ECOLOGICAL FACTORS AFFECTING DISTRIBUTION AND SPECIATION OF POCKET GOPHERS IN OKLAHOMA

By

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PREFACE

Pocket gophers are both widespread and numerous in the state of Oklahoma. Despite this fact the scientific record of their distribution, and even of their classification, has in the past been based on considerably less than one hundred specimens from fewer than forty localities. No attempt has been made to determine all of the species and subspecies present and the complete range of each, or to discover the factors that isolate the forms into geographic races. The factors that prevent pocket gophers from occupying certain areas have not been fully known.

The author, under the supervision of Dr. Walter P. Taylor, began a study of the pocket gophers of the state, in order to determine their classification, the areas that they occupy, and the ecological factors affecting their distribution and speciation. Special thanks are due to Dr. Taylor for his supervision, to the Oklahoma Agricultural and Mechanical College Research Foundation for providing research time and travel funds utilized in this study, and to the Zoology Department of the same institution for providing storage facilities and expendable materials used in the preparation of study specimens.

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on the fossil history of the family Geomyidae.

Miss Elizabeth Thomas, of the Oklahoma A and M College Library deserves much praise for her help in preparing the bibliography. At times her facility for deciphering and locating obscure or baffling citations amounted to sheer divination.

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FOSSIL HISTORY OF THE GEOMYIDAE

The pocket gophers constitute a distinctive group of North American rodents, the family Geomyidae, with known history as far back as the middle Oligocene, where several fossil genera are known from the John Day and other deposits of northwestern United States. That there is a close relationship between this family and the family Heteromyidae, known from early Miocene forward, is well documented by Wood (1935, 1936, 1937). Most authorities class the two families together in the superfamily Geomyoidea. Unfortunately, the common ancestor of these rodent groups is unknown, although there has been much speculation concerning their origin. Wood (1935) reviewed various theories of geomyoid origin, noting the weaknesses in each. Matthew (1910) suggested that the Eocene-Oligocene series Paramys-Sciuravus-Gymnoptychus (= Adjidaumo) might represent the steps in their evolution. However, Wood (loc. cit.) pointed out that the assumed relationship of Gymnoptychus to the Geomyidae is an error based on an inaccurate figure. The Eocene fossil Protoptychus was also ruled out as a possible ancestor, on the basis of the teeth being more advanced than those of any known geomyoid older than Upper Pliocene. Wood also stated that it seems unlikely that the Middle Oligocene Heliscomys, now classed with the Heteromyidae, could be the looked-for ancestor of either of these families, due to its great morphological distinctness from the geomyids of the John Day deposits. In summing up, although several theories have been proposed, the ancestry of the geomyidae prior to Middle Oligocene remains unsolved. It does seem to be well established that this group is properly classed together with the family Heteromyidae in the superfamily Geomyoidea, on the basis of the zygomasseteric structure, and the fur-lined cheek pouches.

It seems also to be accepted generally that both of these families are more closely related to the Sciuridae, Castoridae, and Aplodontidae than to other rodent groups, and together constitute a natural suborder, the Sciuromorpha. All members of this suborder are very likely descended from Paramys stock of the Eocene. The exact lines of descent of the various families, however, have never been discovered.

The oldest known geomyid genus is Gidleumys, known from the White River (Brule) deposits of South Dakota, of Middle Oligocene age. This form is distinct from the Heteromyidae. Wood (1936) stated, however, that it is too specialized in other ways to be directly ancestral to the later members of the family of which the living genera are a part. He did not include this genus in the subfamily Entoptychinae, which name he reserved for a group of genera of Miocene age, which also show specializations which separate them from the living genera.

The Miocene geomyids have been divided into two subfamilies, the Entoptychinae and the Geomyinae. The former are characterized by having the angular portion of the mandible mostly below the alveolar level, the cheek teeth primitively rooted, and the upper incisors usually smooth. The latter have the angular portion of the mandible mostly above the alveolar level, strongly hypsodont teeth, and the upper incisors usually sulcate.

Four genera constitute the Entoptychinae, all from the Lower Miocene deposits of the western United States. Pleurolicus has been reported from the middle and upper John Day beds of Oregon, and the upper and lower Rosebud and Porcupine Creek of South Dakota. Gregorymys occurs in the upper and lower Rosebud of South Dakota, the Lower Miocene Arikaree beds in Wyoming, and the Goolin deposits in Montana. Grangerimus is known from

the upper John Day beds, in Oregon, and from an oil well drilling from Bee County, Texas. Entoptychus is known from the middle and upper John Day beds of Oregon. A specimen reported from Thousand Island Creek, Nevada by Kellogg (1910) was reported by Wood (1937) to be identical with Diprionomys, a heteromyid.

The subfamily Geomyinae, to quote from Wood (1936),

> "represents a higher grade of specialization than do the Entoptychinae, which they seem to have replaced almost as soon as the two groups came into competition. At present nothing is known of the origin, and very little of the evolution of the Geomyinae. The later tertiary forms that have been described are all close to the recent species, and show little or nothing of the origin of the group."

There is one relatively primitive genus, Pikkomys, known from the lower Harrison formation (Lower Miocene) in Nebraska. Wood stated that this is an aberrant form, whose relationship with the later geomyids is not evident. He stated that its relationships are probably with the more specialized members of the family, hence closest to Thomomys.

Many genera of geomyids are known from the late Tertiary and Recent epochs. There seems to be some uncertainty as to the real antiquity of some of the recent genera, some fossil forms that were once placed in living genera having later been transferred into newly described fossil genera. Zittel (1925) stated that Geomys is known from the Miocene, and Romer (1945) listed the genus as being found from the Miocene to the Recent epochs. Wood (loc. cit.) made no mention of Geomys in his discussion of the mid-Tertiary representatives of this family. Matthew (1910) listed Thomomys as being found in the Middle Miocene, a dating that Romer (loc. cit.) considered questionable. Again Wood (loc. cit.) made no mention of this genus. Indeed Wood (1938) listed both of these genera as being questionable in the Miocene, with no valid records extant

for Thomomys below Middle Pliocene, or for Geomys below Upper Pliocene.

Wood mentioned the possibility that the Entoptychinae may have been unsuccessful in competition with the Geomyinae, whose fossorial adaptations are more perfect. Admitting that the lack of the former group in late deposits may be due to incompleteness in the fossil record, he nevertheless pointed out that the latest entoptychines and the earliest geomyines, as far as known, appear in the same deposits.

Wood (1936) had the following to say about the earlier records of the geomyids of the early Pliocene and Miocene:

> "Lower and Middle Pliocene gophers are in a state of considerable confusion.....The recent forms, Geomys and Thomomys, have been reported from the early Pliocene and even from the Miocene. It must be admitted that it seems quite likely that Thomomys, at least, was present by Lower Pliocene time. On the other hand, no adequate description of any gopher material referable to a recent genus and occurring in the Lower and Middle Pliocene has ever been published. Not a single specimen has been figured."

It seems, then, that reliable records of the recent genera of the family are available only from mid-Pliocene onwards. One genus of aberrant pocket gophers, Pliosaccomys, occurs only in the Middle Pliocene deposits from Smiths Valley, in Nevada. According to Wilson (1936) it is aberrant, and of uncertain affinities.

The Pliocene and Pleistocene pocket gophers are so similar to living genera that in most cases they have been listed as congeneric. In a few cases species that were first described under recent genera have been placed in new fossil genera, but in the main specimens from these epochs are regarded as constituting extinct species of still extant genera. The upper Pliocene specimens of Geomys from Benson, Arizona, described by Gidley (1922) have been placed in a separate genus, Nerterogeomys by Gazin (1942). However Geomys quinni is listed by Franzen (1947)

from the Rexroad, a Pliocene site in Kansas. This species is regarded as belonging to Geomys, even after comparison with Nerterogeomys. This seems to indicate that there were two closely related but valid genera in the upper Pliocene. Other records of pocket gophers from the Pliocene include Cratogeomys from Benson, Arizona; and Geomys from Snake Creek, Nebraska. Thomomys is known from Grandview and Hagerman, Idaho; Rexroad, Kansas; and lower Snake Creek, Nebraska.

The geomyids seem to have reached their peak in distribution during the Pleistocene. For many years only recent genera were listed for this epoch, but recently the species from eastern United States, formerly regarded as Thomomys, were placed in a separate genus, Plesiothomomys, by Gidley and Gazin (1933). This genus is known from Cumberland Cave, Maryland, and from a cave in Citrus County, Florida. Other Pleistocene records for Thomomys include middle Loup and Grayson, Nebraska; Fossil Lake, Oregon; Wenatchee, Washington; and the Carpinteria Asphalt, San Pedro, Samwel Cave, Potter Creek Cave, Hawver Cave, and La Brea Tar faunas, all in California. The genus Geomys is known from the following Pleistocene localities: Melbourne, Florida; a fissure near Willcockson, Arkansas; Bulvedere Cave near San Antonio, Texas; the mouth of the Platte River and Sand Draw, Nebraska; the loess deposits of Alton, Illinois; crevices in the lead-mining region of Wisconsin, Illinois, and Iowa; Fossil Lake, Oregon; San Pedro, Arizona; and from many Pleistocene sites in the great plains, particularly in Kansas. Cratogeomys, although known from the upper Pliocene, has never been recovered from any Pleistocene deposits. The Recent genera of pocket gophers that are found only in Mexico, Pappogeomys, Zygogeomys, Orthogeomys, Heterogeomys, and Macrogeomys, have no known fossil history.

From the known distribution of extinct and Recent geomyids it seems that the group had its center of origin in the western part of the North American Continent. Although records are lacking for periods earlier than the Miocene, the family must have been an old one at that time. The early Miocene records from Oregon, South Dakota, Wyoming, Montana, Nebraska, and Texas indicate a long existence in the Oligocene for which there is no known fossil record.

Though the record is obviously incomplete, it seems that the early geomyids of the subfamily Entoptychinae never spread beyond the western part of the North American Continent. The decline of the Entoptychinae coincided with the appearance of the Geomyinae, which in the Pliocene and Pleistocene extended their range eastward. By Pleistocene time geomyines were found all the way to the eastern limits of the Continent. Variation among the Geomyinae occurred mainly in the west. The eastern spread during the Pleistocene however established a second center of variation in the southeast, resulting in the evolution of the genus Plesiothomomys, now extinct, and in the species of Geomys still occupying parts of Georgia, Alabama, and Florida. Subsequent modifications of terrain, probably associated with the end of glaciation and changes in the Mississippi Valley, have resulted in the extinction of one, and the complete isolation of the other. Geomys tuza and related species and subspecies in the Southeast have become adapted to the sandy pinelands of that area, where they constitute a center of survival.

The present distribution of the genus Thomomys in the western highlands, where it is often found at a great elevation, indicates the likelihood of the species having taken advantage of periods of glaciation to extend its range eastward, where evolution of the closely related

Plesiothomomys took place. Extinction of Plesiothomomys undoubtedly followed the last retreat of the ice sheets. By contrast Geomys, a more austral genus, has survived the end of the glacial period.

The main center of variation among the Geomyinae, as noted above, seems to have been in the western half of the United States. By upper Pliocene time all of the living genera had evolved. The occurrence of several Recent genera in Mexico of which there is no fossil record presents an enigma for which there is as yet no satisfactory solution. These Mexican genera should probably be regarded as exemplifying a southern extension of range which probably occurred during the periods of glaciation. Obviously active speciation has occurred, and these genera probably represent another important center of variation near the southern limit of range of the family.

TAXONOMIC HISTORY OF THE GENUS GEOMYS

The name Geomys was first applied to the pocket gophers of North America by Rafinesque (1817), the name Geomys pinetis being applied by him to the gopher of the pine barrens of Georgia. Actually the name Pseudostoma bears line priority over the name Geomys, however the description as given for the former does not fit exactly any known species of mammal, hence it is now regarded as a synonym of Geomys, whose original description is unmistakable. The name pinetis has been replaced by the name tuza, proposed by Ord (1815) as Mus tuza, based on a description of the animal published without a name by Mitchill in 1802. Ord apparently never saw the animal, but based his account solely on Mitchill's written description. He utilized the generic name Mus, that has been frequently applied in the past to numerous distantly related rodents. Recognition of the distinctness of the genus has required acceptance of Rafinesque's name, making the combination Geomys tuza (Ord) as it is now known.

