergence among samples, a multivariate analysis of variance (MANOVA) in SAS was used. Characteristic roots and vectors were then extracted and mean canonical variates computed for each locality. This analysis considers all characters simultaneously and provides weighted combinations of characters that maximize among-sample variance and minimize within-sample variance. For a detailed description of the mechanics of this particular analysis, see Schmidly and Hendricks (1976) and Yates and Schmidly (1977).

Distributional Analysis

Soil samples were collected from the walls of burrows in which pocket gophers were trapped and from areas completely void of gophers. Four soil parameters (clay, silt, sand, and moisture) were measured to investigate the influence of soil texture and moisture on the distribution of *G. bursarius*.

Prior to analysis, all samples were air-dried and passed through a 2-mm. screen. The texture of the soil in each sample was analyzed by the hydrometer method in order to assess the percentage of clay, silt, and sand present (Kilmer and Alexander, 1949). The field capacity of the soil for moisture was determined with a technique described by Milford (1970). The location of all samples was plotted on a county soil map and the soil association corresponding to each location was determined.

The importance of the Brazos River as a boundary between karyotypic races also was investigated. At several locations along that river, pocket gophers were trapped on both banks and karyotyped to determine the distribution of chromosomal races. Oxbow lakes and other major land transfers along the river were located with the aid of aerial photographs and examined for their potential as avenues for dispersal of pocket gophers across this waterway. Other rivers in eastern Texas also were examined to determine their effects on the distribution of the various chromosomal races.

Results

Chromosomal Analyses

Karyotypic Descriptions

More than 183 specimens were karyotyped from the 11-county study area. Of these, 18 had the karyotype of race D; 93, of race E; 30, of race F; 25 of race G; and 17 were of hybrid origin. No polymorphism was found in any of the populations sampled. Representative karyotypes are shown in Figs. 5-7. Karyotypic descriptions follow:

Chromosomal race D (Fig. 5A).—Diploid number, 72; fundamental number, 70. This karyotype consists of 35 pairs of large to small acrocentric autosomes, a large acrocentric X-chromosome, and a small acrocentric Y-chromosome.

Chromosomal race E (Fig. 5B).—Diploid number, 74; fundamental number, 70. The autosomal complement contains 36 pairs of size-graded acrocentric chromosomes. The X-chromosome is a medium-sized submetacentric and the Y-chromosome is a small acrocentric. Kim (1972) described chromosomal race H from Robertson County. However, specimens examined during this study from

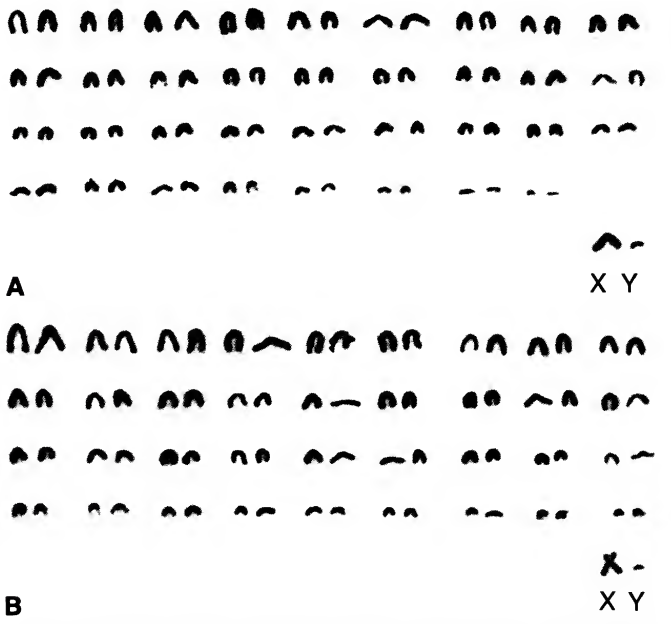

FIG. 5.—Karyotypes of male *Geomys bursarius* representing: A, chromosomal race D from McLennan County near Waco, Texas; B, chromosomal race E from Falls County near Cedar Springs, Texas.

localities given by Kim possessed karyotypes identical to those found for chromosomal race E.

Chromosomal race F (Fig. 6A).—Diploid number, 70; fundamental number, 74. In the autosomal complement there are 31 pairs of large to small acrocentrics, one pair of large submetacentrics, one pair of medium submetacentrics, and a pair of small metacentrics. The X-chromosome is a medium submetacentric and the Y-chromosome a small acrocentric.

Chromosomal race G (Fig. 6B).—Diploid number, 70; fundamental number, 72. The autosomal chromosomes are comprised of 32 pairs of large to small acrocentrics, one pair of large submetacentrics, and a pair of small metacentrics. The X-chromosome is a medium submetacentric, the Y-chromosome, a small acrocentric.

F×G hybrids (Fig. 7A).—Karyotypic differences between these two races center around the number of biarmed chromosomes present in the autosomal complement, and F_1 hybrids can be detected due to this difference. All F_1 individuals have a diploid number of 70 and a fundamental number of 73. The autosomal chromosomes consist of 30 pairs of large to small acrocentrics, one unpaired acrocentric, one pair of large submetacentrics, an unpaired medium submetacentric,

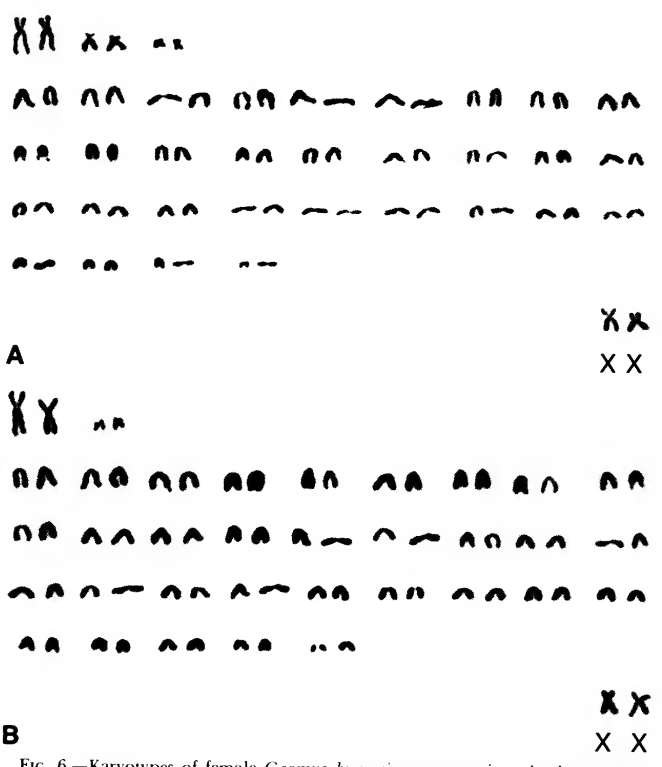

FIG. 6.—Karyotypes of female *Geomys bursarius* representing: A, chromosomal race F from 8.0 km. South of Gause, Milam County, Texas; B, chromosomal race G from northeastern Burleson County, Texas.

and a pair of small metacentrics. The X-chromosome is a medium submetacentric and the Y-chromosome is an acrocentric.

E×G hybrids (Fig. 7B).—The karyotypic distinctions between these two chromosomal races involve differences in diploid number, fundamental number, and the number of biarmed autosomes. Only one F_1 hybrid was found and this individual had a diploid and fundamental number of 72. The autosomal chromosomes consist of 32 pairs of large to small acrocentrics, one unpaired large submetacentric, one unpaired small metacentric, and four unpaired acrocentrics. The X-chromosome is a medium submetacentric.

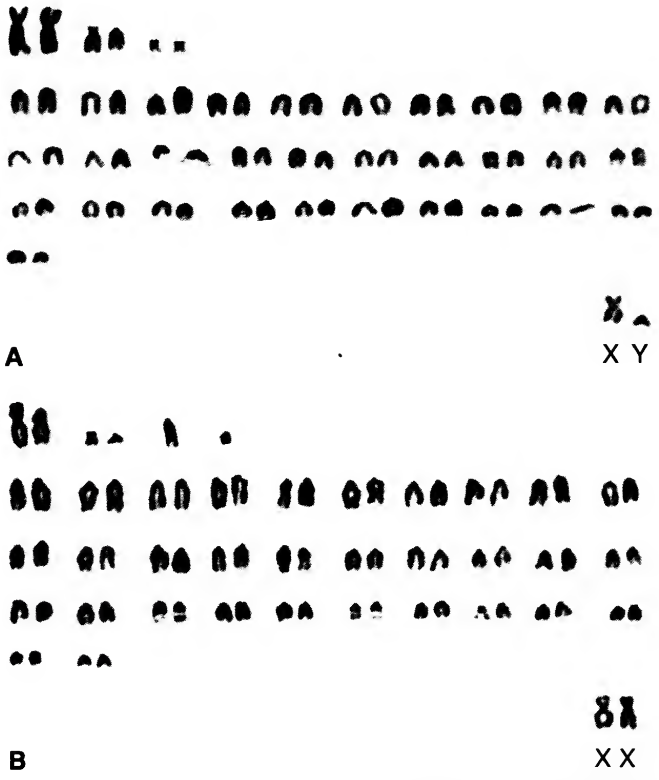

FIG. 7.—Karyotypes of *Geomys bursarius* representing: A, a male F_1 hybrid between chromosomal races F and G from 6.24 km. NW Grant on Highway 50, in Burleson County, Texas; B, a female F_1 hybrid between chromosomal races E and G from 5.76 km. NW Grant on Highway 50, in Burleson County, Texas.

Distribution of Chromosomal Races

The geographic distribution of chromosomal races D, E, F, and G is shown in Fig. 8. All four races maintain distinct distributions in this area as described below.

Chromosomal race D reaches the southern limit of its range in McLennan County. From the northern part of McLennan County to the Falls County line, pocket gophers of this race maintain a

linear distribution along both the east and west banks of the Brazos River. No pocket gophers were found in soil types away from the river. Although ranges of races D and E approach one another near the McLennan-Falls county lines, an hiatus of approximately 12.8 km. separates them.

Chromosomal race E reaches the western limit of its range along the Brazos River. South of Falls County, race E is located primarily on the east bank. However, in Milam and Burleson counties small isolated populations occur on the west bank in areas close to the river. Northward in Falls County, race E is distributed linearly along both sides of the river as far north as the McLennan-Falls county line. With the exception of southeastern Falls County, pocket gophers occur only beside the river. Race E has a continuous distribution east of the Brazos River throughout eastern Texas where soils are suitable.

The distribution of chromosomal race F is limited to Milam, Burleson, and Lee counties. These pocket gophers are found throughout southern Milam County; clay soils apparently inhibit their moving into the northern part of that county and Williamson and Bell counties to the west. The west bank of the Brazos River forms the eastern boundary. Southward, race F extends into northeastern Burleson County, where it is limited to areas along the river, and most of Lee County.

Chromosomal race G reaches its northern and eastern limits just north of the Milam-Burleson county line and thence eastward to the Brazos River. This race has not been found on the east bank of the Brazos. Throughout most of Burleson and Bastrop counties, pocket gophers of race G maintain an almost continuous distribution in areas of suitable soils. They are somewhat limited in distribution in Washington County, however, owing to the presence of clay soils.

Contact Zones

Two zones of contact between chromosomal races occur in the study area. We collected specimens that represent parental types and hybrids in each zone. Assignment of specimens as either parental or hybrid was based entirely on karyotypes. In the following discussion, the term "hybrid" is not used to infer specific status of the various chromosomal races involved but rather to imply interbreeding between chromosomally distinct populations.

The first zone of contact involves races F and G and occurs near Milano and Gause, Milam County, Texas (Fig. 8). The zone

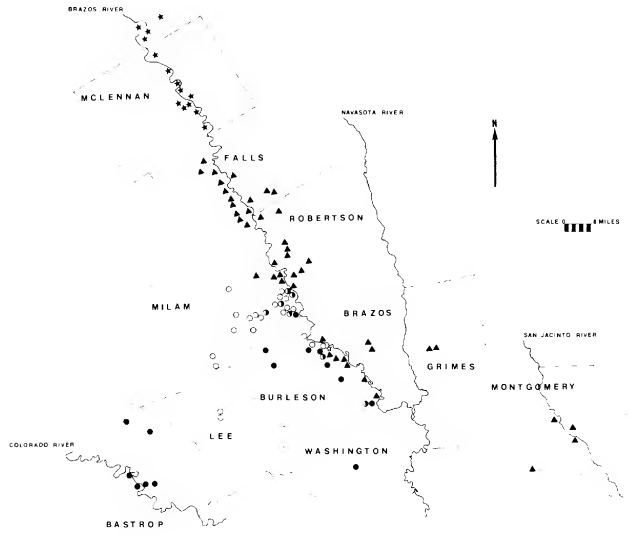

FIG. 8.—Geographic distribution of chromosomal races of *Geomys bursarius* in the 11-county study area. Stars represent chromosomal race D; triangles, race E; open circles, race F; and closed circles, race G. The intermediate circle indicates intergrades between races F and G, and the open star, an intergrade between races E and G.

is approximately 17.6 to 22.4 km. from east to west and has a maximum width of about 14.4 to 16.0 km. from north to south. To the north and west of this area, pocket gophers are represented by race F, to the south, by race G. The Brazos River forms the eastern boundary of the zone.