A darker form, Pseudostoma floridana, was described by Audubon and Bachman (1857), and Merriam (1894), in his monograph of the pocket gophers, retained this form as Geomys tuza floridana for the gophers in the vicinity of St. Augustine, Florida. At the same time he named the subspecies G. tuza mobilensis for the population in the vicinity of Mobile Bay. This form is smaller and darker than typical G. tuza tuza, whose type locality is Augusta, Georgia.

Bangs (1898) proposed the name Geomys colomus for the gophers of the St. Marys region of Florida, basing his separation on their dark coloration. At the same time he proposed the name Geomys cumberlandius for the gophers of Cumberland Island off the coast of Georgia, on the

basis of their large size, rounded zygomata, and bright russet color. A new subspecies of Geomys tuza, G. t. austrinus, was also proposed for the gophers in the vicinity of Bellear, Hillsboro County, Florida. Distinction was claimed mainly on the basis of lighter color.

Recently Geomys fontanelus was described by Sherman (1940) from a restricted area seven miles northwest of Savannah, Chatham County, Georgia. Distinctness was claimed on the basis of characteristic fontanelles in the parietal region of the skull. These four species and their geographic races are the representatives of the genus occupying an area extending across the pine lands of the southeast from Mobile Bay to the Savannah River. This population is at present cut off from its congeners of the midwest and plains by the broad alluvial belt of the Mississippi Valley.

The description of the plains pocket gopher was published many years before the one from the southeast. Shaw (1800) described a specimen designated as being from the upper parts of interior Canada, to which he gave the name Mus bursarius. There has been some uncertainty whether or not Shaw's specimen was actually of the genus Geomys. Until recently the genus Thomomys was the only one known from Canada outside of the valley of the Red River of the North. Merriam (1895) never did come to any conclusions in the matter, and although he pointed out the resemblances between Shaw's illustrations and Thomomys, he used the combination Geomys bursarius (Shaw) for the gopher of the northern plains. Merriam expressed belief that the actual specimen seen by Shaw was not positively known at the time of his writing, and he doubted that it would ever be. In the absence of the original specimen he concluded that the majority of points in the description favored Geomys, which he used. Swenk (1939) supported this position, and it now seems beyond reasonable doubt that

this usage is correct. In view of the doubt cast on the original locality of Shaw, Merriam redefined the type locality of Geomys bursarius as the upper Mississippi Valley. Swenk (1939) further restricted this to the vicinity of Elk River, Sherburne County, Minnesota.

The name that has been in use for the pocket gophers of the southern plains area is Geomys breviceps, proposed by Baird (1855). This species was first described from Prairie Mer Rouge, Morehouse Parish, Louisiana, and was characterized by its small size and dark coloration. The name has been applied since that time to the pocket gophers of eastern Oklahoma and Texas, and adjacent parts of Arkansas and Louisiana. Within this region various geographic races have been described.

A third name of long standing, Geomys lutescens Merriam 1890, was first described as a subspecies of G. bursarius. The type locality was given as Birdwood Creek, Lincoln County, Nebraska. Distinctive of the species is its yellowish color. The form was elevated to the rank of full species by Merriam (1895), when he stated that if intergradation between lutescens and bursarius did occur that it would be between the 98th and 99th meridians. He further mentioned that there was an area in southern Kansas where there was a puzzling population of gophers that seemed to be intergrades between bursarius, lutescens, and breviceps. No attempt was made to solve the problem presented by this population.

Merriam (loc. cit.) also described four new forms for the United States. Geomys breviceps sagittalis from the Galveston Bay region of Texas was distinguished by its smaller size, darker coloration with white throat and forefeet, and by the distinct sagittal crest. Geomys breviceps attwateri from the coastal plain region of Texas south to

Nueces Bay was separated on the basis of larger size, lighter color, angular zygomata, and the hairy condition of the basal third of the tail. Geomys texensis, from the vicinity of Mason, in central Texas was described as being very small, white beneath, and with a short tail. Geomys arenarius from the Rio Grande north of El Paso, Texas, was described as being of medium size, pale in color, with the tail well haired except at the tip. Cranially it was distinguished by the presence of parallel temporal ridges, and by the distal end of the squamosal forming a knob over the middle of the zygoma. The latter species has never been shown to be linked with the main range of the plains pocket gophers.

True (1899) proposed the name Geomys personatus for the gophers found on Padre Island, off the southern coast of Texas. This form was described as being quite large, and of light color, with a nearly naked tail. Cranially it was characterized by a high sagittal crest, and by the zygomata standing out at right angles from the skull. To this species Merriam (loc. cit.) added the subspecies G. personatus fallax to include the mainland form of the species, which he claimed intergraded with the typical island form in the vicinity of Nueces Bay. The new race was characterized by its smaller size, with features otherwise like the island form. The range of Geomys personatus approaches that of breviceps in the vicinity of Nueces Bay. Contiguity and intergradation between the two has not been demonstrated. Davis (1940) indicates by maps that at their closest approximation these forms are separated by Nueces Bay.

As early as 1857 Baird recognized that the mid-continental area of the United States contained two distinctive populations of pocket gophers, which he recognized under the names bursarius and breviceps. The former

was applied to the larger animals of the northern prairies, the latter to the smaller ones of the Gulf Coastal Plain. He also noted the gray coloration of the Illinois pocket gophers that later led Komarek and Spencer (1931) to recognize them as a separate subspecies, restricted to the eastern side of the Mississippi River in Illinois and Indiana.

Vernon Bailey (1895), in his biological survey of the state of Texas, described Geomys breviceps llanensis from the town of Llano, and listed many places in the Texas Panhandle where it had been collected. The larger size, lighter color, and more highly arched skull were regarded as distinctive. This name remained in general use until 1940, when Davis was able to demonstrate that the gophers of the Texas Panhandle all belonged to the group known at that time as Geomys lutescens Merriam. Bailey's form, llanensis, thereby became G. lutescens llanensis, which Davis (1940) further restricted to the vicinity of the type locality. Davis proposed the name Geomys lutescens major for the subspecies occupying the rest of the range formerly assigned to G. breviceps llanensis. The type locality was designated as Clarendon, Donley County, Texas. The form is larger and the skull flatter than in llanensis. The subspecies major differs from typical lutescens in being liver colored rather than yellowish.

In 1931 Komarek and Spencer proposed that the distinctness of the pocket gophers east of the Mississippi River in Illinois and Indiana be recognized taxonomically. The name Geomys bursarius illinoensis was proposed for this population, the distinction being based solely on the lead-gray coloration. Later G. b. illinoensis was raised to full specific rank by Lyon (1936), who reasoned that the two populations could not intergrade while separated by the barrier of the Mississippi. This ranking is not

currently accepted by most taxonomists, and Baker and Glass (1951) list it as a subspecies in the latest list of forms of Geomys bursarius.

Hall (1932) described Geomys arenarius brevirostris from the Tularosa Basin adjacent to the White Sands in New Mexico. Separation was based on the darker color and shorter rostrum.

Davis (1938) separated the gophers of the Brazos River drainage in southeastern Texas into the subspecies Geomys brevicens brazensis on the basis of its small size and distinctive coloration, as well as certain proportions of the skull. He also reduced Geomys texensis Merriam to the rank of a subspecies of G. brevicens, because of the close relationship apparent in all measurements, and because the color distinctions used by Merriam are not trenchant. In 1940 Davis expanded his study to include all parts of Texas, New Mexico, Oklahoma, Arkansas, and Louisiana known to contain gophers. This constitutes the most extensive revision since Merriam's monograph of 1895. Davis pointed out that Prairie Mer Rouge is the only place that pocket gophers possess the distinctive dark coloration described by Baird in the original description of Geomys brevicens, and that the type locality has an isolated population, separated by several miles from the nearest point to the west where pocket gophers occur. Consequently Davis restricted the name Geomys brevicens brevicens to the population in the vicinity of the type locality. He applied the name Geomys brevicens dutcheri, with type locality at Fort Gibson, Oklahoma, to the large population in eastern Oklahoma and Texas thus rendered nameless. He also separated the gophers of southwestern Louisiana and extreme eastern Texas into the subspecies pratincolus with type locality near Liberty, Texas. Characteristically bowed zygomata and distinctive coloration identify this

form. He also designated another form, Geomys breviceps ludemani, from the east side of Galveston Bay, Texas, separating it on the basis of distinctive cranial features. The vicinity of Texas City, west of Galveston Bay, was designated as the type locality of Geomys breviceps terricolus, distinct from G. b. sagittalis Merriam to the north by its larger size, exemplified in several cranial and external measurements. Davis also named Geomys breviceps ammophilus for the population between the Colorado and Guadalupe Rivers in the vicinity of Victoria, Texas. The form was described as being smaller than attwateri, with less divergent zygomata.

In the group of subspecies comprising Geomys personatus, Davis restricted the type subspecies to the Padre and Mustang Islands gophers, and proposed the name Geomys personatus maritimus for the peninsular form found between Nueces and Redfish Bays, Texas. This form is lighter in color than fallax, its nearest relative, and is the largest of the mainland forms. Within this species complex Davis also proposed the names Geomys personatus megapotamus for the gophers along the lower Rio Grande, and Geomys personatus minor for the ones in the vicinity of Carrizo Springs, Texas. Size differences provided the main basis for separation. Davis (1943) substituted the name streckeri for minor, since the latter was preoccupied.

Several new subspecies of Geomys lutescens have been described. Blossom (1938) proposed the name Geomys lutescens hylaeus for the gophers of the Pine Ridge region of South Dakota, distinguishing them from typical lutescens by several distinctive color features. Hooper (1940) proposed the name Geomys lutescens jugosicularis for the

yellow pocket gophers of southeastern Colorado and southwestern Kansas south of the Arkansas River. He predicted that it would be found in Oklahoma, and possibly in Texas, but listed no specimens from those states. Swenk (1940) described two new forms of Geomys lutescens. G. l. levisagittalis was recognized from Spencer, Boyd County, Nebraska on the basis of slightly greater skull proportions and body measurements, and G. l. vinaceus from western Nebraska and adjacent parts of Colorado and Wyoming on the basis of more vinaceous color, and smaller skull.

Swenk's (1939) discussion of the validity of the name Geomys bursarius, and his restriction of the type locality, have already been mentioned. The name Mus saccatus of Mitchill (1802) for the gophers of the region bordering Lake Superior provided Swenk with a logical area within which to select his restricted locality, being the earliest record with a definite location. In the same paper Swenk proposed the name Geomys bursarius majusculus for the unusually large gophers found in eastern Nebraska and the adjacent parts of Iowa. The form was described as being found mainly in regions of predominantly loess soil.

Recently Villa and Hall (1947) published a paper on the pocket gophers of Kansas in which the conclusion was reached that Geomys lutescens and Geomys bursarius intergrade in western Kansas. Consequently all of the distinctions between populations of these forms were reduced to those of subspecies. As a result the form in northeastern Kansas is now designated as Geomys bursarius majusculus, in the northwest Geomys bursarius lutescens, in the southwest Geomys bursarius jugosicularis, and in the south central area Geomys bursarius major. Geomys bursarius industrius, a new form, was described as occupying an area between the four subspecies just mentioned. The most

characteristic feature of the new race is the strong anterior inclination of the occiput, especially in males. Thus after fifty-nine years the form lutescens, and by implication all of its described subspecies, was restored to the species bursarius under which it was originally named.

The status of the plains pocket gophers remained unchanged until within the last twelve months. Recently Baker (1950) placed both Geomys breviceps texensis and Geomys bursarius llanensis in the same species, bursarius, pointing out evidence of intergradation that he had discovered in the vicinity of Llano and Mason, Texas. Both were retained, however, as valid subspecies. Baker and Glass (1951) reduced breviceps to synonymy with bursarius, on the basis of demonstrated intergradation in a portion of the area wherein the ranges of each form come in contact in central Oklahoma.

There remain at the time of writing the following full species in the central portion of the United States; Geomys arenarius Merriam, Geomys bursarius (Shaw), and Geomys personatus True. The published records of the three species, including localities listed here for the first time, are depicted in Fig. 1.

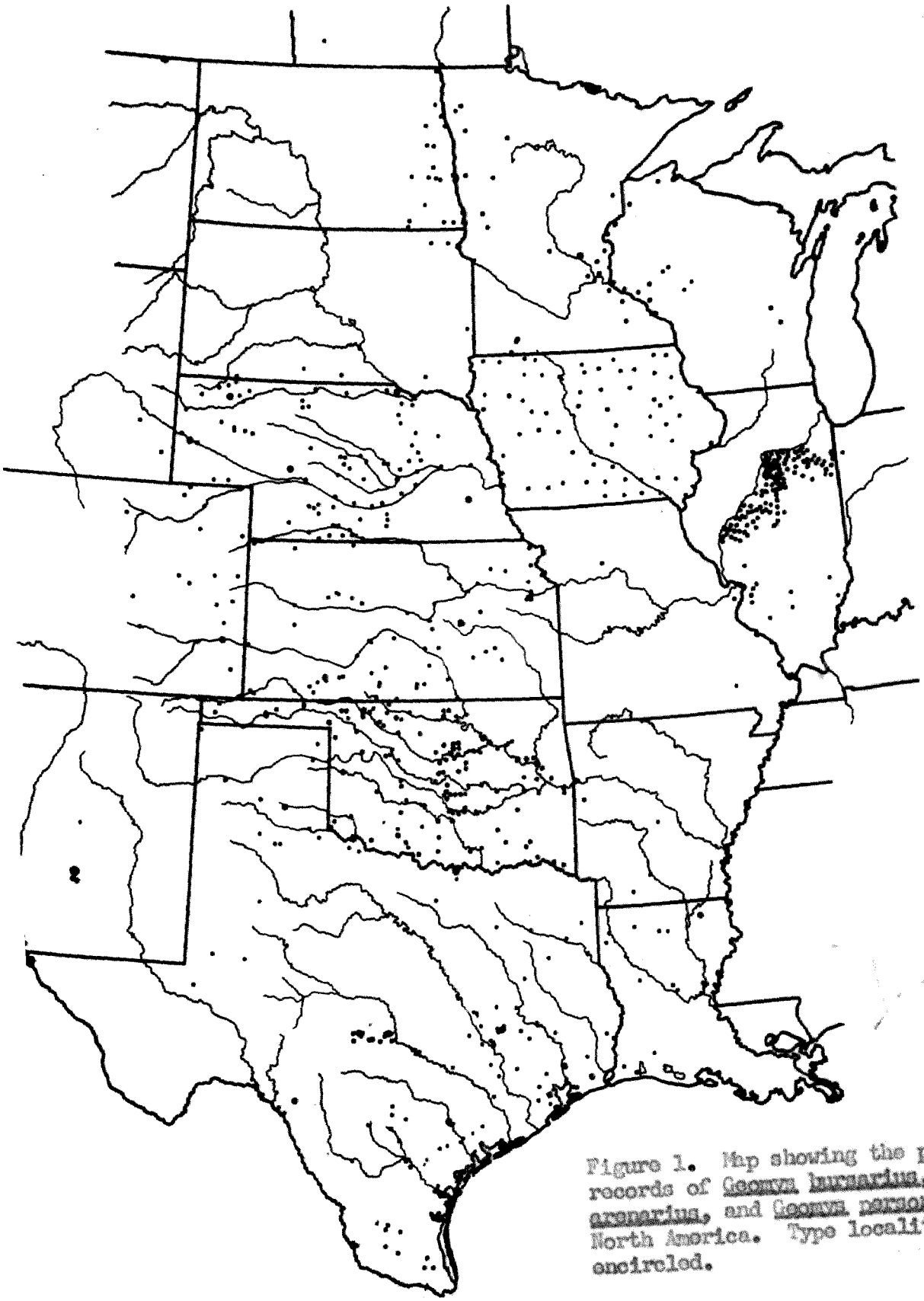

Figure 1. Map showing the published records of Geomys bursarius, Geomys arenarius, and Geomys personatus in North America. Type localities are encircled.

TAXONOMIC HISTORY OF THE GENUS CRATOGEOMYS

The history of the genus Cratogeomys is neither as long nor as involved as that of Geomys. For many years the two were regarded as congeneric, and the North American pocket gophers were divided into only two groups, those with sulcate upper incisors and those whose upper incisors are smooth. The genus Cratogeomys was created by Merriam (1895) when he revised the pocket gophers with grooved incisors. In the genus were placed several forms from Mexico, not considered here, and all of the gophers of the United States whose upper incisors bear only a single groove. At that time only a single form, Cratogeomys castanops (Baird) was recognized north of the Mexican Boundary.

Baird (1852) was the first mammalogist to encounter an individual of this species when he examined a specimen collected by Lt. Abert on the prairie road to Bent's Fort, near the present town of Las Animas, Colorado. The name used by Baird was Pseudostoma castanops. Later in the same year LeConte (1852) showed that the generic name Pseudostoma Rafinesque is untenable in that the description fits no known species of gopher. In its place he proposed that Geomys Rafinesque be used, pointing out that in this instance the description is accurate, and clearly applies to a recognizable form. Pseudostoma has preference over Geomys by line priority only, and LeConte's recommendations have been universally followed by subsequent workers, including Baird (1857), who in his monographic work "Mammals of North America" used the combination Geomys castanops.

The name Geomys clarki[1] was proposed by Baird (1855) to include the population in the vicinity of Presidio del Norte on the Mexican side of the Big Bend of the Rio Grande. Later Baird (1857, 1858a) recorded this species as being found in the Pecos River Valley. This species was suppressed by Merriam (1895) as a synonym of Cratogeomys castanops, and was resurrected by Nelson and Goldman (1934) as a subspecies of C. castanops, limited to the Mexican side of the International Boundary. Being now regarded as a purely Mexican form, the subspecies is considered no further in this study.

As Merriam (1895) recognized no new forms of Cratogeomys for the United States, C. castanops remained the only representative of the genus north of the Mexican Boundary until the revision of the genus by Nelson and Goldman (op. cit.). This publication is the most recent revision of these pocket gophers, and is regarded as the accepted classification at the present time. Cratogeomys castanops castanops (Baird) was therein restricted to southeastern Colorado and northeastern New Mexico. Cratogeomys castanops perplanus was created to include the population of the Staked Plains. The basis for the separation of this form lies mainly in the cranium, the most distinctive feature being the greater extent to which the squamosals encroach upon the external auditory meatus. The type locality of this form is Tascosa, Oldham County, Texas. The name does not appear on many recent maps, but the location is on the South Canadian River in the eastern part of the County, and

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1 Formerly spelled clarkii, now clarki, to conform with a new ruling of the International Commission on Zoological Nomenclature.

is now the site of an eleemosynary institution known as Boy's Ranch. Another form, Cratogeomys castanops lacrimalis was described by Nelson and Goldman to include the gophers of the Pecos River Valley, the type locality being Roswell, Chaves County, New Mexico. The chief characteristic of this form is the larger and heavier lacrimal bones of the skull. An additional form, Cratogeomys castanops hirtus, was described for the peripheral population found in the vicinity of Albuquerque, Bernalillo County, New Mexico. A strong tendency towards melanism characterizes this form, which seems to be limited in distribution to the vicinity of the type locality. Lastly these authors proposed the name Cratogeomys castanops angusticeps for the population occupying the region of Texas east and southeast of the Big Bend of the Rio Grande. Small size characterizes this race, whose type locality is Eagle Pass, Maverick County, Texas. Other forms described by these authors for various parts of Mexico are not discussed here, for they do not come within the scope of this study. The published records of North American subspecies of Cratogeomys, including localities listed here for the first time, are depicted in Fig. 2.

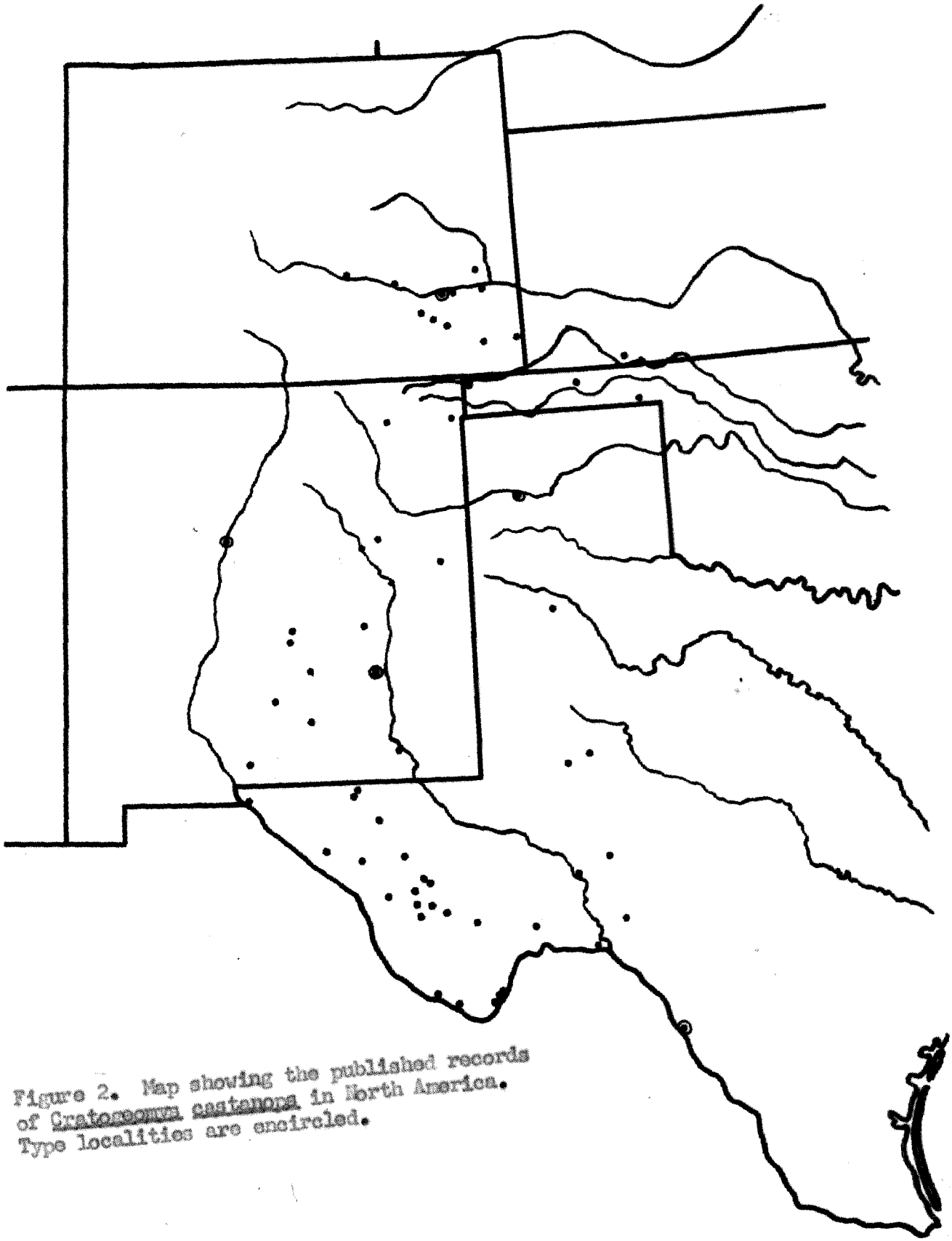

Figure 2. Map showing the published records of Craterocrum castanopsa in North America. Type localities are encircled.

OBJECTIVES AND METHODS

The present study of pocket gophers in Oklahoma has three objectives. The first is to outline the areas of the state in which pocket gophers occur. The second is to confirm or revise the taxonomy of Oklahoma's pocket gophers. The third is to correlate geographic and ecological factors with both occurrence and speciation in the state.