Karyotypic differences between these two races involve the presence or absence of a pair of medium submetacentric autosomes (Figs. 6A and 6B). All F_1 hybrids had an intermediate karyotype with a fundamental number of 73 and five biarmed autosomes (Fig. 7A). Only F_1 hybrids could be identified because backcross individuals resemble either the parental or the F_1 karyotype in gross chromosome morphology. Of 32 specimens collected and karyotyped from this area, 13 (41 per cent) were F_1 hybrids, 18 (56 per cent) exhibited a race F karyotype, and one (3 per cent) exhibited a race G karyotype.

No distributional overlap was found between the two parental types in this zone of contact. The hybrids were associated with chromosomal race F, whereas chromosomal race G remained on the periphery of the zone. This would seem to indicate similar ecological requirements of race F and the hybrids; however, no obvious ecological preferences could be determined for either of the parental types or for the hybrids. All individuals captured occurred in the Lakewood-Tabor-Luverne soil association, which consists of sandy loam soils (Soil Conservation Service and Texas Agricultural Experiment Station, 1961). This particular soil association is prevalent throughout southern Milam County and parts of northern Burleson County. No differences in vegetation or other ecological parameters were noted in this area.

The second contact zone is near the Brazos River in northeastern Burleson County (Fig. 8) where the geographic ranges of three races (E, F, and G) approach one another. The contact zone is limited to a width of approximately 1.6 km. from east to west and a similar distance from north to south. Chromosomal race G occupies the west, northwest, and southwest portion of the zone while race F is found to the northeast and east along the Brazos River and race E to the southeast.

Chromosomal race E differs from races F and G in diploid number and the number of biarmed autosomes (Figs. 5B, 6A, and 6B). Potential hybrid formation in this zone is complicated by the possible occurrence of hybrids between races F and G, F and E, or G and E. If the backcrossing potential of hybrids is considered, the number of possible karyotypes becomes extremely large.

Of the 27 individuals karyotyped from this zone, four (15 per cent) exhibit a race F karyotype; nine (33 per cent), a race G karyotype; 11 (41 per cent), a race E karyotype; and two (7 per cent), a karyotype representing the F_1 hybrid of a cross between races F and G. One individual (4 per cent) is a potential F_1 hybrid between races E and G. This particular individual has a karyotype with a diploid number of 72 and a fundamental number of 72 and is intermediate between races E and G (Fig. 7B).

Soil maps of Burleson County indicate that this contact zone is entirely within the Miller-Norwood soil association, an association containing soils ranging from blocky calcareous clay to silty clay loam (Soil Conservation Service and Texas Agricultural Experiment Station, 1960). No vegetative differences were discernable between this area and that surrounding it.

Influence of Soils on Distribution

Most pocket gophers were found in associations consisting of loamy to sandy loam soils (Fig. 9). These are represented by the Lakewood-Tabor-Luverne, Edge-Tabor, Axtell-Bastrop, Crockett-Wilson, and Gowen-Ochlockonee associations (Soil Conservation Service and Texas Agricultural Experiment Station, 1960, 1961). Chromosomal races found in these soil types maintain a more or less continuous distribution. Two races (F and G) occur only in the Lakewood-Tabor-Luverne and Edge-Tabor associations which represent most of the sandy soils in Milam and Burleson counties. Few pocket gophers are found in clay loam to clay soils except in isolated areas along the Brazos River (see shaded areas on Fig. 9). This is the case in McLennan and Falls counties where chromosomal races D and E occur almost exclusively along the river. With the exceptions of the sandy soils of the Axtell-Bastrop and Axtell-Irving associations, chromosomal races D and E inhabit alluvial soils of the Miller-Norwood-Yahola association. This association contains soils series consisting of clay, represented by the Miller series, silt loam to silty clay, represented by the Norwood series, and silt loam to very fine sandy loam, represented by the Yahola series (Templin *et al.*, 1958). Most pocket gophers were found in isolated areas where sandy soils persisted. These areas probably correspond to the Yahola series. Chromosomal race E also occurs in the Miller-Norwood association, which is located along the Brazos River in Robertson, parts of Brazos, and Burleson counties. In most cases, pocket gophers in this association occurred close to the river or along highway rights-of-way and were scattered in occurrence and rather low in density.

Certain clay soils limited the contact among chromosomal races. The ranges of races D and E approach one another near the McLennan-Falls county line; however, an hiatus of approximately 12.8 km. that separates the two represents land where frequent flooding occurs and clay soils persist. Chromosomal races E and F approach one another in Milam County but remain separated by a belt of heavy clay soils of the Trinity-Catalpa association. This soil belt is about 4.8 km. wide. Although there is a small contact zone in northeastern Burleson County, the ranges of chromosomal races E and G remain separated by a belt of clay soils of the Miller-Norwood association 4.8 to 6.4 km. wide.

Four measurements of soil features (per cent clay, sand, silt, and moisture) were used to assess the influence of soil texture and

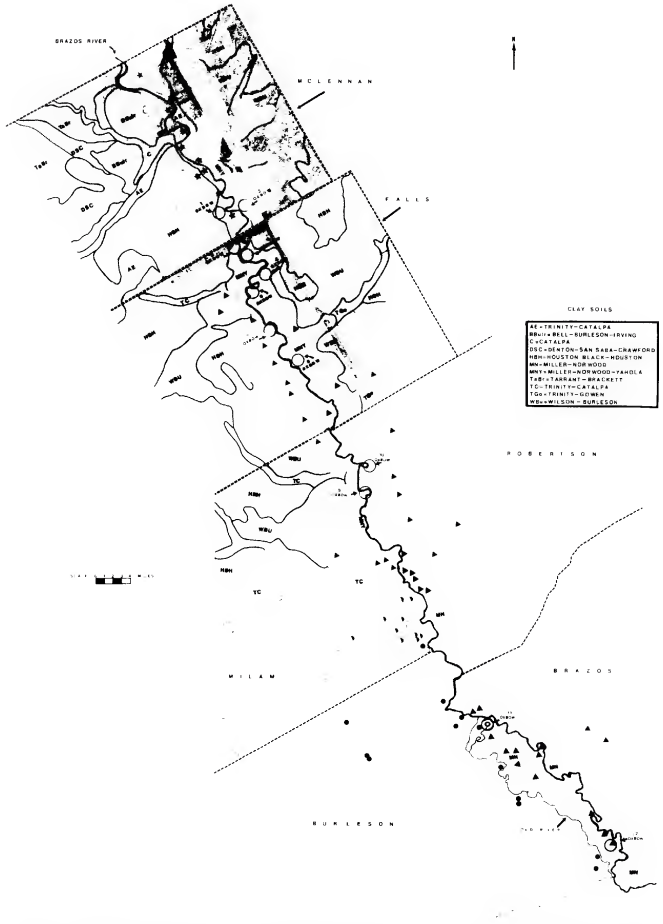

FIG. 9.—Distribution of chromosomal races of *Geomys bursarius* according to soil associations and actions of the Brazos River. Stars represent chromosomal race D; triangles, race E; closed circles, race G; open circles, race F; and half circles, hybrids between races F and G. Shaded areas correspond to clay soil associations identified in the legend; unshaded areas represent sandy soil associations. Potential oxbows are identified by a circle and correspond to the numbers 1 to 12.

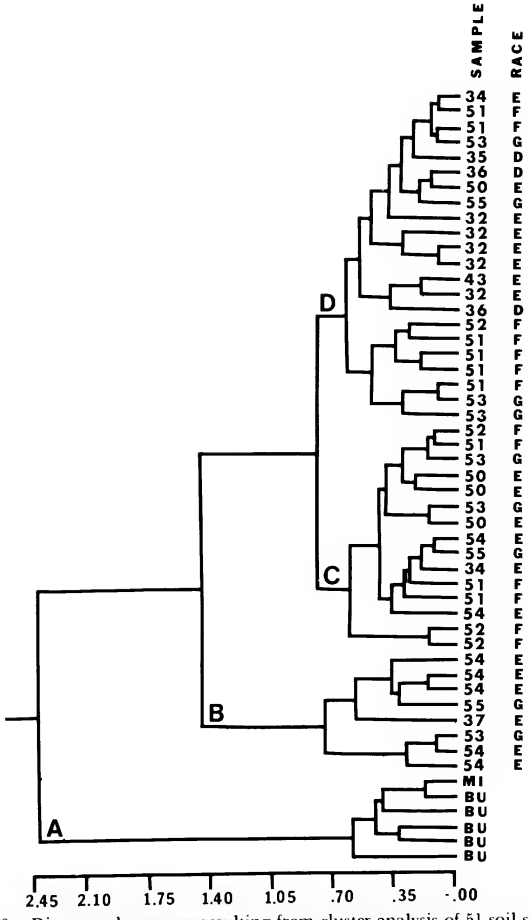

FIG. 10.—Distance phenogram resulting from cluster analysis of 51 soil samples. These samples correspond to areas yielding the four chromosomal races and to the two major clay belts separating the chromosomal races. The cophenetic correlation coefficient is 0.90. The letters D, E, F, and G represent the four chromosomal races. Mi and Bu correspond to the clay belts located in Milam and Burleson counties, respectively. The sample numbers correspond to grouped localities presented in Fig. 4.

maximum moisture content on the distribution of the various chromosomal races.

A NT-SYS clustering analysis was used to determine if the different chromosomal races had distinct soil preferences. Means of the four soil measurements for 51 soil samples (45 of which yielded one of the four chromosomal races and six of which represented the two major clay belts separating the chromosomal races) were used in the analysis. A phenogram diagraming the phenetic relationships of all samples was computed by cluster analysis from distance matrices (Fig. 10). The samples correspond to those used in the morphological analysis (Fig. 4) and the karyotypes represent chromosomal races.

The distance matrix divides the samples into four major clusters with a cophenetic correlation coefficient of 0.90. Cluster A separates the two major clay belts located in Milam and Burleson counties, where gophers were absent, from samples where gophers were present. There is considerable overlap of soil samples in clusters B, C, and D indicating little distinction among the chromosomal races with respect to the four soil parameters. In general, the four groups represented by clusters A to D demonstrate a clustering of samples that show a gradual decrease in the percentage of clay.

Forty-nine of the 51 samples used in the clustering analysis were plotted on a textural triangle to determine in which textural class the various chromosomal races and areas void of gophers would occur. As can be seen in Fig. 11, most of the four chromosomal races occupy sandy loam to sandy clay loam soils. The seven samples in loam and clay loam soils are pocket gophers taken from the Miller-Norwood soil association in Burleson County and are almost exclusively representative of race E gophers from localities near the Brazos River. Open squares at the top of the triangle are samples taken in heavy clay soils from areas void of pocket gophers in Milam and Burleson counties. The Milam County samples are from the belt of Trinity-Catalpa soils separating races E and F, whereas the Burleson County samples are from the belt of Miller-Norwood soils that separate races E and G.

The four soil measurements also were used to determine soil tolerances of the chromosomal races as well as to indicate the overall influence of each particular parameter on the presence or absence of gophers. As revealed in the clustering analysis and plots on the texture triangle, there is a large degree of overlap

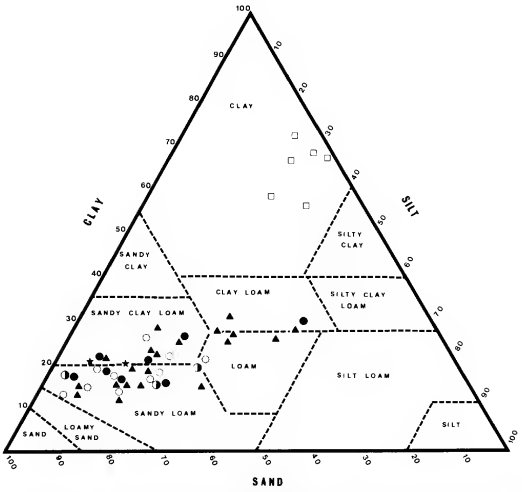

FIG. 11.—Soil textural triangle representing the percentage of clay, silt, and sand in samples taken from localities yielding pocket gophers as well as areas void of pocket gophers. Stars represent samples of chromosomal race D; triangles, race E; open circles, race F; closed circles, race G; and half circles, hybrids between races F and G. Open squares represent the two clay belts located in Milam and Burleson counties where pocket gophers were absent. Scales located on each side of the triangle indicate percentage of clay, silt, and sand. The triangle has been subdivided into 12 textural classes based on these percentages.

among the four chromosomal races with regard to their soil tolerances. As shown in Table 1, chromosomal race E inhabits a wider range of soil types than do races D, F, and G; however, if samples occurring in the Miller-Norwood soils (where a higher than average percentage of clay, silt, and moisture are present) are excluded from this analysis, the tolerance of race E is similar to that of the others.