The author adheres strongly to the theory that isolation is a necessary forerunner to speciation, and that when the latter has occurred, the isolating factors should be demonstrable. In undertaking a study of distribution and speciation, the factors that have contributed to the differentiation of the various geographic races ought to be considered. Therefore a search for the isolating factors that have contributed to the speciation of pocket gophers is an integral part of this distributional study.

Pocket gophers have been known from Oklahoma for many years. Merriam (1895) had specimens from eleven localities in Oklahoma when he wrote his classic revision of the Geomyidae. Elliot (1907) listed two localities not recorded elsewhere. When Blair (1939) prepared his list of records of Oklahoma mammals he had specimens from 24 localities. Davis (1940) examined specimens from 16 locations, most of which also appeared in Blair's list. Baker and Glass (1951) added a series of ten localities. All of these total less than 40 published localities at the present time.

To accomplish the first objective the writer travelled approximately six thousand miles throughout the state, observing the occurrence

or absence of pocket gophers. The presence of pocket gophers within a general area was determined by driving a car at a moderate rate of speed along the highway and keeping a sharp watch for the characteristic mounds of earth. When this method of detection seemed inadequate, the land bordering the road was examined on foot. A quick cruise over from one to three acres of land was usually sufficient to determine the presence of the animals. Examination of the ground on foot was usually necessary in late summer, when high grass made mounds difficult to see from a car. If cruising by car or on foot failed to demonstrate the presence of pocket gophers in an area local farmers or county agricultural agents were contacted to determine the presence or absence of the animals. It was noticed that in regions where pocket gophers were common everyone interviewed was familiar with them. In regions where they were not found, pocket gophers were almost invariably confused with moles. Failure on the part of local residents to verify the presence of pocket gophers, plus their inability to recognize the description, was taken to indicate virtual or complete absence of these animals.

Another method of detection proved useful in eastern Oklahoma. Price (1949) proposed the theory that pocket gophers might have been the architects of the structureless mounds known as "mima" mounds, found abundantly in various parts of the United States coastal plain. These mounds, usually about 6 feet in diameter and 12 to 18 inches high, are common in the hay meadows of eastern Oklahoma. During the wet season of the summer of 1950 pocket gophers concentrated their activity around these structures. The presence of "mima" mounds

proved to be an invariable indicator of the presence of pocket gophers. Where the mounds were absent, diligent search usually failed to reveal the presence of the animals. These structures are only apparent in natural meadows that have long been used for commercial hay production. Cultivation of the land, especially with the use of mechanized farm equipment, apparently eradicates the mounds, for they are rarely seen in tilled fields.

To accomplish the second objective, collections of pocket gophers were made from representative areas throughout the state. When collecting was completed, specimens had been taken from 91 new localities and the total number of specimens available for study in the Oklahoma A and M College Museum of Zoology (OAM) amounted to 475, of which 463 are from Oklahoma. The remaining 12 (from Texas) were used for comparison. An additional 138 specimens were procured by loan from Kansas University (KU), the University of Michigan (UMMZ), and the United States National Museum (USNM), or were studied at the University of Oklahoma (UOMZ). Of the loan specimens, 128 were from Oklahoma, while 10 were from Texas, New Mexico, and Colorado. The total number of specimens from all sources used in this study amounted to 613.

Weights and body measurements for comparison were taken in the field from freshly killed specimens. Skull measurements were made with a vernier caliper to the nearest 0.1 mm. Averages and percentages were computed on a slide rule accurate to the third figure. Color comparisons were made using Ridgway's color standards.[2] Capitalized color names in the synopsis of species are from Ridgway.

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[2]Ridgway, R. 1912. Color Standards and Color Nomenclature. Washington, D. C. 43 pp. 53 pls.

To accomplish the third objective, vegetative, soil, geologic, and physiographic maps of the state were assembled in an attempt to correlate the presence or absence of pocket gophers, and the distribution of subspecific races, with definite physical or ecological regions.

CLASSIFICATION AND DISTRIBUTION OF OKLAHOMA POCKET GOPHERS

The results obtained in attaining the first objective of the study are illustrated in Figures 3, 4, and 9. Pocket gophers are quite generally distributed in Oklahoma except for four mountainous areas. In regions other than montane they may be locally uncommon or absent, due to special local conditions, but these four areas are the only extensive ones from which gophers seem to be entirely excluded. The areas are the Ozark Plateau in the northeast, the Ouachita Mountains in the southeast, the Arbuckle Mountains in the south central region, and the Wichita Mountains in the southwest. These areas will be discussed more fully in the section on ecological factors.

Discovery of *Cratogeomys castanops* in the state by an Oklahoma A and M College field party (Glass 1951) has added another species to the state faunal list, and specimens taken in the summer of 1950 have extended the range through the full length of the Oklahoma Panhandle. There are no color variations in the Oklahoma specimens of *Cratogeomys*, and they are all referable to the single species *castanops*. Slight distinctions in the skull have made it possible to refer specimens from the eastern Panhandle to the subspecies *C. c. perplanus*, while specimens from the Black Mesa region are referred to the subspecies *C. c. castanops*. The detailed comparions are given under the respective synopses.

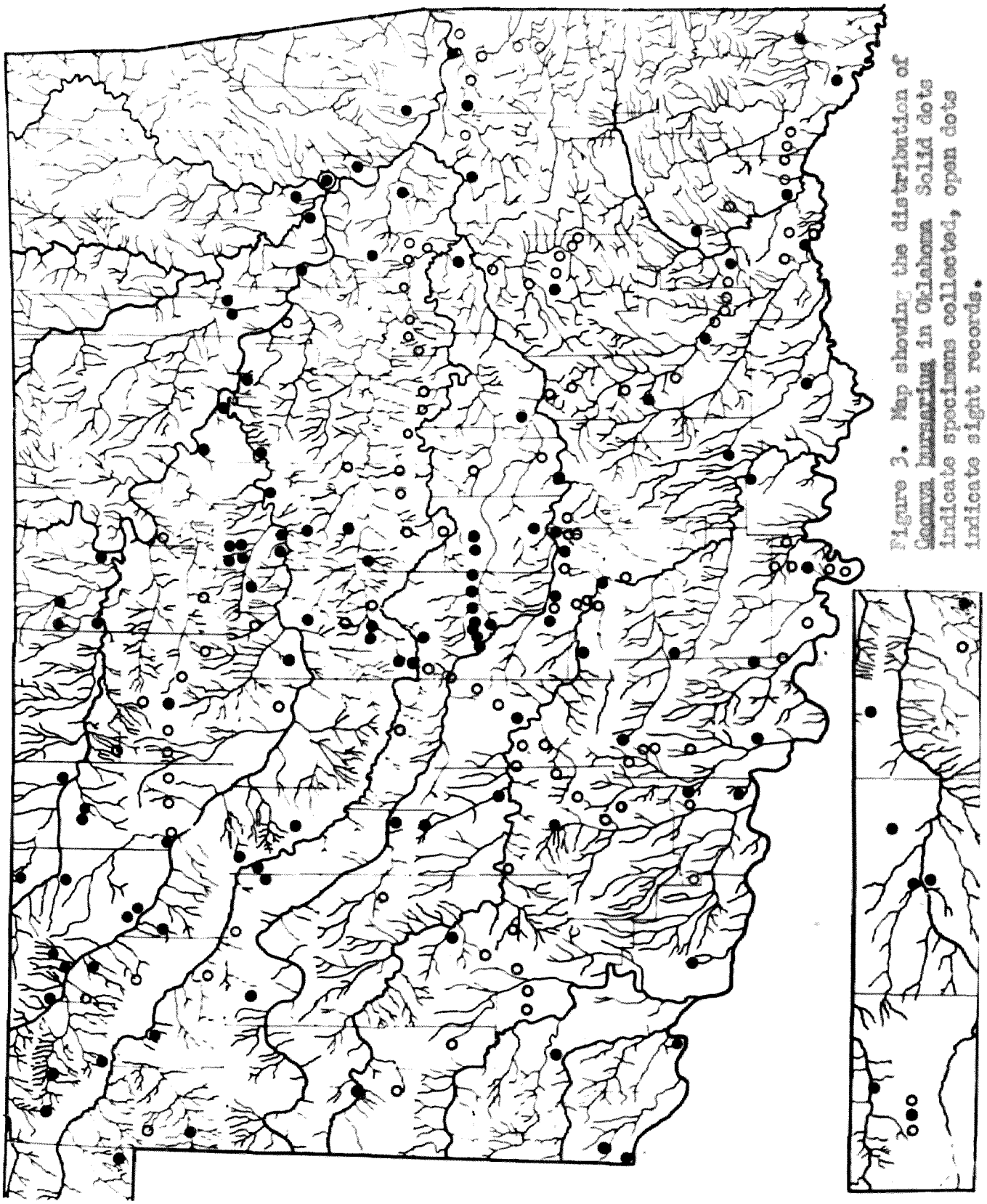

Figure 3. Map showing the distribution of Cocnua hurnarius in Oklahoma. Solid dots indicate specimens collected, open dots indicate light records.

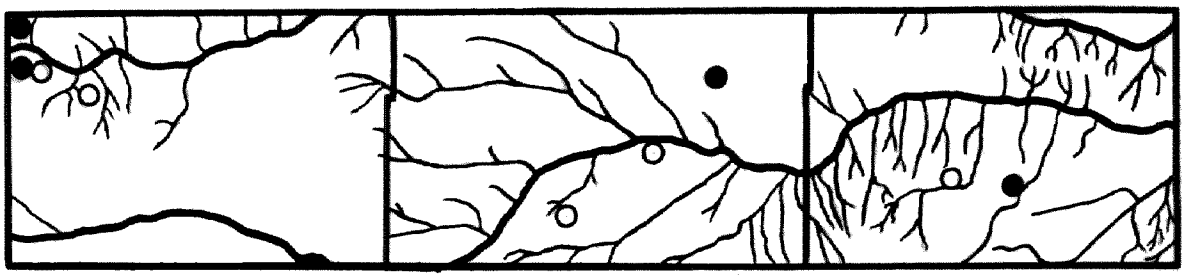

Figure 4. Map showing the distribution of Cratogeomys castanops in the Oklahoma Panhandle. Solid dots indicate specimens collected, open dots indicate sight records. Specimens from the northwestern corner of Cimarron County are C. c. castanops. Those from Texas and Beaver counties are C. c. perplanus.

The subspecies G. b. industrius, described by Villa-R. and Hall (1947) from Kansas has as its only distinguishing feature the "strongly inclined occiput, especially in males." Among the 296 specimens of G. b. major and G. b. jugosicularis examined, 46 have been found to possess this character. However, they are from scattered locations throughout the state, and nowhere is the presence of the character universal. Consequently the subspecies industrius is not included in the Oklahoma fauna, but is regarded as being confined to the state of Kansas.

The taxonomic confusion surrounding the genus Geomys in Oklahoma stems from the fact that two species were originally named for what has now proven to be a continuous population. Merriam (1895) did not indicate that G. lutescens and G. breviceps actually had contiguous ranges. Blair (1939) regarded specimens from the entire state as G. breviceps, but Davis (1940) implied through maps and distribution records that two species existed, whose ranges did not actually meet at any point. At the time of writing the only proven area of intergradation is the region between Norman, Cleveland County, and Tecumseh, Pottawatomie County (Baker and Glass 1951).

As long as the ranges of the two gophers were thought to be separated geographically, morphological characters could be supplemented by distributional data in making identifications. Now that the populations are known to meet and intergrade, it becomes necessary to evaluate the physical characters used in separating them. Merriam (1895) utilized size, coloration, and several cranial characters in distinguishing G. lutescens and G. breviceps, but commented that in most respects the skulls of the two were remarkably alike. Davis (1940) used only two measurements, the length of the hind foot and the length of the dorsal exposure of the jugal compared with the width of the rostrum below the infraorbital opening. He also stated that the coloration of G. b. major was liver brown.