Most pocket gophers were found in soils having a low content of clay (mean, 19; range, 12 to 39%) and a high content of sand (mean, 63; range, 19 to 22%). Conversely, pocket gophers are absent from soils having a high clay content (mean, 65; range, 56 to 72%) and low sand content (mean, 8; range, 1 to 16%). Moisture also seems to be correlated with the local presence or absence of pocket gophers. On the average, soils capable of containing a high moisture content (mean, 24; range, 23 to 33%) excluded

TABLE 1.—*Mean soil tolerances of chromosomal races D, E, F, and G of* Geomys bursarius. *Minimum and maximum values are given in parentheses.*

Chromosomal races	% Clay	% Sand	% Silt	% Moisture
Race D	19.65	68.96	11.39	11.57
	(18.32-20.32)	(64.96-70.96)	(08.72-14.72)	(09.56-12.63)
Race E	19.77	60.40	19.80	14.13
(with Miller-Norwood samples)	(12.88-39.44)	(19.84-81.84)	(06.72-45.44)	(08.75-23.15)
Race E	16.55	67.62	17.41	12.64
(without Miller-Norwood samples)	(12.16-26.16)	(51.84-81.84)	(06.00-33.24)	(08.75-16.95)
Race E	28.26	44.64	28.52	17.42
(Miller-Norwood samples)	(21.44-39.44)	(19.84-68.56)	(10.00-45.44)	(12.48-23.15)
Race F	18.78	63.98	17.24	14.20
	(12.88-26.88)	(48.40-82.40)	(04.00-30.00)	(12.64-16.61)
Race G	20.88	60.62	18.58	15.25
	(16.16-30.32)	(24.96-78.40)	(04.72-44.72)	(12.24-18.51)

gophers. Per cent of silt did not affect the distribution of gophers in the study area.

Influence of Rivers on Distribution

In the major floodplain of the Brazos River from southern Falls County to Washington County, chromosomal race E is limited primarily to the east bank and chromosomal races F and G to the west (Fig. 8). Other rivers considered in the course of this study did not appear to effectively limit the distribution of chromosomal races. The Navasota and San Jacinto rivers located east of the Brazos River, for example, had chromosomal race E distributed along both the east and west banks; likewise, chromosomal race G occupied both banks of the Colorado River in south-central Texas.

Several areas reflected exceptions to the general distribution of chromosomal races along the Brazos. Outside the major floodplain to the north in Falls and McLennan counties, chromosomal races D and E were found on both the east and west banks. Within the floodplain, chromosomal race E occurred on the west bank of the river in Milam and Burleson counties. Both of these locations represent isolated areas near the river.

In an effort to explain the presence of race E in Milam and Burleson counties, we investigated certain actions of the Brazos River. Using aerial photographs and ground surveys, we found 12 oxbow lakes along the river (Fig. 2). Two of them were on the west bank in Falls and Milam counties and in the general vicinity of chromosomal race E in Milam County. In the region of Burleson County, also occupied by race E, two more oxbow lakes were located as well as a major shift of the streambed; Old River

represents a meander scar or old river bed of the Brazos. We suggest that populations of pocket gophers belonging to race E and presently occupying the west bank of the Brazos historically occurred on the eastern bank. Shifts in the course of the river, as indicated by the meander scar, effectively isolated portions of the once contiguous distribution of race E and placed them on the western side of the river.

Morphological Analyses

The following morphological analyses were conducted to examine the degree of correlation between chromosomal and morphological variation in *Geomys bursarius*. Chromosomal races served as a population index in grouping specimens for morphological consideration.

Univariate Analysis

Four cranial characters (greatest length of skull, palatal length, length of rostrum, and mastoidal breadth) were examined for clinal variation in size among populations of *G. bursarius* in Texas. Three geographical transects (north to south, east to west, and northeast to southwest) were constructed for each character. All four characters fit a single pattern with only minor deviations; therefore, only greatest length of skull is illustrated by Dice-Leraas diagrams in Fig. 12.

Along the north-south transect, greatest length of skull shows a clinal decrease in size from the larger pocket gophers in northern Texas (samples 3, 7, and 17), representing the *lutescens* group, to the smaller gophers in southern Texas (samples 25, 24, 20, 22, and 21), which are representative of the *attwateri* group. Two samples from the Texas coast in Aransas County (21 and 22) show a significant increase in size, and the mean values are reminiscent of pocket gophers from farther to the north.

Along the east-west transect from Jasper and Newton counties (sample 45) to Winkler County (sample 15), there is a smooth clinal increase in greatest length of skull. Three size groups can be recognized based on slight deviations or breaks along the cline. These include the small gophers of the *breviceps* group (samples 45, 44, 43, 32, and 33), the medium-sized gophers of the *attwateri* group (samples 51 and 53), and the large gophers of the *lutescens* group (samples 17, 16, 14, and 15). Sample 16 from Mason County also shows a shift in the cline and gophers from there

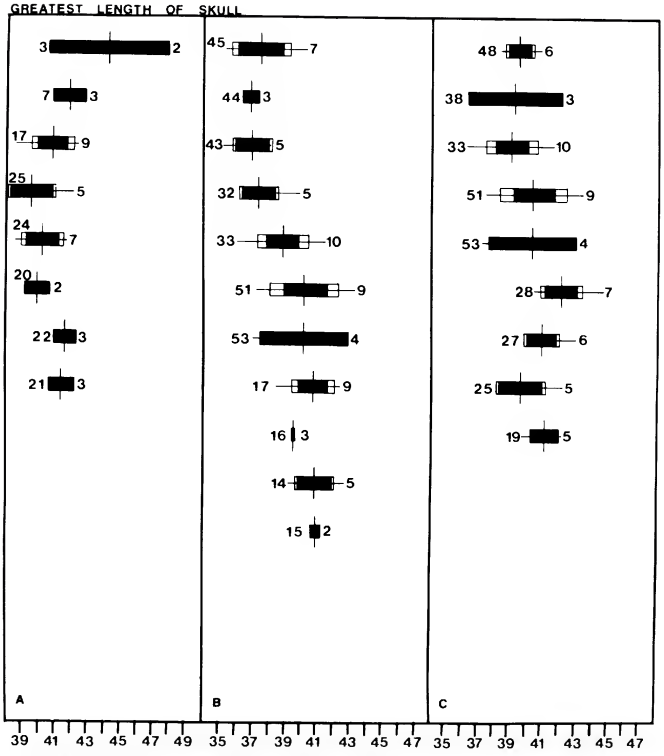

FIG. 12.—Clinal variation in greatest length of skull as expressed by Dice-Leraas diagrams. A, a north to south cline; E, east to west; and C, northeast to southwest. Measurements in millimeters (mm) are given along the horizontal axis. For each diagram, the horizontal line represents the range; the vertical line, the mean; the unshaded part of the rectangle, one standard deviation; and the shaded part of the rectangle, two standard errors of the mean. The locality number is to the left of the diagram and the sample size is to the right. For a key to samples, see Fig. 4.

average slightly smaller than those from samples to the east and west.

Clinal trends along the northeast-southwest transect are somewhat erratic with the exception of adjacent samples in rather localized areas. There is a gradual increase in size from specimens in Louisiana (sample 48) to sample 28 in central Texas. This situation is reversed and size decreases beginning with sample 28

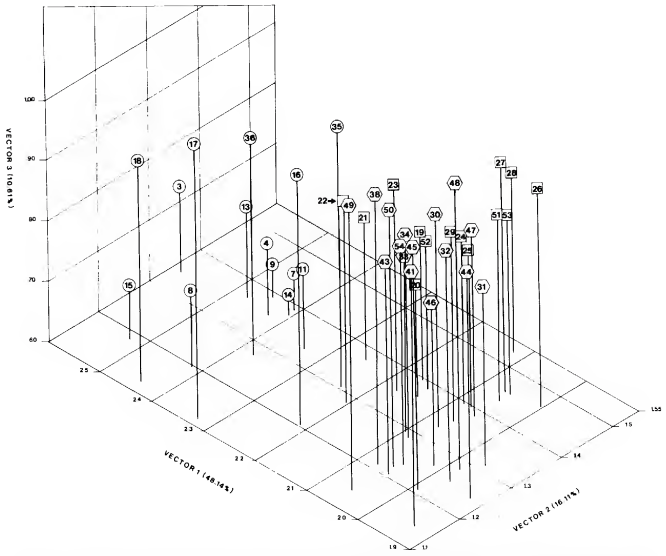

FIG. 13.—Three-dimensional projections of the 44 samples of *Geomys bursarius* females onto the first three canonical vectors. Circles represent the *lutescens* chromosome group; squares, the *attwateri* group; and hexagons, the *breviceps* group.

and continuing to sample 25; gophers in sample 19 from southern Texas are slightly larger than those represented by sample 25 from Guadalupe and Gonzales counties.

Multivariate Analysis

A multivariate analysis of variance (MANOVA) with projection onto canonical axes was used to describe the amount of variation among 44 samples by considering all characters simultaneously. Four different criteria (Wilk's Criterion, Roy's Maximum Root Criterion, Hotelling-Lawley's Trace, and Pilla's Trace) were used to test the hypothesis of no significant morphological difference among samples. All four tests produced F-values that were significant at $P<0.0001$; therefore, significant morphological differences among samples were assumed to exist.

The first three characteristic roots were significant at the $P<0.00001$ level and their canonical variates (vectors) accounted

TABLE 2.—*Variable coefficients for canonical variates I, II, and III with an estimate of the per cent influence of each character on each vector for 44 samples of* Geomys bursarius.

Character	Vector I		Vector II		Vector III	
	Variable Coefficient	Per cent Influence	Variable Coefficient	Per cent Influence	Variable Coefficient	Per cent Influence
Greatest length of skull	0.0877	22.52	−0.0104	4.05	−0.0364	16.14
Basal length	0.0386	8.99	−0.0247	8.74	0.0250	10.06
Breadth of rostrum	0.0775	4.54	−0.0291	2.59	0.0956	9.64
Zygomatic breadth	−0.0206	3.24	−0.0304	7.26	−0.0353	9.61
Interorbital breadth	−0.0230	0.83	0.0712	3.90	−0.0862	5.37
Breadth of braincase	−0.0553	6.06	0.0428	7.12	0.0309	5.85
Mastoidal breadth	0.0570	8.27	0.0589	12.97	−0.0534	13.38
Length of nasals	0.0564	4.69	−0.0087	1.10	0.0050	0.72
Length of rostrum	−0.1453	15.33	−0.0584	9.36	0.0885	16.15
Length of maxillary toothrow	−0.0090	0.47	0.0129	1.03	0.1032	9.41
Palatal length	−0.1163	17.13	0.1403	31.38	−0.0043	1.09
Palatofrontal depth	0.0876	7.93	−0.0764	10.50	0.0166	2.60

for the greatest percentage (VI, 48.14%; VII, 16.11%; and VIII, 10.61%) of the total variance. A three-dimensional plot of the means of the first three canonical variates is shown in Fig. 13. The per cent contribution of each character to these three canonical variates is given in Table 2.

Vector I primarily separates samples of the *lutescens* group (represented by circles) from those of the *attwateri* and *breviceps* groups (represented by squares and hexagons, respectively). Characters having the highest per cent influence on this vector reflect size, especially in skull length. Greatest length of skull, length of rostrum, and palatal length all exert a heavy influence on this vector. In all these characters, gophers of the *lutescens* group average larger than those from either the *attwateri* or *breviceps* groups. No overlap occurs among these three chromosomal complexes along Vector I; however, samples 21 and 22 of the *attwateri* group are closely associated with the larger gophers of the *lutes-*

cens group. No distinct geographic trends with regard to taxonomically recognized subspecies are indicated along this vector.

Vector II separates the *attwateri* group from the *breviceps* group. Characters with the highest influence on this vector are mastoidal breadth, palatal length, and palatofrontal depth. These measurements are wider and deeper in gophers of the *attwateri* group than those of the *breviceps* group. Overlap between these two groups along Vector II is evident in sample 47, which is associated with the *attwateri* group, although it has a *breviceps* karyotype. A slight geographic trend is evident among the *lutescens* group along this vector as illustrated by the separation of samples 8, 15 to 18, 35, and 36 from samples 3, 4, 7, 9, 11, 13, and 14. The former assemblage represents the recognized subspecies, *G. b. knoxjonesi* (samples 8 and 15), *G. b. texensis* (sample 16), *G. b. llanensis* (samples 17 and 18), and *G. b. major* (samples 35 and 36 from central Texas). The latter assemblage of samples represents *G. b. major* from northwestern Texas.

Vector III separates samples within each major chromosomal group. The primary contributing characters are greatest length of skull, length of rostrum, and mastoidal breadth. Most of the separation occurs within the *lutescens* group with samples 16, 17, 18, 35, and 36 (representing gophers from the eastern edge of the Edwards Plateau) splitting away from other samples of the group. No other geographic trends are indicated along this vector.

In order to compensate for some of the disadvantages of ordination techniques, a NT-SYS clustering analysis was performed with the 12 canonical variates from the MANOVA for each of the 44 samples of females. A phenogram diagraming the phenetic relationships of the 44 samples computed by clustering from distance matrices is presented in Fig. 14. Chromosomal and subspecific designations for each sample are also included. The distance phenogram is subdivided into three major clusters. Starting from the top, the first cluster includes samples 3, 4, 7 to 9, 11, 13 to 18, and 36, representing pocket gophers of the *lutescens* group. All of these samples, with the exception of sample 36 from McLennan and Hill counties in central Texas, represent specimens from the western part of the state. Within this first cluster, two subdivisions are evident. The first (samples 3, 13, 4, 7 to 9, 11, 14, and 15) represents two subspecies, *G. b. major* (chromosome race D) and *G. b. knoxjonesi* (chromosome race A), which are known from northwestern Texas. The second subcluster (samples 16 to 18 and 36) includes three subspecies, *G. b. texensis* (chromosome

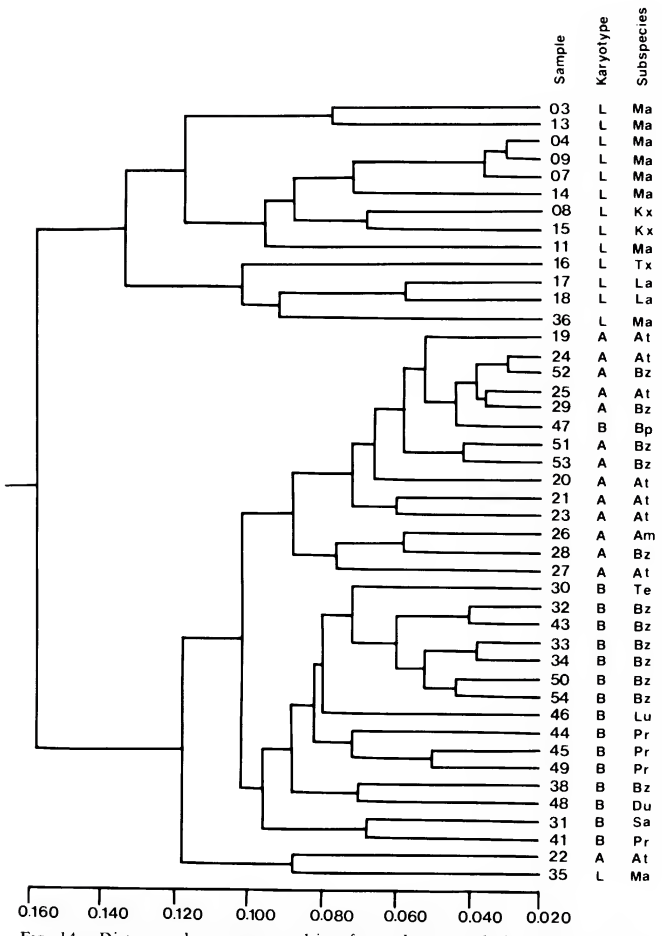

FIG. 14.—Distance phenogram resulting from cluster analysis of 44 samples of female *Geomys bursarius*. The cophenetic correlation coefficient is 0.797. L, A, and B represent the *lutescens*, *attwateri*, and *breviceps* chromosome groups. Subspecies abbreviations are as follows: Ma, *G. b. major*; Kx, *G. b. knoxjonesi*; Tx, *G. b. texensis*; La, *G. b. llanensis*; At, *G. b. attwateri*; Bz, *G. b. brazensis*; Bp, *G. b. breviceps*; Am, *G. b. ammophilus*; Te, *T. b. terricolus*; Lu, *G. b. ludemani*; Pr, *G. b. pratincola*; Du, *G. b. dutcheri*; and Sa, *G. b. sagittalis*.

race A), *G. b. llanensis* (chromosome race A), and *G. b. major* (chromosome race D), which are known from the eastern edge of the Edwards Plateau and central Texas.

The second major cluster contains samples 19 to 21, 23 to 34, 38, 41, and 43 to 54; these are pocket gophers from central and east Texas and Louisiana. Two main subclusters can be seen readily. One contains samples 19 to 21, 23 to 29, 47, and 51 to 53. All of these samples, with the exception of 47, belong to the *attwateri* group and are located in central and southern Texas. Sample 47 (from Mer Rouge, Louisiana) represents the subspecies, *G. b. breviceps*, and, although chromosomally identical to populations in eastern Texas with a *breviceps* group karyotype, it is morphologically similar to populations of larger gophers in central and southern Texas with an *attwateri* group karyotype. The arrangement of samples in this subcluster does not indicate that morphological differences exist between chromosomal races F and G or among the currently recognized subspecies occurring in this geographic area. Rather, it represents pocket gophers that are intermediate in size between western and eastern samples of *G. bursarius*, and that exhibit the *attwateri* group karyotype. The second subcluster is composed of samples 30 to 34, 38, 41, 43 to 46, 48 to 50, and 54 from central and eastern Texas that possess a *breviceps* group karyotype. A total of six described subspecies (*G. b. pratincolus*, *G. b. terricolus*, *G. b. dutcheri*, *G. b. brazensis*, *G. b. saggitalis*, and *G. b. ludemani*) are represented by these samples and it is evident from the clustering that only minor patterns of geographic differentiation exist among them.

The third major cluster contains two samples, 22 and 35, from diverse areas in the distribution of the species. Sample 22, of the *attwateri* chromosome group and the subspecies *G. b. attwateri*, is from Aransas County in southern Texas. Sample 35 is located in McLennan and Bosque counties in north-central Texas and represents the *lutescens* chromosome group and the subspecies *G. b. major*. The univariate analysis, as well as the MANOVA, shows a strong association of sample 22 with the samples of larger pocket gophers from the *lutescens* group. When considered independent of one another, samples 22 and 35 show similarities to samples possessing similar karyotypes. Sample 22 has an average distance coefficient of 0.105 to samples of the *attwateri* group as compared to 0.137 from samples of the *lutescens* group. Sample 35 has an average distance coefficient of 0.106 to samples of the *attwateri* group and 0.104 to samples of the *lutescens* group.

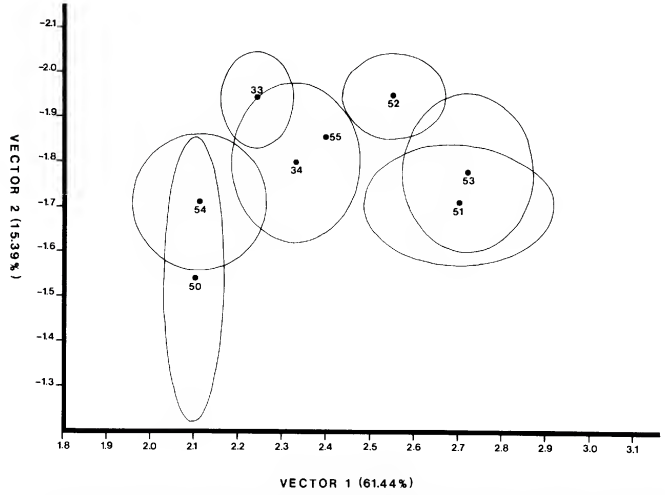

FIG. 15.—Projections of the first two canonical vectors for eight samples of *Geomys bursarius* females in Robertson, Brazos, Milam, and Burleson counties in east Texas. The numbers are positioned near the mean value for each sample in the character space; the ellipse surrounding each number represents one standard deviation around the mean.

To investigate the extent to which patterns of morphological variation shown throughout the state compare to variation in a more localized area, eight samples (50 to 55, 33, and 34) from four counties in the east Texas study area were analyzed using a MANOVA (Fig. 15).

The first two canonical variates account for 76.83 per cent (VI, 61.45%; and VII, 15.39%) of the total variation. Fig. 15 gives a two-dimensional plot of the means of the first two canonical variates. The ellipsoid curves represent one standard deviation to either side of the mean for each vector. The per cent infuence of each character is given in Table 3.

Characters most influential along Vector I are palatal length, mastoidal breadth, breadth of braincase, and palatofrontal depth. Two main groups of gophers can be distinguished. The first consists of samples 50, 54, 55, 33, and 34; these represent the *breviceps* group karyotype and the subspecies *G. b. brazensis*. The second group, samples 52, 53, and 51, represents the *attwateri* group karyotype and the subspecies *G. b. brazensis*. As can be

TABLE 3.—*Variable coefficients for canonical variates I and II with an estimate of the per cent influence of each character on each vector for eight samples of* Geomys bursarius *in a four county area.*

Character	Vector I		Vector II	
	Variable Coefficient	Per cent Influence	Variable Coefficient	Per cent Influence
Greatest length of skull	0.2597	18.53	−0.2513	30.73
Basal length	−0.4289	27.81	0.0305	3.39
Breadth of rostrum	−0.0007	0.01	−0.1982	5.53
Zygomatic breadth	−0.1670	7.46	−0.0192	1.47
Interorbital breadth	−0.1173	1.21	−0.2207	3.88
Breadth of braincase	0.0330	1.04	0.1768	9.49
Mastoidal breadth	0.1036	4.22	−0.0831	5.80
Length of nasals	−0.1559	3.59	−0.1370	5.40
Length of rostrum	−0.1838	5.42	0.4768	24.08
Length of maxillary toothrow	0.2200	3.29	0.1069	2.73
Palatal length	0.6087	25.10	0.0239	1.69
Palatofrontal depth	−0.0915	2.32	0.1336	5.81

seen by the ellipses, considerable overlap occurs within each chromosomal group but none between the two groups. Although the degree of difference between these two complexes is rather small, samples of the *attwateri* group average larger than those of the *breviceps* group in measurements that exert the greatest influence on this vector. The morphological variation along this vector does not separate the two chromosomal races of the *attwateri* group karyotype, which are represented by samples 51 (chromosome race F) and 53 (chromosome race G), nor does it indicate the intermediate size of the intergrades between these two races (represented by sample 52).

DISCUSSION

Chromosomal Variation

In light of the chromosomal variation found within *Geomys bursarius*, two questions concerning the systematics of this species

in Texas need to be answered. First, does the chromosomal divergence found indicate that more than one species is represented in the state? Second, how does this variation relate to currently recognized subspecies of *G. bursarius*?

Recent studies of chromosomal variation throughout the range of *G. bursarius* have repeatedly pondered the matter of populational relationships within this species (Hart, 1971; Kim, 1972; Hart, 1978). Both Hart and Kim concluded that some of the chromosomal divergence seen within *G. bursarius* could represent karyotypic differences among cryptic species. Studies of other fossorial animals also have indicated that karyotypic differences may be indicative of species-level differentiation (Patton and Dingman, 1968; Patton, 1973; Reig and Kiblisky, 1969; Thaeler, 1968*a*, 1968*b*, 1974; Wahrman *et al.*, 1969). However, as revealed by recent investigations of contact zones between chromosomally distinct populations, not all karyotypic differences warrant species recognition (see Baker *et al.*, 1975, for a review). According to Baker *et al.* (1975), and Thaeler (1974), the true role of karyotypic variation in speciation can be determined only by examining interactions of chromosomal forms in zones of contact.

To date three contact zones between chromosomal forms of *G. bursarius* have been studied (Hart, 1971; Pembleton and Baker, 1978). Two of these involve chromosomal races considered in this study. Hart (1971) examined a contact zone between chromosomal races D and E in Oklahoma. From this preliminary study, he concluded that some genetic exchange between these chromosomal races was occurring; however, he did indicate that a more detailed analysis was needed. Pembleton and Baker (1978) surveyed a contact zone between chromosomal races B and C in New Mexico. They found a low level of F_1 hybrid production as well as reduced hybrid fertility but refrained from concluding that species level differences existed because of the presence of an apparently fertile F_1 female and the inability to detect backcross individuals with the use of chromosomal differences.

No contact zones between chromosomal races occurring in eastern Texas have been examined prior to this study. Hart (1971) suggested that chromosomal differences between races G and E could be related to specific differences and that studies of areas of contact should elucidate this. The two contact zones found in eastern Texas during our work reveal two different types of interactions. The zone of contact between races F and G in Milam County involves chromosomal races that differ in fundamental

number but not in diploid number. This chromosomal variation involves the presence or absence of a pair of biarmed chromosomes. Even though the two races maintain distinct distributions, F_1 hybrid formation is high (41 per cent), suggesting extensive interbreeding. Unfortunately, the degree of gene exchange cannot be determined because of an inability to recognize backcross individuals. Chromosomal diversity between these two races could be indicative of subspecific differentiation, although an alternative interpretation is possible: the second arms of the two biarmed chromosomes in race F could be heterochromatic, in which case no meiotic penalties would result during interbreeding with race G. Baker and Genoways (1975) considered chromosomal differences between races A and B to represent such a mechanism and, therefore, relegated them to the same subspecies (*G. b. knoxjonesi*). Further studies using electrophoresis and chromosome banding are needed before any conclusions can be drawn concerning the amount of gene flow between chromosomal races F and G. However, even if gene flow is reduced, two important questions still remain to be answered. First, how did the chromosomal differences arise, and second, why do they persist in this particular area of Texas?