From the beginning of the study it has been apparent that there are three very distinct color phases in Oklahoma and that each color is typical of a certain geographic area. In the eastern part of the state the gophers are dark, with deep brown heavily intermixed with black on the back and sides. Most individuals have a distinct blackish stripe down the back. The under side is also quite dark. Some individuals tend to be melanistic. An abrupt change occurs in the central part of the state, with the dark brown animals being replaced by ones of a reddish color. The western animals usually have little intermixture of black, and only rarely possess a dark middorsal stripe. The under side is lighter than in the eastern form. Transition from typical reddish coloration to the darker shade has been observed to occur in the space of from three to six miles between Wayne and Rosedale, McClain County, between Norman and three miles east of Norman, Cleveland County, between Oklahoma City and Tinker Field, Oklahoma County, and between Stillwater and six miles west of Stillwater,

Payne County. Transition over a slightly greater distance has been demonstrated between Edmond, Oklahoma County, and Wellston, Lincoln County, with specimens from five miles east of Edmond being almost exactly intermediate. Transition also occurs between Guthrie and Coyle in Logan County. Along all of these routes the population of pocket gophers is continuous. South of the Arbuckle Mountains the population in the vicinity of Ringling, Jefferson County, seems to be exactly intermediate. The reddish coloration characterizes the pocket gophers of the entire western part of the state. Another abrupt color change occurs in western Harper County and eastern Beaver County, and the Geomys of the Panhandle are a light yellowish or buffy shade. Transition from reddish to buffy occurs between Buffalo Creek, three miles west of Buffalo, and Doby Springs, ten miles west of Buffalo, both in Harper County. The yellowish form represents the subspecies jugosicularis, known from Colorado and Kansas, but hitherto unreported from Oklahoma.

The three color variants are so distinctive, and the transition from one to the next is so abrupt, that they form the logical basis for designating subspecies of Geomys bursarius. The writer has had no difficulty in assigning the specimens examined to one or the other of the three subspecies on the basis of color alone. The only exceptions have been from Ringling, Edmond, and just east of Norman, where some of the specimens seem to be exactly intermediate. If specimens from the exact zone of transition are excluded, virtually 100 percent separation may be made on the basis of color. None of the other characteristics used by various authors, or used here for the first time, are as easily detected, or as unvarying, although they do provide additional evidence of the distinctness

of the three groups. Therefore the zones of color change are recognized as the subspecific boundaries.

Davis (1940) proposed that the relationship between the interorbital width measured ventral to the interorbital aperture and the length of the dorsal exposure of the jugal be used as a means of separating G. b. dutcheri and G. b. major. According to Davis the rostral measurement exceeds that of the jugal in G. b. dutcheri, with the opposite being true in G. b. major. Separation on the basis of this character is only 73 percent accurate in the case of G. b. dutcheri, 66.5 percent in the case of G. b. major, and 56 percent in the case of G. b. jucosiccularis.

Table 1. Relation of the rostral width measured ventral to the infraorbital aperture to the dorsal exposure of the jugal in 491 specimens of Geomys bursarius of both sexes.

	Rostral width greater	Rostral width equal	Rostral width less
G. b. dutcheri	186	18	53
G. b. major	63	10	145
G. b. jucosiccularis	4	3	9

Davis (loc. cit.) also used the length of the hind foot in the female as a means of separating dutcheri and major. The former was described as having the hind foot less than 30 mm. in length, the latter as having the hind foot greater than 30 mm. in length.

Table 2. Length of hind foot in 303 female specimens of G. bursarius.

	Less than 30 mm	30 mm	greater than 30 mm
G. b. dutcheri	150	5	1
G. b. major	64	21	32
G. b. jucosiccularis	0	4	6

The character (Table 2) applies to G. b. dutcheri with 96 percent accuracy. If "hind foot 30 mm. or over" is substituted for "hind foot over 30 mm." the character applies to G. b. major with only 48 percent accuracy, and to G. b. jugosicularis with 100 percent accuracy.

Merriam (1895) mentioned that in G. lutescens (used to include all of the gophers of western Oklahoma and Texas) the zygomata were more divergent, while in breviceps they were more or less parallel.

Table 3. Comparison of the zygomatic shape in 453 specimens of G. bursarius of both sexes.

	sides divergent	sides parallel
G. b. dutcheri	53	190
G. b. major	124	59
G. b. jugosicularis	19	8

Using this character (Table 3) G. b. dutcheri may be identified with 78 percent accuracy, G. b. major with 68 percent accuracy, and G. b. jugosicularis with 70 percent accuracy. The skulls of G. b. major and G. b. jugosicularis both possess a character most useful in distinguishing them from G. b. dutcheri. In G. b. dutcheri the frontal bone is usually flat, or has a slight rounded depression anteriorly, between the orbits. G. b. major and G. b. jugosicularis have the parietal ridges more highly developed, and encroaching upon the posterior part of the frontal on each side, creating a pair of ridges between which the median part of the bone is depressed into an elongated trough which extends the full length of the frontal bone. The trough seems to become more apparent with age, but is quite evident even in sub-adult individuals. By

contrast, even fully mature males of dutcheri rarely develop such a feature.

Table 4. Nature of the frontal in 464 specimens of G. bursarius of both sexes.

	frontal flat or depressed anteriorly	frontal troughlike
G. b. dutcheri	229	36
G. b. major	18	173
G. b. jugosiccularis	3	25

Using the character (Table 4) G. b. dutcheri may be identified with 86.5 percent accuracy, G. b. major with 90.6 percent accuracy, and G. b. jugosiccularis with 89.4 percent accuracy.

A tendency has been noted for the interorbital region of the frontal bone of Geomys to be narrower in G. b. major and G. b. jugosiccularis than in G. b. dutcheri. The measurement apparently does not increase with age after the animal once obtains its growth. An attempt was made to correlate this with the basilar length. The latter measurement was found to vary so much with age that when the results were plotted no separation was apparent between G. b. dutcheri and the other subspecies. A search was made for some other body measurement that becomes established at an early age and does not increase thereafter. It was found that this is true in the measurement of the hind foot. In series of specimens containing both adult and sub-adult individuals (so judged by having a molt line that had progressed at least halfway down the back, replacing juvenile hair with adult hair) the latter had foot measurements that agreed consistently with those of the former. Tables were drawn up for

both males and females expressing the interorbital width as a percentage of the length of the hind foot (Figs. 5 and 6).

Various authors have used variation in size as a criterion in distinguishing the forms here referred to as G. b. dutcheri and G. b. major. In the present study weights and total lengths have been used to test the validity of claims to distinctness based on size. Adult females only have been used for comparison because of the great variability in size of adult males. Averages were computed for all individuals from each locality, and the averages were plotted on charts (Figs. 7 and 8). G. b. dutcheri always averages less than 235 mm. in total length, with the greatest number falling between 220 and 230 mm. By contrast G. b. major varies greatly from one locality to the next. Adult females of G. b. major from some localities average no larger than G. b. dutcheri, while elsewhere the length averages much greater. The size range for G. b. major varies from 215 to 260 mm., with approximately one half of the localities averaging larger than the maximum size of G. b. dutcheri. On the other hand G. b. fugosiccularis averages consistently large, the size range varying from 245 to 255 mm.

Average weights of adult female G. b. dutcheri are consistently less than 150 gm. except from localities near the zone of intergradation, where they sometimes average considerably larger. The majority of series average below 140 gm., with the greatest concentration near 135 gm. Again G. b. major shows considerable variation, with weights averaging from 130 to nearly 190 gm. By far the majority, however, average above 140 gm. Average weights of G. b. fugosiccularis are more variable than body measurements, for they vary from 144 to 192 gm.

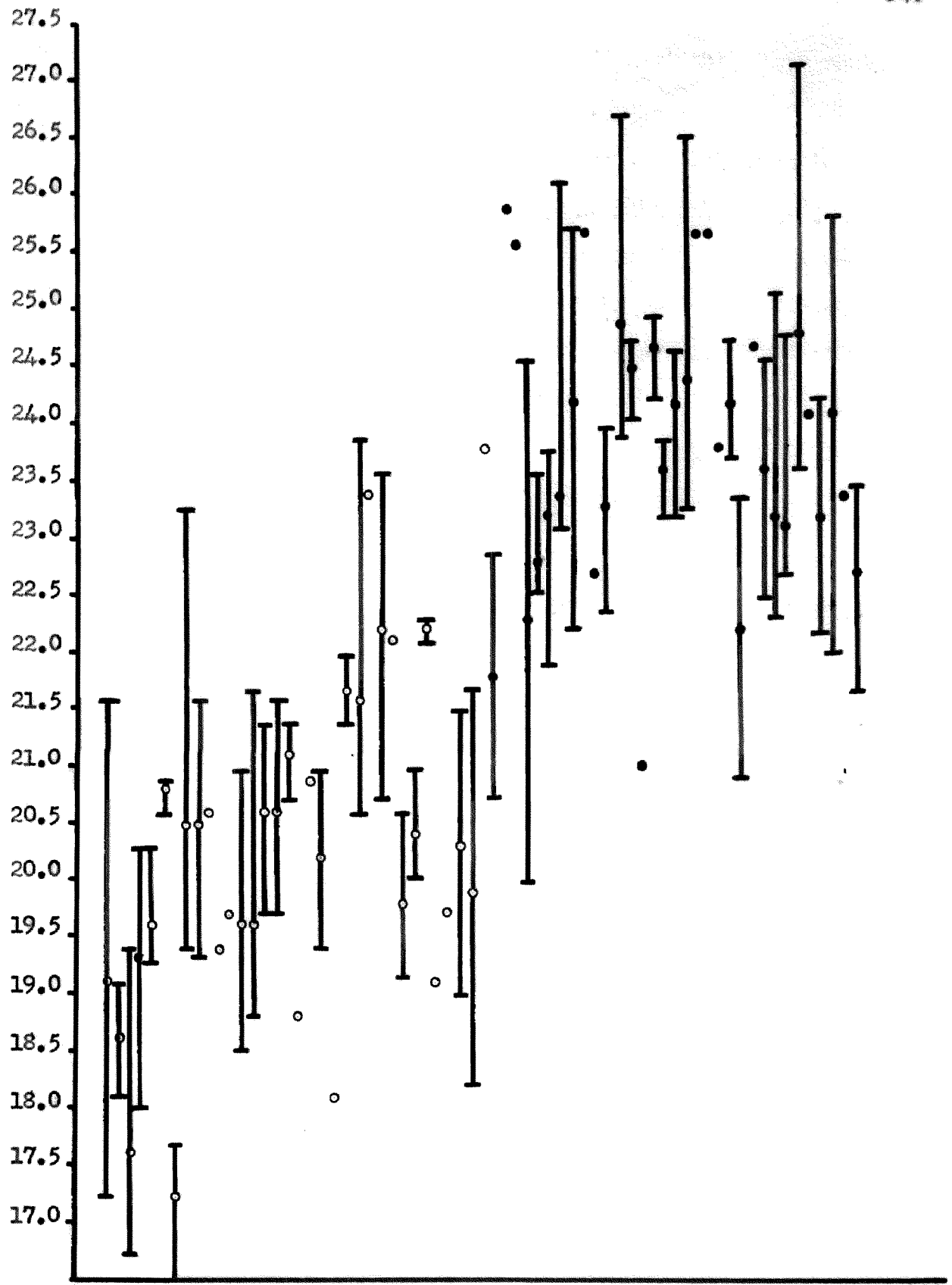

Figure 5. Ratio of interorbital width to length of hind foot in male Geomys bursarius. Each dot indicates the average for a series from one locality. Vertical lines indicate deviation from the average. Solid dots are dutcheri, open dots are major, and half-dots are jugosiccularis, as determined by color. Arrangement of the collections from left to right corresponds to geographic distribution from west to east.