The second contact zone located during this study involves chromosomal races E, F, and G. However, only one F_1 hybrid with an intermediate karyotype between races E and G has been found, and none between races E and F. This indicates considerable reduction in gene exchange between races F and G, which are found west of the Brazos, and race E, occurring primarily east of the Brazos River. This is expected because chromosomal differences between these two major groups include differences in both diploid and fundamental numbers. Similar instances, involving this magnitude of chromosomal differentiation, have been reported for other pocket gopher populations (Patton, 1973; Thaeler, 1974). A taxonomic decision on the specific status of these two chromosomal races will be deferred until further studies can be conducted in this contact zone.

Davis (1940) recognized nine subspecies throughout central and eastern Texas and western Louisiana; however, chromosomal variation in these areas does not correspond to the ranges of the subspecies defined by Davis. This is especially true for chromosomal races E, F, and G. As indicated in the chromosomal analysis, race E persists throughout parts of central Texas, eastern Texas, eastern Oklahoma, and western Arkansas and Louisiana

with no apparent variation. This area spans the ranges of seven described subspecies. Likewise, the ranges of chromosomal races F and G correspond to three subspecies.

Distribution of Chromosomal Races

The distributional patterns of chromosomal races A, B, C, and D occurring in northwestern Texas have been investigated previously by Baker *et al.* (1973). Hart (1971) and Kim (1972) conducted preliminary studies on the overall distribution of chromosomal races D, E, F, and G throughout Texas and the neighboring states; however, neither author described the details of this distribution, although they did indicate that all four chromosomal races inhabit eastern Texas. As a result, investigations during this study were directed toward determining the distributional patterns of chromosomal races D, E, F, and G (in an 11 county study area) in eastern Texas (Fig. 2).

Several distributional patterns are evident within and among chromosomal races D, E, F, and G in the study area. Although local populations may conform to an island type distribution, the chromosomal races are, for the most part, continuously distributed wherever suitable soils exist. At the edge of their ranges along the Brazos River, the races maintain a linear distribution throughout alluvial soils close to the water. In the case of race D in McLennan County and race E in Falls County, this distribution is restricted to areas along both sides of the river and can best be described as a double dendritic distribution, as defined by Kennerly (1964). With few exceptions, the Brazos River represents a boundary that separates race E on the east bank from races F and G on the west bank. No localities have been found where the chromosomal races are sympatric, although the ranges of certain races approach one another at several localities and actually contact at two places. In all situations where chromosomal races are not in contact, either the Brazos River or indurate soils exist between them.

Factors Affecting Distribution of Chromosomal Races

Previous studies have shown that the distribution of *Geomys bursarius* is correlated with sandy soils and that clay soils act as an effective barrier to dispersal (Davis, 1938, 1940; Davis *et al.*, 1938; Russell, 1953; Miller, 1964; Downhower and Hall, 1966). Major rivers also have been discussed as potential barriers to the distribution of this pocket gopher (Davis, 1940; Kennerly, 1954;

Miller, 1964). Both of these factors were found to influence the distribution of chromosomal races D, E, F, and G in eastern Texas.

Overall distribution patterns of the four chromosomal races are influenced directly by certain soil associations (Fig. 9). Chromosomal races were found consistently in soils ranging from loam to sandy loam; soils consisting of clay loam and clay appeared to act as effective barriers. Chromosomal races along the Brazos River were situated in isolated areas of well-drained alluvial soils or soils containing a high sand content. As indicated by Kennerly (1954, 1963), alluvial soils provide avenues for dispersal through areas of otherwise unfavorable soils. This is the case in McLennan and Falls counties where chromosomal races D and E occur almost exclusively in the Miller-Norwood-Yahola soil association. Dispersal of chromosomal race D into McLennan County probably was from counties (Hill and Bosque) to the north by way of these soils. Dispersal of race E from Falls County along alluvial soils also could explain the occurrence of that chromosomal race on the west bank of the Brazos River in Milam County. Support for this idea can be shown by the fact that race E appears in an isolated area representing the southernmost extension of the Miller-Norwood-Yahola soil association in Milam County. Barriers between chromosomal races were represented by two soil associations. The Trinity-Catalpa association separates chromosomal races E and F in Milam County and the Miller-Norwood separates races E and G in Burleson County.

From studies of chromosomal races in areas of contact, some authors have indicated differences in soil preference between chromosomal races (Patton, 1973; Pembleton and Baker, 1978). No differences were found among chromosomal races D, E, F, and G. Both contact zones examined in the course of this study failed to reveal any chromosomal race having preference for a particular soil type. As indicated by the clustering analysis and plots on the soil triangle, the distribution of chromosomal races overlapped with respect to the four soil parameters measured (per cent of clay, silt, sand, and moisture). The only differences found involved samples of race E, which occurred in the Miller-Norwood association in Burleson County and parts of Robertson County.

Miller (1964) noted that in Colorado *G. bursarius* was adapted to the narrowest range of soil conditions and was limited in distribution by soil tolerances. Likewise, Downhower and Hall

(1966) indicated a direct influence of the per cent clay and sand on the distribution of *G. bursarius* in Kansas. The distribution of chromosomal races D, E, F, and G in eastern Texas is governed, we think, by three soil parameters, namely per cent sand, clay, and moisture. In general, chromosomal race E has a wider tolerance to these parameters than the other three; it occupies soils with a higher than average percentage of clay, sand, and moisture. This wider tolerance is related to the presence of these pocket gophers in the Miller-Norwood association in Burleson County. With the exclusion of these samples, the general distribution of all the chromosomal races corresponds to soils having a low clay content, low soil moisture, and high sand content (Table 1).

The Brazos River is a significant factor affecting the distribution of the four chromosomal races in eastern Texas. It not only provides an avenue for dispersal through alluvial soils along its banks for chromosomal races occurring in Falls and McLennan counties, but it also acts as an effective barrier to the distribution of chromosomal races E, F, and G in the floodplain. Two major questions may be posed regarding the importance of this river to the distribution of the plains pocket gopher. First, why is the Brazos River a barrier in the floodplain? Second, how does the Brazos River affect the dispersal of chromosomal races in the floodplain?

As indicated by Davis (1940), rivers that cut transversely across the range of pocket gophers and that have a good flow of water at all seasons could act as effective barriers. As seen in Fig. 9, the Brazos River pursues such a course across the range of chromosomal races E, F, and G. The Brazos River is also one of the major waterways in Texas. Average annual streamflow for the years 1940 to 1965 was seven million acre-feet (Texas Water Development Board, 1968). The Brazos has a maximum discharge and minimum flow equal to, if not slightly larger than, the Trinity, Nueces, and Sabine rivers in eastern Texas, and greatly exceeds that of the Colorado, San Jacinto, and Navasota rivers.

Kennerly (1963) indicated that swimming probably represents the major means of dispersal across waterways, and that width of a river dictates, therefore, the amount of dispersal that can occur. Grinnel (1914) and Goldman (1931, 1935) studied the distribution of pocket gophers along the Colorado River in the Southwest and noted that it, in combination with its floodplain, constitutes a barrier to pocket gopher distribution. Both authors concluded

that transfers of land from one side to the other could account for the distribution of pocket gophers along the lower part of the Colorado. The dispersal of race E into Burleson County is best explained by this type of action. Oxbow lakes (which represent minor land transfers) cannot account for the wide distribution of race E; however, the major land transfer represented by Old River correlates well with this distributional pattern. Two alternative explanations may be considered for the dispersal of race E in Milam County. First, the oxbow lake in the vicinity of race E may have been a source for dispersal of pocket gophers from Robertson County. Second, dispersal could have occurred from the north in Falls County along the Miller-Norwood-Yahola soil association.

The above information may explain the appearance of chromosomal race E on the west bank of the Brazos; however, the factor or factors restricting races F and G to the west bank are not as obvious. Two possible explanations are: 1) the occurrence of races F and G into the vicinity of the Brazos may be the result of a relatively recent dispersal into the area when compared to race E; 2) races F and G may be limited in their distribution by race E.

Morphological Variation

As stated by Jackson (1971), changes in chromosome morphology do not necessarily indicate similar changes in external phenotypic characters; however, the two may be partially correlated. This seems to be the case with *Geomys bursarius* in Texas where morphological differences, for the most part, correspond with chromosomal differences. This correlation is especially good when gross chromosomal changes, such as those represented by the *lutescens*, *attwateri*, and *breviceps* chromosomal groups, are considered.

Single morphological characters, as shown in the analysis of clinal variation, cannot explain entirely the patterns of geographic variation in *G. bursarius*. They reveal a clinal increase in size from east to west across Texas corresponding to the regions occupied by the three chromosomal groups. However, major morphological separation was not apparent in the univariate analysis. Multivariate statistical techniques provided a better means for analyzing the variation seen with *G. bursarius*.

Four generalizations can be made from both the MANOVA and cluster analyses used to interpret morphological variation of *G. bursarius* in Texas. First, three main groups of pocket gophers

can be recognized on the basis of morphology and karyotype. These are the large pocket gophers from northwestern Texas with the *lutescens* group karyotype, the intermediate-sized gophers from central and southern Texas with the *attwateri* group karyotype, and the small gophers from central and eastern Texas with the *breviceps* group karyotype. One important aspect to note when viewing this overall trend is that there is more morphological variation among samples with the *lutescens* group than there is between samples of the *attwateri* and *breviceps* complexes. This correlates with a greater amount of chromosomal variation and polymorphism among chromosomal races of the *lutescens* group. Second, within each chromosomal group, certain chromosomal races are not distinguished by morphological differences. Variation with the *lutescens* group, for example, does not effectively separate chromosomal races A, B, C, and D into morphologically distinct units. Chromosomal races F and G of the *attwateri* group also are morphologically indistinguishable. Third, peripheral isolates of certain chromosomal races are morphologically distinctive. Sample 47 (race E) occurs at the easternmost part of the range of chromosomal race E in an isolated area of Louisiana. Individuals in this sample are morphologically larger in size than those in adjacent samples of race E, and are more like the intermediate-sized gophers of the *attwateri* group. Sample 22 is the southernmost extension of chromosomal race G. It occupies an isolated area along the coast in Aransas County. In size, it resembles the larger pocket gophers of the *lutescens* group. Samples 16, 17, and 18 occur in isolated areas of the Edwards Plateau. Karyotypically, they are related to chromosomal race A; however, morphologically, they are nearer in size to pocket gophers of race D, as represented by samples 35 and 36 from the eastern edge of the Edwards Plateau. Samples 35 and 36 also are the southernmost extension of chromosomal race D in central Texas. These samples are the smallest pocket gophers of the *lutescens* group. Fourth, a large numer of subspecies recognized prior to our study in central and eastern Texas do not reveal either morphological or karyological differences. These include the *breviceps* chromosome group representing the subspecies *G. b. brazensis*, *G. b. tericolus*, *G. b. sagittalis*, *G. b. ludemani*, *G. b. pratincolus*, *G. b. dutcheri*. The only exception is sample 47, *G. b. breviceps*, which is noticeably larger in size. The subspecies *G. b. ammophilus*, which occurs in central Texas, is allied karyotypically with chromosomal race G and is morphologically similar to other samples represented by this race.

The morphological variation occurring throughout the state also is evident when a more localized area is considered. This is illustrated by the separation of the *attwateri* and *breviceps* groups into morphologically distinct units in the 11-county study area of eastern Texas.

Although chromosomal variation does not coincide completely with morphological variation, the two do correspond in many respects. This supports use of the karyotype as another character for grouping individuals in morphological analyses, especially within species demonstrating chromosomal variation throughout their geographic range. The morphological and chromosomal concordance seen within *G. bursarius* indicates that, at least in central and eastern Texas, misinterpretations have been made in the recognition of subspecies. It also implies that the three chromosomal groups may be different genetic units. However, we have retained these as a single interbreeding unit (under the name *G. bursarius*) until further studies from zones of contact can be conducted.

Taxonomic Conclusions

In recognizing subspecies, we have followed Mayr's (1969) definition that "a subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species." We interpret the morphological and karyological data as revealing seven distinct sub units of *Geomys bursarius* present in Texas and adjacent states (Fig. 16). Table 4 gives some mean values for the major morphological characters distinguishing the seven subspecies.