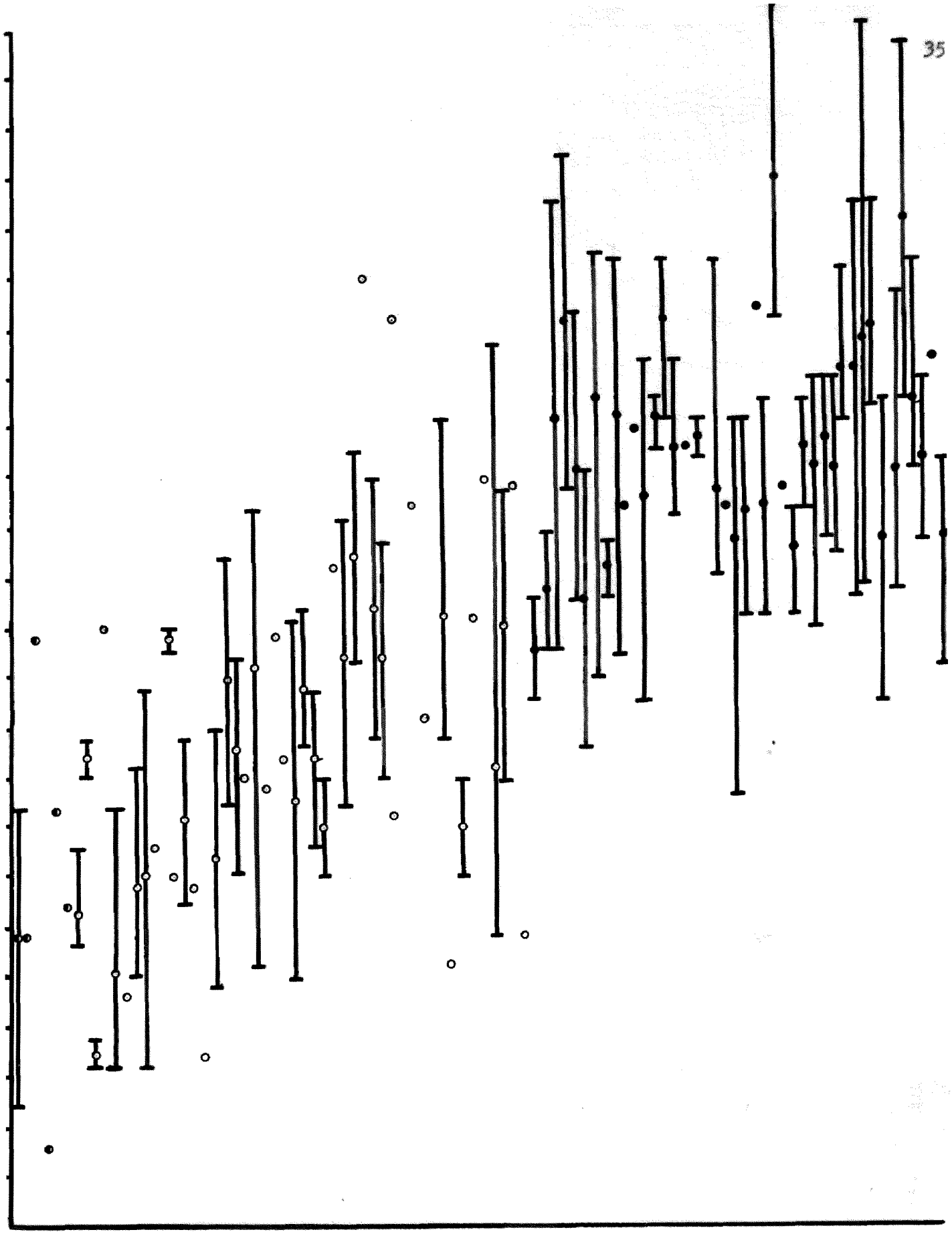

Figure 6. Ratio of interorbital width to length of hind foot in female Geomys bursarius. Meaning of symbols same as in Fig. 5.

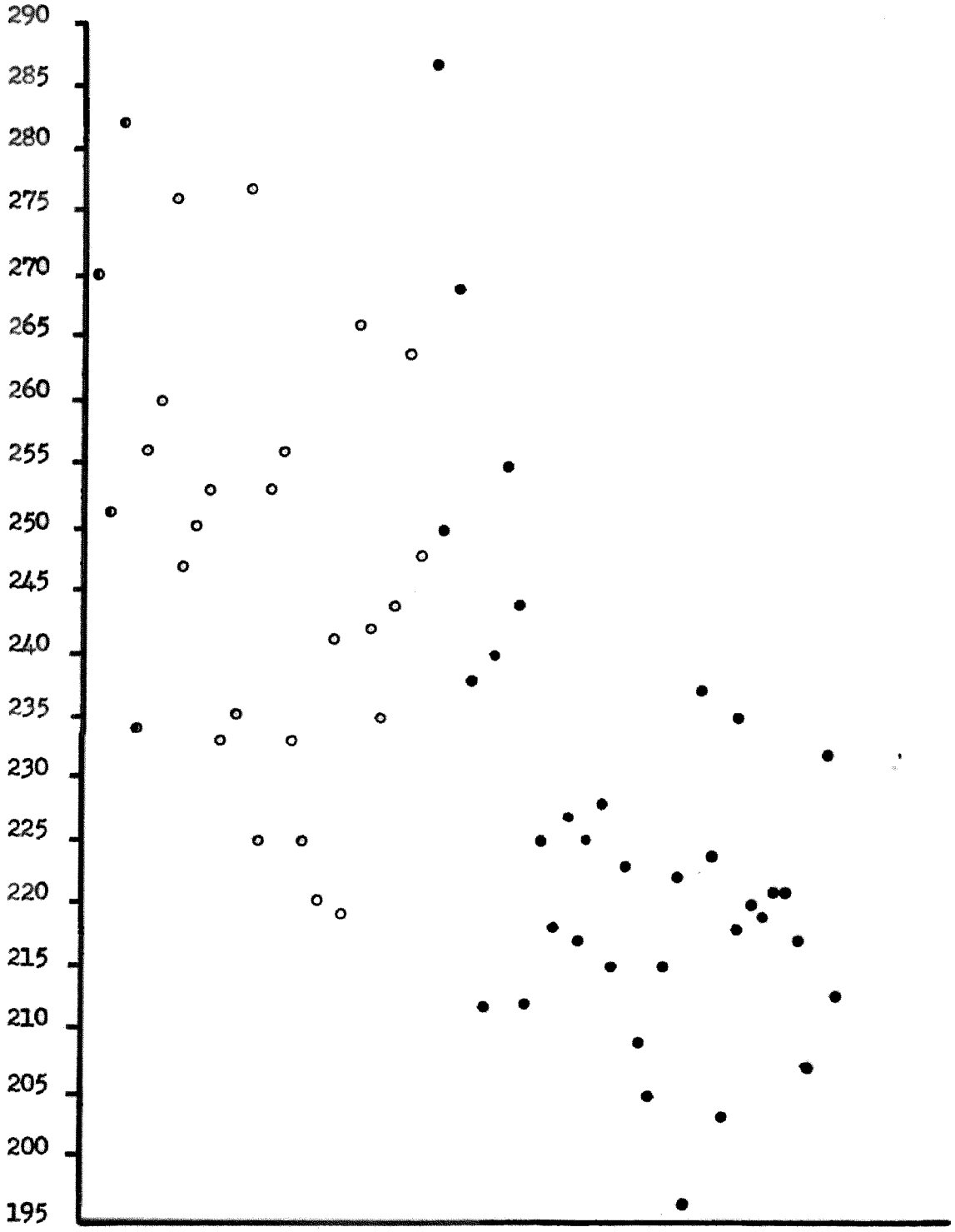

Figure 7. Average weights in grams of adult female Geomys bursarius. Each dot indicates the average for a series from one locality. Solid dots are G. b. dutcheri, open dots are G. b. major, and half-dots are G. b. lutosicularis, as determined by color. Arrangement of collections from left to right corresponds to geographic distribution from west to east.

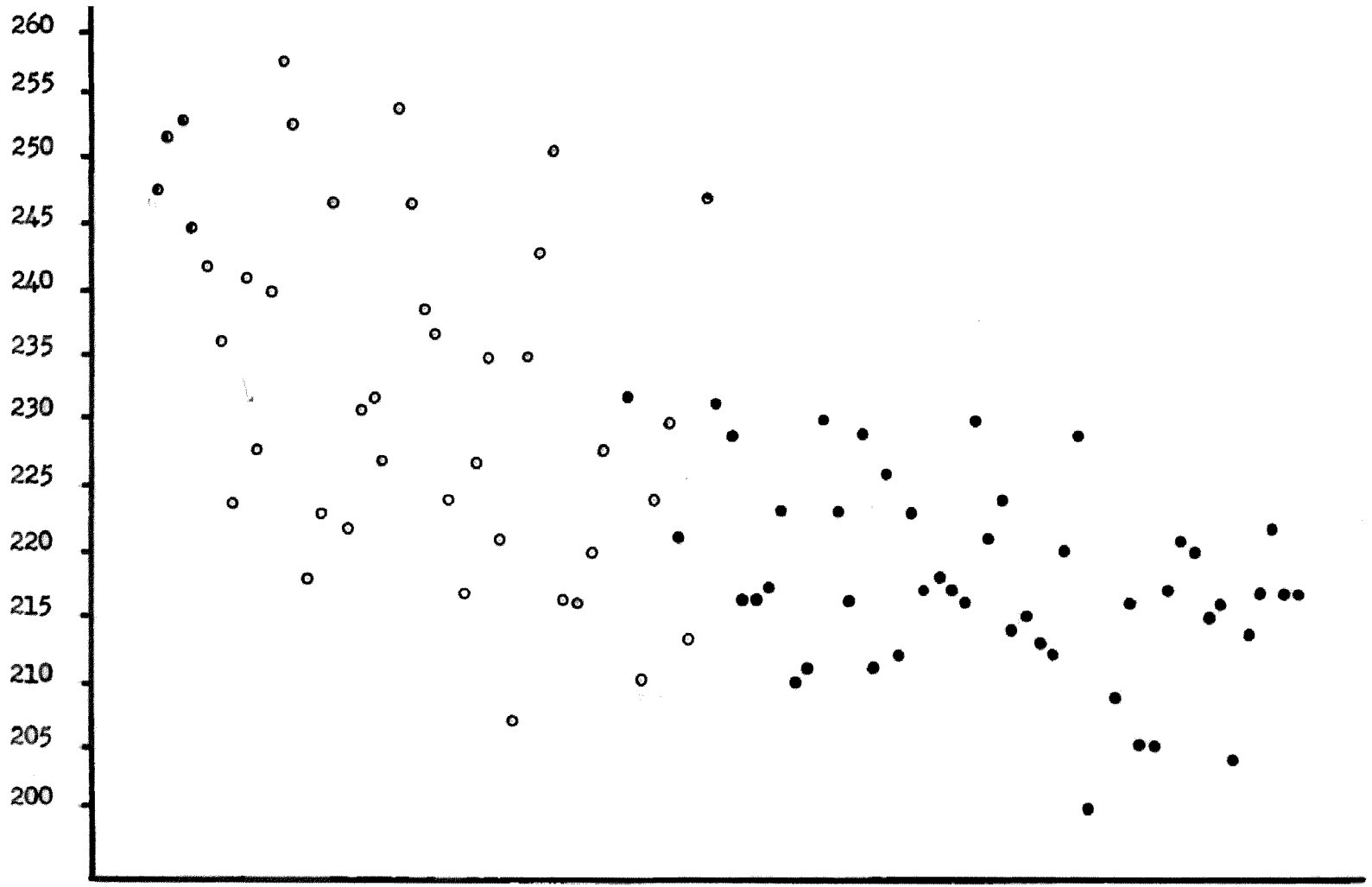

Figure 8. Average total lengths in millimeters of adult female Geomys bursarius. Each dot indicates the average for a series from one locality. Solid dots are G. b. dutcheri, open dots are G. b. maior, and half-dots are G. b. jugosicularis, as determined by color. Arrangement of the collections from left to right corresponds to geographic distribution from west to east.

Geomys bursarius dutcheri Davis

Geomys brevicens Baird, Proc. Acad. Nat. Sci. Phila., 7: 335. April, 1855.