The first subspecies is characterized by a diploid number of 74 and a fundamental number of 70. It represents the largest individuals of chromosomal race E and occurs in Mer Rouge, Louisiana. To this group the trinomial name *G. b. breviceps* Baird applies. Reasons for retaining this subspecies have to do with its disjunct distribution and large size. Another subspecies, *G. b. sagittalis* Merriam, ranges from the Brazos River in central Texas, eastward through extreme eastern Texas and western Louisiana, and northward into eastern Oklahoma and Arkansas. This subspecies encompasses samples formerly referred to as *G. b. brazensis, G. b. sagittalis, G. b. terricolus, G. b. ludemani, G. b. pratincolus,* and *G. b. dutcheri.* Morphological and karyotypic analyses show these six taxa to be indistinguishable from one another. They all represent chromosomal race E and have a diploid number of 74

and a fundamental number of 70. In size, they are the smallest subspecies of *G. bursarius*. The trinomen *G. b. sagittalis* Merriam has priority over the other five names. The third subspecies, *G. b. attwateri* Merriam, occupies a range from southern Texas near the San Antonio River to central Texas along the west bank of the Brazos River. The distribution of this subspecies coincides with that formerly recognized for *G. b. attwateri*, *G. b. ammophilus*, and *G. b. brazensis*; the oldest available name is *G. b. attwateri* Merriam. *G. b. attwateri*, as defined here, is represented by chromosomal races F and G and has a diploid number of 70 and a fundamental number of either 70 or 72. It also is characterized as being of intermediate size. The four remaining subspecies, *G. b. major*, *G. b. llanensis*, *G. b. texensis*, and *G. b. knoxjonesi* are the largest pocket gophers and occupy parts of central and western Texas, western Oklahoma, and eastern New Mexico. From McLennan County in central Texas, *G. b. major* Davis is characterized by a diploid number of 72 and a fundamental number of 70; however, some populations throughout its range exhibit chromosomal polymorphisms ranging from a diploid number of 70 to 72 with a fundamental number of 70. *G. b. llanensis* Bailey and *G. b. texensis* Merriam have limited distributions along the eastern edge of the Edwards Plateau in Llano and Mason counties, respectively. These two karyotypically indistinguishable subspecies show morphological differences but these are less pronounced than those seen among *G. b. attwateri*, *G. b. sagittalis*, and *G. b. major* from eastern Texas. At this time we retain these two subspecies with the hope that future studies will reveal more clearly the systematic relationships between them. The last subspecies, *G. b. knoxjonesi* Baker and Genoways, occurs in western Texas and eastern New Mexico. Baker and Genoways (1975) characterized this race as being both chromosomally and morphologically more closely related to *G. b. llanensis* and *G. b. texensis* than to adjacent populations of *G. b. major*. Our study of both the MANOVA and NT-SYS clustering analyses indicate *G. b. knoxjonesi* to be morphologically similar to *G. b. major* and less similar to populations of *G. b. llanensis* and *G. b. texensis*. There are two explanations for this discrepancy. First, Baker and Genoways placed high value on length of tail in distinguishing this subspecies from *G. b. major*, but we did not include external measurements in our analysis. Second, our sample of *G. b. knoxjonesi* consisted of only six individuals from Texas. These variations in procedure could account for the

TABLE 4.—*Comparison of the mean differences in selected measurements for adult females among seven subspecies of* Geomys bursarius. *Minimum and maximum values are given in parentheses.*

Subspecies	*N*	Greatest length of skull	Length of rostrum	Palatal length	Mastoidal breadth	Palotofrontal depth
G. b. breviceps	10	39.7	16.3	23.1	22.3	13.8
		(38.6-40.5)	(15.7-17.1)	(22.2-24.0)	(21.8-22.9)	(13.3-14.3)
G. b. sagittalis	74	38.2	15.7	21.8	21.4	13.6
		(34.0-41.7)	(13.7-17.7)	(19.3-24.0)	(18.9-23.9)	(12.4-15.0)
G. b. attwateri	71	40.6	16.9	23.8	23.1	14.3
		(37.1-44.6)	(15.1-19.1)	(21.0-27.8)	(21.2-25.4)	(12.8-15.7)
G. b. major	49	42.3	17.1	24.0	24.1	14.7
		(39.3-46.0)	(14.7-20.6)	(22.2-26.6)	(22.2-26.7)	(13.8-16.3)
G. b. llanensis	11	40.9	17.1	22.8	22.1	14.5
		(38.5-42.4)	(15.8-18.2)	(20.8-24.0)	(21.3-24.1)	(13.3-15.7)
G. b. texensis	3	39.6	15.9	22.1	21.7	13.6
		(39.5-39.7)	(15.7-16.1)	(21.8-22.4)	(21.6-21.8)	(13.3-13.9)
G. b. knoxjonesi	6	39.5	15.2	21.4	22.8	14.0
		(38.1-41.1)	(13.9-16.3)	(20.5-22.6)	(22.0-23.8)	(13.4-14.7)

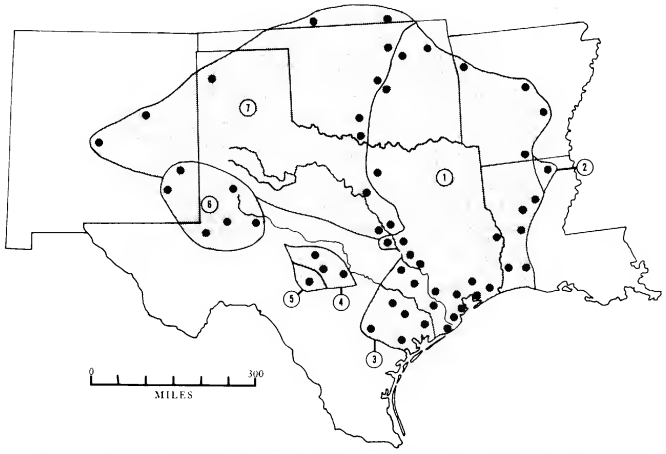

FIG. 16.—Geographic distribution of subspecies of *Geomys bursarius* in Texas and adjacent states: 1) *G. b. sagittalis*; 2) *G. b. breviceps*; 3) *G. b. attwateri*; 4) *G. b. llanensis*; 5) *G. b. texensis*; 6) *G. b. knoxjonesi*; and 7) *G. b. major*.

difference in results and we, therefore, retain *knoxjonesi* as a distinct subspecies.

Subspecific recognition of sample 22, which represents a peripheral isolate of *G. b. attwateri*, does not seem appropriate at this time. Further studies need to be conducted in this area before any taxonomic conclusions can be made.

ACCOUNTS OF SUBSPECIES

Geomys bursarius breviceps Baird

1855. *Geomys breviceps* Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:335.
1951. *Geomys bursarius breviceps*, Baker and Glass, Proc. Biol. Soc. Washington, 64:57, 13 April.

Type locality.—Prairie Mer Rouge, Louisiana.

Distribution.—Known only from the vicinity of Mer Rouge, Morehouse Parish, Louisiana.

Comparisons.—Compared with *G. b. sagittalis*, *G. b. breviceps* is larger in most cranial measurements (see Table 4): greatest length of skull averaging 39.7 mm. as opposed to 38.2 mm.; rostrum seldom less than 16.3 mm.; palatal length not less than 22.2 mm.; skull wider with mastoidal breadth not less than 21.8 mm. *G. b. breviceps* differs from *G. b. attwateri* in having: skull shor-

ter with greatest length seldom exceeding 40.5 mm.; length of rostrum averaging 16.3 mm. as opposed to 16.9 mm.; width of skull not exceeding 22.9 mm.; shallower skull with palatofrontal depth not exceeding 14.3 mm.; a diploid number of 74 and a fundamental number of 70 as opposed to a diploid number of 70 and fundamental numbers of 70 or 72 for *G. b. attwateri*.

Remarks.—*G. b. breviceps* represents a peripherally-isolated population of *G. bursarius*. Chromosomally, it is indistinguishable from *G. b. sagittalis*, and morphologically, it is intermediate in size between *G. b. sagittalis* from eastern Texas, western Louisiana, and Arkansas, and *G. b. attwateri* from central and southern Texas. Most individuals of this subspecies also have a melanistic coat color not found in the other subspecies.

Specimens examined (12).—LOUISIANA: *Morehouse Parish*: 1 mi. W Mer Rouge, 3 (TCWC); 1 mi. S Mer Rouge, 7 (TCWC); 2.5 mi. S Mer Rouge, 1 (TCWC); 3.5 mi. S Mer Rouge, 1 (TCWC).

Geomys bursarius sagittalis Merriam

1895. *Geomys breviceps sagittalis* Merriam, N. Amer. Fauna, 8:134, 31 January.
1938. *Geomys breviceps brazensis* Davis, J. Mamm., 19:489, 14 November.
1940. *Geomys breviceps dutcheri* Davis, Texas Agr. Exp. Sta. Bull., 590:12, 23 October.
1940. *Geomys breviceps ludemani* Davis, Texas Agr. Exp. Sta. Bull., 590:19, 23 October.
1940. *Geomys breviceps pratincolus* Davis, Texas Agr. Exp. Sta. Bull., 590:18, 23 October.
1940. *Geomys breviceps terricolus* Davis, Texas Agr. Exp. Sta. Bull., 590:17, 23 October.
1951. *Geomys bursarius sagittalis*, Baker and Glass, Proc. Biol. Soc. Washington, 64:57, 13 April.

Type locality.—Clear Creek, Galveston Bay, Galveston County, Texas.

Distribution.—From the Brazos River in central Texas throughout eastern and northern Texas, western Louisiana, southwestern Arkansas and eastern Oklahoma.

Comparisons.—For a comparison of *G. b. sagittalis* with *G. b. breviceps* see account of the latter. *G. b. sagittalis* differs from *G. b. attwateri* as follows: smaller size; length of skull shorter, averaging 38.2 mm. as opposed to 40.6 mm.; width of skull narrower; depth of skull shallower; diploid number of 74 and fundamental number of 70 as opposed to a diploid number of 70 and a fundamental number of either 70 or 72, for *G. b. attwateri*. From *G. b. major*, *G. b. sagittalis* differs as follows: smaller size; skull shorter in length; mastoidal breadth averaging 21.4 mm. as opposed to

24.1 mm.; depth of skull not exceeding 15.0 mm.; diploid number of 74 with fundamental number of 70 as opposed to diploid numbers of 70, 71, or 72 and fundamental number of 70 for *G. b. major*; X-chromosome submetacentric as opposed to acrocentric.

Remarks.—*G. b. sagittalis* is the smallest subspecies of *G. bursarius* in Texas. Generally, size in this species increases from east to west across Texas with the smallest pocket gophers occurring in eastern and central Texas. Davis (1938) recognized six subspecies within the range here attributed to *G. b. sagittalis*; however, our analyses revealed neither morphological nor chromosomal differences among any of the previously recognized subspecies. Davis (1938) also depicted the range of *G. b. sagittalis* as extending into central Texas near the Colorado River. Both chromosomal and morphological analyses indicate that the range of *G. b. sagittalis* does not extend west of the Brazos River except in localized areas in Burleson and Milam counties.

Specimens examined (199).—LOUISIANA: *Caddo Parish*: 2 mi. SW Shreveport, 6 (TCWC). *Webster Parish*: 5 mi. E Minden, 2 (TCWC); 4 mi. E Minden, 1 (TCWC). *Lincoln Parish*: 4 mi. E Cloudrant, 1 (TCWC). *Vernon Parish*: 4.2 mi. NE Louisiana border, Fm. Rd. 692, 1 (TCWC); 2 mi. E Texas-Louisiana border, Fm. Rd. 692, 1 (TCWC). *Beauregard Parish*: De Ridder, 1 (TCWC). TEXAS: *Newton Co.*: Newton, 5 (TCWC); 12 mi. NE Burksville, 1 (TCWC); 13 mi. NE Kirbyville, 1 (TCWC); 3 mi. NE Kirbyville, 1 (TCWC). *Jasper Co.*: 2.2 mi. N Buna, 1 (TTU); 7 mi. SW Buna, 1 (TCWC); 15 mi. N Jasper, 1 (TCWC); Clark Farm Study Site, 1 (TCWC). *Sabine Co.*: 3 mi. N Bronson, 1 (TCWC); 2 mi. N Bronson, 1 (TCWC); 7 mi. W Hemphill, 1 (TCWC); 8 mi. W Hemphill, 1 (TCWC). *San Augustine Co.*: 8 mi. S San Augustine, 1 (TCWC). *Shelby Co.*: 7 mi. S Center, 1 (TCWC); 10 mi. S Center, 1 (TCWC). *Panola Co.*: 4 mi. NE Carthage, 2 (TCWC). *Rusk Co.*: 12 mi. S Hendrickson, 1 (TCWC). *Nacogdoches Co.*: 11 mi. SW Nacogdoches, 1 (TCWC); 5 mi. S Nacogdoches, 1 (TCWC). *Tyler Co.*: 17 mi. S Woodville, 3 (TCWC). *Hardin Co.*: 5 mi. N Kountze, 2 (TCWC); Silsbee, 1 (TTU). *Polk Co.*: 3 mi. W Livingston, 2 (TCWC). *Upsher Co.*: 1 mi. W Gilmer, 1 (TCWC); 7 mi. W Gilmer, 2 (TCWC). *Wood Co.*: 4 mi. S Winnsboro, 2 (TCWC); Mineola, 1 (TCWC). *Jefferson Co.*: 7 mi. SW Fannett, 3 (TCWC). *Chambers Co.*: 4.7 mi. N Anahuac, 1 (TTU). *Liberty Co.*: 2 mi. E Liberty, 4 (TCWC). *Anderson Co.*: Palestine, 1 (TCWC); 1 mi. W Palestine, 1 (TCWC). *Trinity Co.*: 13.5 mi. S, 3.5 mi. W Grove, 1 (TTU); Trinity, 1 (TTU). *San Jacinto Co.*: 3 mi. SW Evergreen, 1 (TCWC); 2 mi. W Evergreen, 1(TCWC); Shepherd, 4 (TTU); 2 mi. S Shepherd, 2 (TTU). *Montgomery Co.*: 2 mi. S Conroe, 3 (TCWC); 5 mi. W conroe, 1 (TCWC); 5 mi. S Conroe, 1 (TCWC); 1.6 mi. E Decker Prairie, 3 (TCWC); 2 mi. E Decker Prairie, 1 (TCWC); 7 mi. E Tomball, 1 (TCWC). *Harris Co.*: 4 mi. N Huffman, 1 (TCWC); 3 mi. N Mason's Bay, Laporte, 1 (TCWC); 3 mi. NE Webster 1 (TCWC). *Galveston Co.*: 1 mi. N Texas City, 4 (TCWC); 2 mi. N Texas City, 2 (TCWC); 1.4 mi. S, 2.3 mi. W Hitchcock, 2 (TTU). *Walker Co.*: 6 mi. S Huntsville, 1 (TCWC); 17 mi. W on the Huntsville-Bedias Rd., 1 (TCWC). *Grimes Co.*: 2 mi. E Shiro, 1 (TCWC); 5 mi. E Kurten, 1 (TCWC); 2 mi. E Carlos, Hwy. 30, 1 (TCWC); 0.8 mi. E Carlos, 2 (TTU). *Leon Co.*: 13 mi. E Centerville, 1 (TCWC); 7

mi. N Normangee, 2 (TCWC). *Brazos Co.*: TAMU, College Station, 6 (TCWC); 1 mi. S Hwy. 30-Hwy. 6 intersection, College Station, 2 (TCWC); 6.2 mi. S College Station, 1 (TCWC); 7 mi. S College Station, 1 (TCWC); 2 mi. SE College Station, 1 (TCWC); 4 mi. SE College Station, 1 (TCWC); 3 mi. SW College Station, 1 (TCWC); 6 mi. SW College Station, 3 (TCWC); 7 mi. SW College Station, 2 (TCWC); 3 mi. E Kurten, 1 (TCWC); Bryan, 1 (TCWC); 0.7 mi. E Brazos River Bridge, Hwy. 21 (TCWC); 0.2 mi. E Brazos River Bridge, Hwy. 21, 1 (TCWC). *Robertson Co.*: 1 mi. W Bremond, 2 (TCWC); Sander's Turkey Farm, 1 (TCWC); 7 mi. NW Hearne, 1 (TCWC); 4 mi. NE Hearne, 1 (TCWC); 4 mi. W Hearne, 1 (TCWC); 5 mi. W Hearne, 1 (TCWC); 7 mi. N, 1 mi. W Hearne, 1(TCWC); 0.5 mi. N Calvert, Hwy. 6, 2 (TCWC); 2.3 mi. N Calvert, Hwy. 6, 2 (TCWC); 2.3 mi. N, 1.6 mi. W Calvert, 1 (TTU); 3.4 mi. N, 2 mi. W Calvert, 7 (TTU); 5 mi. SW Calvert, 1 (TCWC); 7 mi. S Calvert, Fm. Rd. 1644, 1 (TCWC); 8 mi. S Calvert, Fm. Rd. 1644, 1 (TCWC); 3.6 mi. SW Bremond, 1 (TCWC); 0.3 mi. S Eloise, Fm. Rd. 1373, 1 (TCWC). *Falls Co.*: 2.8 mi. SW Marlin, Fm. Rd. 712, 1 (TCWC); 3.1 mi. SW Marlin, Fm. Rd. 712, 1 (TCWC); 12.3 mi. SE Marlin, Hwy. 6, 1 (TCWC); 0.3 mi. S Cedar Springs, Fm. Rd. 2027, 1 (TCWC); 1.7 mi. S Cedar Springs, Fm. Rd. 2027, 1 (TCWC); 4.4 mi. N Cedar Springs, Fm. Rd. 2027, 1 (TCWC); 1.9 mi. SE Reagen, Hwy. 6, 2 (TCWC); 0.5 mi. E Highbank, Fm. Rd. 413, 1 (TCWC); 1 mi. N Eloise, Fm. Rd. 1373, 1 (TCWC); 2.3 mi. E Wilderville, Fm. Rd. 413, 1 (TCWC); 3.8 mi. E Wilderville, Fm. Rd. 413, 1 (TCWC); 0.8 mi. N Wilderville, Fm. Rd. 2027, 1 (TCWC); 0.6 mi. S Wilderville, Fm. Rd. 2027, 1 (TCWC); 0.4 mi. E Chilton, Hwy. 7, 1 (TCWC); 2.5 mi. NE Chilton, 1 (TCWC). *Freeston Co.*: Fairfield, 1 (TCWC). *Milam Co.*: 2 mi. E Maysfield, Hwy. 190, 1 (TCWC); 6.8 mi. E Maysfield, 2 (TCWC); 1.2 mi. SE Branchville, Hwy. 190, 1 (TCWC); 2.1 mi. SE Branchville near Brazos River, 1 (TCWC); 3.8 mi. SE Branchville, Hwy. 190, 1 (TCWC); 2.4 mi. S Wilderville, Hwy. 413, 1 (TCWC). *Burleson Co.*: 2.4 mi. NE Clay, 1 (TCWC); 3.0 mi. NE Clay, 3 (TCWC); 3.2 mi. NE Clay, 1 (TCWC); 6.1 mi. N Clay near Brazos River, 1 (TCWC); 17 mi. E Caldwell on W bank of Brazos River near Koppes Bridge, 2 (TCWC); 0.1 mi. SE Grant, Hwy. 50, 1 (TCWC); 1.4 mi. SE Grant, Hwy. 50, 1 (TCWC); 3.1 mi. SE Grant, near Brazos River, 1 (TCWC); 3.4 mi. SE Grant, near Brazos River, 1 (TCWC); 3.8 mi. SE Grant, Hwy. 50, 1 (TCWC); 0.6 mi. NW Grant, Hwy. 50, 1 (TCWC); 0.7 mi. NW Grant, Hwy. 50, 1 (TCWC); 0.8 mi. NW Grant, Hwy. 50, 1 (TCWC); 2.1 mi. NW Grant, Hwy. 50, 1 (TCWC); 2.3 mi. NW Grant, Hwy. 50, 1 (TCWC); 2.5 mi. NW Grant, Hwy. 50, 1 (TCWC); 2.8 mi. NW Grant, Hwy. 50, 1 (TCWC); 3.6 mi. NW Grant, Hwy. 50, 6 (TCWC); 3.8 mi. NW Grant, Hwy. 50, 1 (TCWC).

Geomys bursarius attwateri Merriam

1895. *Geomys breviceps attwateri* Merriam, N. Amer. Fauna, 8:135, 31 January.
1940. *Geomys breviceps ammophilus* Davis, Texas Agr. Exp. Sta. Bull., 590:16, 23 October.
1951. *Geomys bursarius attwateri*, Baker and Glass, Proc. Biol. Soc. Washington, 64:57, 13 April.

Type locality.—Rockport, Texas.

Distribution.—From the Brazos River in central Texas to southern Texas near the San Antonio River and along the coast as far south as Rockport, Aransas County.

Comparisons.—For comparisons with *G. b. breviceps* and *G. b. sagittalis* see accounts of same. *G. b. attwateri* differs from *G. b. major* as follows: smaller size; skull shorter with greatest length of skull averaging 40.6 mm. as opposed to 42.3 mm.; mastoidal breadth narrower; depth of skull shallower.

Remarks.—In size *G. b. attwateri* is intermediate between *G. b. sagittalis* to the east and *G. b. major* to the north and west. This subspecies represents two chromosomal races (see text for information pertaining to them). Both races contact in central Texas near the Brazos River, and a zone of intergradation is formed; however, the degree of chromosomal difference separating the two is not thought to be representative of distinct subspecies. Although there is an overlap in diploid and fundamental numbers between *G. b. attwateri* and *G. b. major*, the two are distinct in the morphology of the X-chromosome and the morphology of chromosomes in their autosomal complements. *G. b. attwateri* contacts *G. b. sagittalis* in Burleson County. To date only one chromosomally intermediate individual has been found in this area of contact.

Davis (1938) indicated that *G. b. attwateri* was not present north of the Colorado River. Morphological and chromosomal data indicate that the range of this subspecies extends to the west bank of the Brazos River.

Specimens examined (223).—Texas: *Milam Co.*: Gause, 1 (TCWC); 6 mi. SW Hearne, Hwy. 79, 2 (TCWC); 1.7 mi. E Gause, Hwy. 79, 1 (TCWC); 3 mi. E Gause, 1 (TCWC); 3.8 mi. E Gause, 1 (TCWC); 1 mi. W Gause, 1 (TCWC); 4.4 mi. W Gause, 1 (TCWC); 6.3 mi. W Gause, 1 (TCWC); 2.5 mi. S Gause, 1 (TCWC); 2.6 mi. S Gause, 1 (TCWC); 3.2 mi. S Gause, 1 (TCWC); 4.1 mi. S Gause, 1 (TCWC); 4.3 mi. S Gause, 1 (TCWC); 5 mi. S Gause, 1 (TCWC); 5.6 mi. S Gause, 1 (TCWC); 2.4 mi. NE Gause, 1 (TCWC); 2.6 mi. NE Gause, 1 (TCWC); 3 mi. NE Gause, 6 (TCWC); 2.2 mi. SE Gause on Two Mile Rd. 2 (TCWC); 2.7 mi. SE Gause, 1 (TCWC); 5.7 mi. SE Gause, 2 (TCWC); 6.3 mi. SE Gause, 1 (TCWC); 7 mi. SE Gause, 1 (TCWC); 8.7 mi. SE Gause, 1 (TCWC); 1.3 mi. N, 3 mi. E Milano, 2 (TTU); 1.1 mi. N, 2.5 mi. E Milano, 6 (TTU); 0.8 mi. N, 1.3 mi. E Milano, 3 (TTU); 1.3 mi. S, 3.3 mi. W Milano, 1 (TTU); 2.8 mi. S Milano, 1 (TCWC); 9.1 mi. SE Cameron, Hwy. 36, 1 (TCWC); 4.1 mi. SE Cameron, 1 (TCWC); 7.5 mi. S Rockdale, 1 (TCWC); 4.2 mi. SW Rockdale, Fm. Rd. 2116, 1 (TCWC); 1 mi. S Rockdale, 1 (TCWC); *Burleson Co.*: 1.3 mi. NE Clay, 1 (TCWC); 2.6 mi. W Tunis, Fm. Rd. 166, 1 (TCWC); 2.4 mi. NE Clay, 2 (TCWC); 0.2 mi. E Snook, 1 (TCWC); 13 mi. NE Caldwell, Hwy. 50, 2 (TCWC); 3 mi. N Caldwell, Hwy. 36, 2 (TCWC); 3.3 mi. N Caldwell, Hwy. 36, 1 (TCWC); 7.4 mi. N Caldwell, Hwy. 36, 1 (TCWC); 12 mi. E Caldwell, Rt. 3, 5 (TCWC); 3.6 mi. NW Grant, Hwy. 50, 5 (TCWC); 4 mi. NW Grant, Hwy. 50, 8 (TCWC); 4.1 mi. NW Grant, Hwy. 50, 1 (TCWC). *Washington Co.*: 13 mi. W Brenham, 1 (TCWC); 1 mi. W Brenham, 2 (TCWC); Brenham, 1 (TTU). *Lee Co.*: 2.7 mi. S, 1.6 mi. E Lexington, 1 (TCWC); 3.5 mi. S, 1.6 mi. E Lexington, 3 (TCWC). *Austin Co.*: 2

mi. NE Bellville, 3 (TCWC). *Colorado Co.*: 6.2 mi. S Eagle Lake, 14 (TTU); 6.2 mi. S Eagle Lake, 1 (TTU). *Bastrop Co.*: 3 mi. N, 3.7 mi. W Bastrop, 3 (TTU); 3 mi. N, 3.7 mi. W Bastrop, 3 (TTU); 0.8 mi. N, 2.5 mi. E Bastrop, 1 (TTU); 5 mi. E Bastrop, 1 (TCWC); 1.7 mi. W Bastrop, 2 (TTU); Bastrop, 4 (TTU); 1.5 mi. E Elgin, 1 (TTU); 1.9 mi. W Elgin, 4 (TTU); 1.5 mi. W Elgin, 1 (TTU); 0.7 mi. N, 2.6 mi. W Butler, 2 (TTU); 0.5 mi. N, 2.1 mi. W Butler, 1 (TTU); 1 mi. S Butler, 2 (TTU). *Travis Co.*: 0.7 mi. N, 5.7 mi. E Manor, 2 (TTU). *Fayette Co.*: E LaGrange, 1 (TCWC); 6 mi. W LaGrange, 2 (TCWC). *Caldwell Co.*: Luling, 10 (TTU). *Fort Bend Co.*: 1 mi. S Beasley, 2 (TCWC). *Lavaca Co.*: 9.1 mi. S, 9.8 mi. E Yoakum, 2 (TTU); 1.1 mi. W Halletsville, 1 (TTU). *DeWitt Co.*: Hochheim, 5 (TTU); Cuero, 1 (TTU). *Guadalupe Co.*: 12.1 mi. S, 0.7 mi. E Seguin, 12 (TTU); 12 mi. S Seguin, 2 (TCWC). *Gonzales Co.*: 1 mi. W Nixon, 2 (TCWC); 2.2 mi. N Nixon, 3 (TTU). *Victorio Co.*: 6 mi. S Victorio, 1 (TCWC); 3 mi. SW Victorio, 4 (TCWC). *Goliad Co.*: 8 mi. W Goliad, 3 (TCWC); 3 mi. E Goliad, 2 (TCWC); 3.5 mi. N Goliad, 2 (TCWC); 8 mi. SW Goliad, 2 (TCWC). *Wilson Co.*: 1 mi. W Floresville, 2 (TCWC). *Atascosa Co.*: 2 mi. NW Campbellton, 3 (TCWC); 2 mi. N Pleasanton, 2 (TCWC). *Frio Co.*: 1 mi. N Moore, 3 (TCWC). *Aransas Co.*: Rockport, 1 (TCWC); 8 mi. SW Rockport, 5 (TCWC); 10 mi. SE Austwell, 8 (TCWC); C.C.C. Camp, Aransas Refuge, 4 (TCWC). *San Patricio Co.*: between Aransas Pass and Ingleside, Hwy. 361, 5 (TTU).