Geomys breviceps breviceps, Merriam, U. S. Biol. Surv., N. Amer. Fauna 8: 129. January 31, 1895.

Geomys brevicens dutcheri Davis, Texas Agric. Exp. Sta. Bull., 590: 12. October 23, 1940.

Geomys bursarius dutcheri, Baker and Glass, Proc. Biol. Soc. Wash., 64: 55. April 13, 1951.

Type locality. - Fort Gibson, Muskogee County, Oklahoma.

Distribution in Oklahoma. - East of a line connecting eastern Noble County on the north with eastern Jefferson County on the south. Generally absent north and east of the Arkansas River except within a few miles of the river. Absent from the Ouachita and Arbuckle Mountain regions (See Fig. 9).

Diagnosis. - A small dark-colored gopher, frequently melanistic; usually a blackish mid-dorsal stripe; sides of nose sooty. Frontal usually flat or with a rounded depression between the orbits. Rostral width ventrad to infraorbital aperture usually exceeding length of dorsolateral exposure of jugal.

Color. - Back Sayal Brown to Tawny Olive, sometimes near Hair Brown in individuals that tend towards melanism. Hairs Deep Neutral Gray at base, brown distally, and tipped with black. Blackish coloration tending to be concentrated in middorsal region in most specimens, forming a distinct middorsal stripe. Black around tip of nose. Belly hair Neutral Gray at base, tipped with Pinkish Cinnamon. Considerable variation in

color, even in individuals from the same location taken at the same season. A widespread tendency towards melanism. Belly color variable, but usually darker than in major, varying from Pinkish Cinnamon in most specimens to near Avellaneous. Variable white patches on belly occasionally present, occurring in specimens from scattered localities. General appearance brown with blackish middorsal stripe, never reddish. Some melanistic individuals have general appearance of Bister or Olivaceous-Black on back. Color of juvenile hair usually some shade of gray.

External features. - Size consistently small, adult females averaging from 200 to 235 mm. total length. Hind foot of adult females rarely equalling 30 mm. in length. Average weight of adult females less than 150 gm., except near zone of intergradation with major, where some populations average much heavier.

Skull. - General appearance rather smooth, without strongly developed ridges, zygomata rather weak with sides usually parallel. Frontal bone either entirely flat above, or with a rounded depression directly between the orbits. Rostral width ventrad to infraorbital aperture usually greater than dorsolateral exposure of jugal. Interorbital region rather wide, ratio of interorbital width to length of hind foot usually above 23 percent.

Comparisons. - From Geomys bursarius major, this subspecies differs in its consistently smaller size, exemplified in several proportionate measurements; in its brown color with heavy admixture of black, rather than a uniformly reddish appearance; and in the character of the frontal, which in major has an elongated trough involving the full length of the bone. The width of the rostrum ventrad to the infraorbital aperture

usually is greater than the dorsolateral exposure of the jugal, (see Table 1), and there is a tendency for the interorbital region to be wider than in major. (see Figs. 5 and 6).

Specimens examined 289, as follows. - Atoka County: 5 mi. E. Atoka 3 (OAM). Bryan County: 1 mi. S. Blue 8 (OAM). Choctaw County: Sawyer 3 (OAM), across Red River from Arthur, Texas 2 (USNM). Cleveland County: 3 mi. E. Norman 4 (KU), 5 mi. E. Norman 1 (UOMZ), 7 mi. E. Norman 3 (KU), 12 mi. E. Norman 5 (KU), 17 mi. E. Norman 3 (KU). Coal County: 1 mi. W. Coalgate 3 (OAM). Creek County: Oilton 1 (OAM). Haskell County: Keota 2 (OAM), Whitefield 5 (OAM). Hughes County: Holdenville 5 (OAM). Jefferson County: 1 mi. E. Ringling 7 (OAM). Johnston County: Milburn 1 (OAM), S. side Washita River at Ravia 3 (OAM). Lincoln County: Agra 3 (OAM), Chandler 7 (OAM), Wellston 7 (OAM). Logan County: Coyle 6 (OAM). Love County: 7 mi. S. Marietta 11 (OAM). McClain County: S. side S. Canadian River at Asher 3 (OAM), 2 mi. W. Byars 5 (OAM), Rosedale 1 (OAM). McCurtain County: 13 mi. SE. Broken Bow 1 (UOMZ), 2 mi. SE. Idabel 3 (OAM). McIntosh County: Eufaula 9 (OAM). Muskogee County: Braggs 13 (OAM), Fort Gibson 15 (OAM) 8 (USNM), 3 mi. E. Wainwright 2 (UOMZ), 1 mi. E. Warner 5 (OAM). Oklahoma County: 5 mi. E. Edmond 4 (OAM), 2 mi. E. Tinker Field 4 (OAM). Pawnee County: ½ mi. W. Cleveland 3 (OAM), 4 mi. N. Keystone 1 (OAM). Payne County: 5 mi. E. Perkins 1 (OAM), 1 mi. W. Perkins Corner 10 (OAM), Stillwater 18 (OAM), 3 mi. NW. Stillwater 1 (UMMZ), 6 mi. N. Stillwater 1 (OAM), 2 mi. W. Stillwater 1 (OAM), 2 mi. SW. Yale 4 (OAM). Pittsburg County: McAlester 8 (OAM). Pontotoc County: Tyrola 2 (OAM). Pottawatomie County: Asher 7 (OAM), Tecumseh 6 (KU) 1 (OAM), 6 mi. W. Tecumseh 5 (KU). Pushmataha County:

Antlers 4 (OAM), 2 mi. S. Finley 2 (OAM). Sequoyah County: Redland 1 (USNM), 2 mi. E. Vian 4 (OAM). Tulsa County: Garnett 4 (UMMZ), Mohawk Park 7 (OAM) 11 (UMMZ), 8 mi. W. Red Fork 3 (USNM), 5 mi. W. Sand Springs 7 (OAM), Tulsa 1 (USNM). Wagoner County: S. side Arkansas River at Coweta 7 (OAM), 4 mi. NW. Okay 3 (OAM), 1 mi. S. Vann's Lake 1 (OAM).

Geomys bursarius major Davis

Geomys bursarius lutescens Merriam, U. S. Biol. Surv., N. Amer. Fauna 4: 51. October 8, 1890.

Geomys lutescens Merriam, U. S. Biol. Surv., N. Amer. Fauna 8: 127. January 31, 1895.

Geomys breviceps llanensis Bailey, U. S. Biol. Surv., N. Amer. Fauna 25: 130. 1905.

Geomys lutescens major Davis, Texas Agric. Exp. Sta. Bull., 590: 32. August, 1940.

Geomys bursarius major, Villa-R. and Hall, Univ. Kans. Publ., Mus. Nat. Hist., 1 (11): 229. November 29, 1947.

Type locality. - Eight miles west of Clarendon, Donley County, Texas.

Distribution in Oklahoma. - West of a line connecting eastern Noble County on the north with eastern Jefferson County on the south, except for the Panhandle and extreme northwestern corner of the main part of the state. Absent from the Wichita Mountains region. (See Fig. 9).

Diagnosis. - A reddish-colored gopher, generally with very little admixture of black, and only rarely with any mid-dorsal dark stripe or sooty coloration about the nose. Size quite variable. Frontal usually with an elongated trough extending the full length of the bone. Rostral width ventrad of interorbital aperture usually failing

o equal length of dorsolateral exposure of jugal.

Color. - Back hairs Neutral Gray at base, tipped with Cinnamon ufous or Russet, very little black on extreme tips of hairs. Belly air Neutral Gray at base, Light Ochraceous-Buff at tips. Occasional ndividuals have belly hairs nearly white to the base. Usually no endency towards a mid-dorsal dark stripe, and no concentration of black bout the nose. General appearance distinctly reddish, belly generally ighter-appearing than in dutcheri. Some summer specimens have an area n each side of the face and shoulder where the hairs have the basal gray much lighter, giving the area a lighter tone. This is a tendency owards a condition that occurs uniformly in jugosicularis. Color of uvenile hair usually clear Cinnamon, with basal gray almost completely bsent.

External features. - Size varying from small to quite large, adult emales averaging from 215 to 260 mm. in total length. Hind foot of dult females frequently equalling or exceeding 30 mm. Average weight f adult females varying from 130 to 200 gm.

Skull. - General appearance somewhat more rugose than dutcheri, ygomata frequently with sides more or less divergent. Frontal bone ith a trough-like depression extending the full length from the nasals o the parietals. Rostral width ventrad to infraorbital aperture sually less than dorsolateral exposure of jugal. Interorbital region ather narrow, ratio of interorbital width to length of hind foot usually ess than 23 percent.

Comparisons. - Compared with Geomys bursarius jugosicularis this orm differs chiefly in coloration, being distinctly reddish in tone,

ather than pale tawny yellow. In size major is more variable than jugosiccularis, which is consistently large (see Fig. 8). Series of ndividuals of major from different locations show an astonishing mount of variability, with some series averaging no larger than dutcheri, hile other series average as large or larger than jugosiccularis. In ranial characters major and jugosiccularis are closely similar, both aving a pronounced trough in the frontal bone, and a narrow interor- bital region. The angularity of the zygomata shows considerable vari- bility, with some series having the sides strongly divergent, while in thers they are nearly or quite parallel.

Specimens examined 265, as follows. - OKLAHOMA: Alfalfa County: ½ mi. S. 2 E. Cherokee 1 (UOMZ), Great Salt Plains Wildlife Refuge (OAM), Wheatland Experimental Farm 8 (OAM). Blaine County: Canton (OAM), Roman Nose State Park 5 (OAM). Caddo County: 1 mi. N. Anadarko (OAM), Apache 2 (OAM) 1 (USNM), Hinton 4 (OAM). Carter County: 2 mi. . Ratliff City 5 (OAM). Cleveland County: Norman and vicinity 20 (USNM) 4 (UOMZ) 5 (KU) 4 (OAM), 1.4 mi. E. Norman 2 (KU), 2 mi. E. Norman 1 KU). Comanche County: Lawton 1 (USNM), Mt. Scott P.O. 3 (USNM). otton County: 8 mi. E. Walters 5 (OAM). Dewey County: 5 mi. SW. Canton (KU), 5 mi. SE. Vici 5 (OAM). Ellis County: Shattuck 5 (OAM). Garfield ounty: Enid 1 (KU). Garvin County: 3 mi. E. Lindsay 2 (OAM), Pauls alley 2 (OAM). Grady County: 2 mi. E. Chickasha 10 (OAM). Greer County: angum 5 (OAM). Harmon County: 1 mi. SW. Hollis 9 (OAM). Harper County: uffalo Creek 3 mi. W. Buffalo 4 (OAM), Southern Plains Experimental Range -5 mi. N. Ft. Supply 3 (USNM) 19 (OAM). Jefferson County: 3 mi. S. aurika 4 (OAM). Kay County: Blackwell 2 (OAM), 10 mi. W. Blackwell 1

(OAM), Ponca Agency 3 (USNM), Ponca City 4 (OAM), 10 mi. W. Tonkawa 2 (OAM). Logan County: Crescent 1 (OAM), Guthrie 1 (OAM). Major County: Cimarron River near Cleo Springs 1 (UOMZ), Ewers Creek 4 (OAM). McClain County: Wayne 4 (OAM). Oklahoma County: Oklahoma City 1 (USNM) 2 (OAM), Edmond 2 (OAM). Payne County: 4½ mi. W. Stillwater 2 (OAM), 6 mi. W. Stillwater 1 (OAM). Roger Mills County: 1 mi. N. Cheyenne 4 (OAM). Stephens County: 1 mi. E. Marlow 5 (OAM). Tillman County: Frederick 4 (OAM). Washita County: 4 mi. E. Cordell 7 (OAM). Woods County: Alva 2 (OAM), 12 mi. N. Alva 2 (OAM), 3 mi. E. Camp Houston 2 (OAM), E. side Cimarron River at U.S. 64 8 (OAM), Freedom 1 (OAM), Waynoka 3 (UMMZ). Woodward County: Alabaster Cavern 2 (OAM), Woodward 8 (USNM).