Geomys bursarius major Davis

1940. *Geomys lutescens major* Davis, Texas Agric. Exp. Sta. Bull., 590:32, 23 October.

1947. *Geomys bursarius major*, Villa and Hall, Univ. Kansas Publ., Mus. Nat. Hist., 1:229, 29 November.

Type locality.—8 mi. W Clarendon, Donley County, Texas.

Distribution.—Central Texas (McLennan County) north to western Oklahoma, west throughout northwestern Texas and into parts of eastern New Mexico.

Comparisons.—For a comparison of *G. b. major* with *G. b. sagittalis* and *G. b. attwateri* see accounts of same. *G. b. major* differs from *G. b. llanensis* as follows: size larger, greatest length of skull averaging 42.3 mm. as opposed to 40.9 mm.; palatal length longer; skull wider. *G. b. major* differs from *G. b. texensis* and *G. b. knoxjonesi* in being larger for almost all cranial measurements.

Remarks.—*G. b. major* represents the largest subspecies of *G. bursarius* in Texas and adjacent states. Chromosomally, certain populations throughout its range in western Texas demonstrate varying degrees of chromosomal polymorphism making it difficult to compare distinct differences among *G. b. major*, *G. b. texensis*, *G. b. llanensis*, and *G. b. knoxjonesi* (see Baker *et al.*, 1973, for a discussion of this variation).

Specimens examined (127).—Texas: *McLennan Co.*: E Waco, 4 (TCWC); 0.2 mi. S Waco, Fm. Rd. 434, 1 (TCWC); S Waco, 1 (TCWC); 1 mi. S Waco, 18 (TTU); 6

mi. S Waco, 5 (TCWC); 1 mi. SE Waco, Fm. Rd. 434, 1 (TCWC); 1.3 mi. E Bosqueville, 1 (TCWC); 4.5 mi. NE Bosqueville, 1 (TCWC); 3.3 mi. SE Bosqueville, 1 (TCWC); 2.5 mi. SE Downville, 1 (TCWC); 3 mi. NE Downville, 1 (TCWC); 0.4 mi. N Gholson, 1 (TCWC). *Hill Co.*: 21 mi. NW Waco, Fm. Rd. 933, 2 (TCWC); 5.8 mi. SW Aguilla, Willis Camp, 2 (TCWC). *Bosque Co.*: 1 mi. SE Smith's Bend, Fm. Rd. 2114, 1 (TCWC). *Cooke Co.*: 5.5 mi. SE Gainsville, 1 (TTU). *Montague Co.*: 3.1 mi. E Jct. Texas 59-Fm. Rd. 1758, 2 (TTU). *Hardeman Co.*: ¼ mi. W Chilli Exp. Sta. No. 12, Chillicothe, 1 (TCWC). *Dickens Co.*: 10 mi. E Dickens, 3 (TTU). *Knox Co.*: 5 mi. SE Benjamin, 1 (TCWC). *Collingsworth Co.*: 0.1 mi. W Wellington, 13 (TTU); 2 mi. E, 1.5 mi. N Wellington, 1 (TTU); 0.5 mi. N county courthouse in Wellington, 4 (TTU); 2 mi. N, 9 mi. W Wellington, 7 (TTU); 0.2 mi. W Wellington, 3 (TTU); 3 mi. E Wellington, Hwy. 83, 1 (TTU); Wellington, 1 (TTU). *Hemphill Co.*: 18 mi. E Canadian, 1 (TTU); 5 mi. NE Canadian, 1 (TTU). *Donley Co.*: 1 mi. NW Clarendon, 1 (TTU); 11 mi. W Clarendon, 1 (TTU). *Garza Co.*: 4.5 mi. NW Post, Hwy. 84, 1 (TTU); 4 mi. E Justiceburg, 2 (TTU). *Lubbock Co.*: Lubbock, 1 (TTU); Jct. loop 289-Hwy. 84, Lubbock, 2 (TTU); 6.5 mi. S, 0.4 mi. E Lubbock, 1 (TTU); 5 mi. S, 4 mi. E Lubbock, 1 (TTU); 1 mi. E intersection of Hwy. 84-SE Drive, Lubbock, 1 (TTU); 6 mi. SE Lubbock, 2 (TTU); 4 mi. SE Lubbock, 6 (TTU); Slaton, 1 (TTU); 4 mi. N Slaton, 1 (TTU); 11 mi. S Idalou, 1 (TTU). *Mitchell Co.*: 3 mi. N, 0.3 mi. E Colorado City, 9 (TTU). *Howard Co.*: 2 mi. NE Big Spring, 2 (TTU); 2 mi. N Big Spring, 1 (TTU). *Midland Co.*: 3 mi. E Jct. 349 on Hwy. 80, Midland, 1 (TTU); 4 mi. E Jct. 349 on Hwy. 80, Midland, 1 (TTU); 3 mi. N Midland, 1 (TTU); 5 mi. S Stanton, 2 (TTU). *Lamb Co.*: 2 mi. N Fieldton, 1 (TTU); 2 mi. NW Sudan, 1 (TTU). *Bailey Co.*: 2 mi. SE Muleshoe, 2 (TTU); 22 mi. S Muleshoe, Wildlife Refuge, 2 (TTU). *Dallam Co.*: 2.5 mi. E Dalhart, 1 (TTU).

Geomys bursarius llanensis Bailey

1905. *Geomys breviceps llanensis* V. Bailey, N. Amer. Fauna, 2:4, 1 February.

1947. *Geomys bursarius llanensis*, Villa and Hall, Univ. Kansas Publ., Mus. Nat. Hist., 1:234, 29 November.

Type locality.—Llano, Llano Co., Texas.

Distribution.—Eastern edge of the Edwards Plateau of Texas in Llano and Gillespie Counties.

Comparisons.—For a comparison of *G. b. llanensis* to *G. b. major* see account of the latter. Individuals of *G. b. llanensis* average larger than those of *G. b. texensis* and *G. b. knoxjonesi* for most cranial measurements (see Table 4). These differences are as follow: greatest length of skull longer, averaging 40.9 mm.; length of rostrum not less than 17.1 mm.; mastoidal breadth wider, averaging 22.1 mm.; deeper in skull depth.

Remarks.—*G. b. llanensis*, *G. b. texensis*, and *G. b. knoxjonesi* in Texas are chromosomally indistinguishable with diploid numbers of 70 and a fundamental number of 68 (Kim, 1972; Baker and Genoways, 1975). Hart (1971) described a diploid number of 71 and a fundamental number of 69 for *G. b. texensis*

and *G. b. llanensis*, which may indicate chromosomal polymorphisms within certain populations. The morphological analyses used in this study show certain morphological distinctions; however, they are less than those shown by other subspecies. If mean cranial measurements are considered, *G. b. llanensis* and *G. b. texensis* can be separated, based on size (Table 4). It is possible that these two subspecies are not taxonomically distinct, but the small size of samples prevents us from making a formal taxonomic change at this time.

Specimens examined (31).—TEXAS: *Llano Co.*: Castell, 1 (TTU); 2.6 mi. N, 1.8 mi. E Castell, 5 (TTU); Oatman Creek, 3 mi. S Llano, 3 (TCWC); Drier Creek, 7 mi. E Llano, 9 (TCWC); 51.6 mi. W Austin, Hwy. 71, 1 (TTU); 0.2 mi. N, 8.7 mi. W Llano, 3 (TTU); 8 mi. S, 0.9 mi. W Kingsland, 4 (TTU); 9.2 mi. S, 1.1 mi. E Kingsland, 1 (TTU); 10 mi. S, 1.8 mi. E Kingsland, 2 (TTU). *Gillispie Co.*: 1 mi. N Fredricksburg, 2 (TTU).

Geomys bursarius texensis Merriam

1895. *Geomys texensis* Merriam, N. Amer. Fauna, 8:137, 31 January.
1950. *Geomys bursarius texensis*, Baker, J. Mamm., 31:349, 21 August.

Type locality.—Mason, Mason County, Texas.

Distribution.—Mason County.

Comparisons.—For a comparison of *G. b. texensis* to *G. b. major* and *G. b. llanensis* see accounts of same. *G. b. texensis* compared to *G. b. knoxjonesi* differs as follows: palatal length averaging 22.1 mm. as opposed to 21.4 mm.; mastoidal breadth narrower, averaging 22.1 mm. as opposed to 22.8 mm.; skull shallower with palatofrontal averaging 13.6 mm. as compared to 14.9 mm.

Remarks.—Several mean cranial measurements of *G. b. texensis* and *G. b. knoxjonesi* are similar (Table 4). These similarities are best depicted by measurements of greatest length of skull and length of rostrum.

Specimens examined (22).—TEXAS: *Mason Co.*: 1 mi. E Mason, 4 (TTU); 6.5 mi. E Mason, Hwy. 29, 1 (TTU); 9.4 mi. W Mason, U.S. 377, 1 (TTU); 0.3 mi. S, 1.5 mi. W Castell, 3 (TTU); 0.3 mi. S, 0.9 mi. W Castell, 1 (TTU); 0.3 mi. S, 0.8 mi. W Castell, 1 (TTU); 0.7 mi. S, 2.1 mi. W Castell, 3 (TTU); 1.0 mi. S, 2.3 mi. W Castell, 1 (TTU); 2.0 mi. S, 2.7 mi. W Castell, 1 (TTU); 2.6 mi. S, 3 mi. W Castell, 1 (TTU); 3.6 mi. N, 1.5 mi. W Mason, 1 (TTU); 1 mi. N, 1.1 mi. W Mason, 4 (TTU).

Geomys bursarius knoxjonesi Baker and Genoways

1975. *Geomys bursarius knoxjonesi* Baker and Genoways, Occas. Papers Mus., Texas Tech Univ., 29:1, 25 April.

Type locality.—4.1 mi. N, 5.1 mi. E Kermit, Winkler County, Texas.

Distribution.—Southern Cochran, Yoakum, Terry, Gaines, northwestern Martin, Andrews, Winkler, and Ward counties in western Texas and Chavez, Eddy, and Lea counties in southeastern New Mexico.

Comparisons.—For a comparison of *G. b. knoxjonesi* to *G. b. major, G. b. llanensis,* and *G. b. texensis* see accounts of same.

Remarks.—Baker and Genoways (1975) described *G. b. knoxjonesi* as consisting of two chromosomal races with populations in Texas differing in fundamental number from those in New Mexico. These authors also indicated that *G. b. knoxjonesi* is morphologically more similar to *G. b. texensis* and *G. b. llanensis* than to *G. b. major.* Although multivariate analyses used in this study failed to substantiate this claim, if one examines only mean cranial measurements (as shown in Table 4) these indicate that it averages smaller than *G. b. major* for all measurements and is indeed more similar to *G. b. texensis* and *G. b. llanensis.* This discrepancy can be explained by the fact that the calculated values for pooled populations of *G. b. major* would tend to compensate for any small-sized populations, thus emphasizing its overall larger size.

Specimens examined (34).—TEXAS: *Cochran Co.*: 1 mi. W Lehman, 5 mi. W Morton, 1 (TTU); 1 mi. N, 0.4 mi. W Whiteface, 1 (TTU); 1 mi. N, 0.9 mi. W Whiteface, 2 (TTU); 1 mi. W Morton, 1 (TTU). *Gaines Co.*: 0.8 mi. S, 15 mi. E Seminole, 11 (TTU); 5 mi. SW Seagraves, Hwy. 385, 1 (TTU); 3 mi. N Seminole, 3 (TTU); 0.6 mi. S, 14 mi. E Seminole, 1 (TTU). *Andrews Co.*: 2.5 mi. E Andrews, 1 (TTU). *Winkler Co.*: 0.3 mi. N, 2.5 mi. E Kermit, 6 (TTU); 4.1 mi. N, 5.1 mi. E Kermit, 4 (TTU); 8.5 mi. S, 3.3 mi. E Kermit, 1 (TTU).

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