TEXAS: Floyd County: 6 mi. S. Quitaque 6 (OAM). Garza County: Post 5 (OAM).

Geomys bursarius jugosiccularis Hooper

Geomys bursarius lutescens Merriam, U. S. Biol. Surv., N. Amer. Fauna 4: 51. October 8, 1890.

Geomys lutescens Merriam, U. S. Biol. Surv., N. Amer. Fauna 8: 127. January 31, 1895.

Geomys lutescens jugosiccularis Hooper, Occ. Pap. Mus. Zool., Univ. Mich., (420): 1. June 28, 1940.

Geomys bursarius jugosiccularis, Villa-R. and Hall, Univ. Kans. Publ., Mus. Nat. Hist., 1 (11): 226. November 29, 1947.

Type locality. - Lamar, Prowers County, Colorado.

Distribution in Oklahoma. - The Panhandle and extreme northwestern corner of main part of state. Not found in the canyon region of northwestern Cimarron County (see Fig. 9).

Diagnosis. - A pale-colored gopher, never distinctly reddish in tone. Size consistently large, adult females averaging 245 mm. or more in total length. Skull characters as in major.

Color. - Hairs on back Light Neutral Gray at base, Cinnamon to Pinkish-Cinnamon at tips. Pure Cinnamon-Buff on cheeks and shoulders with basal gray much lighter. Belly hairs Light Neutral Gray at base, Pinkish-Buff, Tilleul-Buff, or White at tips, occasionally white to base of hairs. Juvenile hair Pale Neutral Gray at base, Light Pinkish Cinnamon at tips.

External features. - Size consistently large, adult females averaging from 245 to 255 mm. in total length. Hind foot of adult females always 30 mm. or more in length. Average weight of adult females varying from 144 to 192 gm.

Skull. - General features as in major. Large males tend to have the skull more rugose, with more protruberances, and with greater angularity, than major.

Comparisons. - Specimens from Forgan, Doby Springs and Slapout show a tendency towards major in having a slightly more reddish cast than the ones from Guymon and Boise City. Specimens from Shattuck and Buffalo are regarded as major tending towards fuscosiccularis in their slightly paler color and in having areas of pure Cinnamon on the cheeks and shoulders.

Specimens examined 31, as follows. - Beaver County: 2 mi. W. Forgan 5 (OAM), 3 mi. S. and 3 E. Slapout 1 (OAM). Cimarron County: 12 mi. N. Boise City 1 (OAM), 8 mi. W. Boise City 16 (OAM). Harper County: Doby Springs 4 (OAM). Texas County: Guymon 3 (OAM), Hooker 1 (OAM).

Cratogeomys castanops castanops (Baird)

Pseudostoma castanops Baird, Report of Stanbury's Expedition to Great Salt Lake, p. 13. June, 1852.

Geomys castanops, LeConte, Proc. Acad. Nat. Sci. Phila., 6: 163. 1852.

Cratogeomys castanops, Merriam, U. S. Biol. Surv., N. Amer. Fauna 8: 159. January 31, 1895.

Cratogeomys castanops castanops, Nelson and Goldman, Proc. Biol. Soc. Wash., 47: 136. June 13, 1934.

Type locality. - "Prairie road to Bent's Fort," near Las Animas, Bent County, Colorado.

Distribution in Oklahoma. - The canyon region of northwestern Cimarron County (see Fig. 4).

Diagnosis. - A yellowish pocket gopher, 250-300 mm. in total length, with unisulcate upper incisors. Braincase moderately arched.

Color. - Hairs of back deep Neutral Gray at base, between Clay Color and Tawny Olive distally. Belly hair Neutral Gray, tipped with Tilleul-Buff. Cheeks Clay Color with bases of hairs much lighter gray. Skin of feet and tail mottled with black pigment. Tail with distal half sparsely clothed with blackish hairs, sometimes with white hairs at tip.

Skull. - The unisulcate upper incisors distinguish these pocket gophers from all other species in North America. In large mature males the parietal ridges meet to form a strong sagittal crest. In mature females the parietal ridges barely meet, and do not form a sagittal crest.

Remarks. - These large pocket gophers were first reported from the state by Glass (1951). At that time the species was known only from the

immediate vicinity of Black Mesa, in the sandstone canyons of northwestern Cimarron County.

Specimens examined 15, as follows. - COLORADO: Bent County: Las Animas 2 (USNM). Otero County: La Junta 2 (USNM), Olney 1 (USNM). NEW MEXICO: Colfax County: Chico Springs 2 (USNM). OKLAHOMA: Cimarron County: 6 mi. N. Kenton 5 (OAM), Tesequite Canyon 3 mi. E. and 7 S. Kenton 3 (OAM).

Cratogeomys castanops perplanus Nelson and Goldman

Pseudostoma castanops Baird, Report of Stansbury's Expedition to Great Salt Lake, p. 13. June, 1852.

Geomys castanops, LeConte, Proc. Acad. Nat. Sci. Phila., 6: 163. 1852.

Cratogeomys castanops, Merriam, U. S. Biol. Surv., N. Amer. Fauna 8: 159. January 31, 1895.

Cratogeomys castanops perplanus Nelson and Goldman, Proc. Biol. Soc. Wash., 47: 136. June 13, 1934.

Type Locality. - Tascosa, Oldham County, Texas.

Distribution in Oklahoma. - High plains of Texas and Beaver Counties (see Fig. 4).

Diagnosis. - Color and size as in castanops. Braincase slightly flatter, and lateral portion of squamosals more expanded than in castanops, skull otherwise as in castanops.

Comparisons. - In the series of Cratogeomys castanops from the eastern part of the Oklahoma Panhandle the characteristics of the subspecies perplanus are distinguishable in some individuals, while in others the arching of the braincase and the character of the squamosals resemble

the subspecies castanops. Lack of a large series of specimens from the high plains of Texas makes it impossible to evaluate the validity of the characters ascribed to the two subspecies. In the ten specimens from the United States National Museum three are paratypes of perplanus, and the 7 castanops were used by Nelson and Goldman in their revision of the genus. The points of distinction claimed by Nelson and Goldman are detectable in these specimens, but they do not seem to be as salient as the original text would lead one to believe. Since Nelson and Goldman did not describe their method of comparison it is difficult to repeat their study. Under these circumstances it is best to regard the two as valid but very closely similar subspecies. The Oklahoma specimens are regarded as perplanus on the basis of their distribution on the high plains, and on their possession of the cranial characters of perplanus in some individuals. In Oklahoma the range is separated from that of typical castanops by a wide belt of deep sandy soil in which only Geomys occurs.

Remarks. - Evidence of the presence of these gophers was obtained at two additional points in the Oklahoma Panhandle; one mile northeast of Goodwell, and the south side of the North Canadian River two miles northeast of Guymon. At both locations burrows fully five inches in diameter were discovered, but no specimens were obtained. The largest Geomys burrow excavated was a tight fit for the arm at the elbow, while that of any Cratogeomys easily admitted the arm up to the shoulder.

Specimens examined 13, as follows. - NEW MEXICO: Guadalupe County: Cuervo 1 (USNM). OKLAHOMA: Beaver County: 1 mi. E. Elmwood P. O. 4 (OAM). Texas County: Hooker 5 (OAM). TEXAS: Dawson County: 8 mi. NE. Lamesa 1 (OAM). Howard County: Big Springs 1 (USNM). Oldham County: Tascosa 1 (USNM).

ECOLOGICAL FACTORS AFFECTING DISTRIBUTION

The distribution of a fossorial animal such as the pocket gopher is naturally affected by the nature of the medium in which it lives. It has not been surprising to learn that the presence or absence of these animals is largely determined by the structure of the soil strata at or near the surface of the ground. Some authors, notably Davis (1940a) and Davis, Ramsey, and Arendale (1938), have discussed the function of sand as a limiting factor in the distribution of pocket gophers. Davis (loc. cit.) correlated the distribution of the pocket gophers of Texas and Oklahoma with the distribution of sandy soils as outlined in a soils map by W. T. Carter (1931). Other authors have referred at times to the preference of pocket gophers for certain soil types. Swenk (1939) remarked that G. bursarius majusculus was found mainly in regions where loess soils predominate. Bailey (1907) described Cratogeomys as occupying regions of mellow soil, and Warren (1942) claimed that the same genus was ecologically separated from Geomys, the former being found in thin gravelly upland soils, and the latter in the deeper softer soils of the river valleys.

Pocket gophers do not occupy mountainous areas in Oklahoma. The Wichita Mountains in the southwestern part of the state are of igneous origin, being composed of granite. The mountains themselves are nearly devoid of soil, except in the crevices. The flats between the peaks are mostly paved with small round boulders, and wherever there is a considerable depth of soil it is permeated with granite gravel. Pocket gophers are not found in this type of soil. The specimens referred to by Davis as having come from Mount Scott were actually from Mount Scott

Post Office, which was located on Cache Creek, on the flats or plains east of the mountains. Pocket gophers are found on all sides of the Wichita Mountains where the gravelly soil is replaced by soil of a more homogeneous texture.

The Arbuckle Mountains are composed of upended strata of sedimentary rock, mainly limestone and sandstone. The soil is thin and full of stones, a condition that persists for some distance around the area of the mountains proper. The mountains are bisected by the Washita River, which has a sandy floodplain varying in width up to about a mile. Pocket gophers are found in the vicinity of Wynnewood, north of the mountains, but not in the river bottom in the mountains themselves. All parts of the Arbuckle region traversed by the author were found to be completely devoid of pocket gophers.

The Ouachita Mountains are composed of tilted strata of sedimentary rocks, mainly sandstone and shale, which form range after range of high parallel ridges. The soil in the valleys of the larger rivers is quite sandy, but is full of pieces of rock washed down from the slopes of the hills. Near the edge of the mountain mass the streams have worn wide valleys where a considerable amount of sandy soil, relatively free from stones, has accumulated. In some of these river plains, such as those of the Poteau River, Gaines Creek, and Kiamichi River, pocket gophers are found, but they are never found in the hills, nor very far into the hill region along the rivers. The wide flat plain of the Kiamichi River in the vicinity of Albion and Talihina is uninhabited by pocket gophers, and only the lower reaches of the Poteau River Valley seem to be inhabited by them.

The Ozark Mountain Region is composed of sedimentary rocks, mainly sandstone, limestone, and chert, lying east of the Grand River and north of the Arkansas. The soils are thin and full of stones. Pocket gophers are found only on the southern and southwestern borders of this region where the hills give way to the Arkansas River Valley.

West of the Ozark Hills there is an extensive area of hills and prairies lying north of the Arkansas River where pocket gophers are generally absent. The hilly portion lies mainly in Osage County and forms the northern end of a long chain of sandstone hills that extends southward approximately two thirds of the way across the state. The Arkansas, Deep Fork, and North and South Canadian rivers cut their way through these hills, forming river valleys where pocket gophers are found in great abundance. The hills themselves are more eroded and dissected in the southern part, forming many upland meadows. Here in many places the sandstone has more or less completely disintegrated, forming a sandy soil in which pocket gophers are always found. North of the Arkansas River the hills are less eroded, and the soil is usually more rocky. Pocket gophers are not found in these hills.

The prairies lying between the Osage Hills and the Ozarks are commonly called the Cherokee Prairies. They are open grasslands, and seemingly should prove attractive to pocket gophers. However, the animals seem to be absent from all except the southern part; where the prairies meet the Arkansas River Valley between Tulsa and Wagoner. The reason for the absence of pocket gophers lies in the structure of the subsurface soil layers. In most places the topsoil is quite shallow, often six inches or less in depth, and is underlaid by layers of sandstone and

shale. These seem to form an effective barrier to the spread of pocket gophers. There may be isolated spots within the Cherokee Prairie where the soil is deep and in which pocket gophers have become established. If so they are small in area and widely scattered, and their occurrence has not been detected in this study. In general the underlying layers are undisturbed, with very little breaking up of the strata. Where decomposition has occurred, the shale breaks up into smaller pieces of stone, whereas the sandstone usually breaks down into fine sand. When sandstone and shale, or shale alone, constitute the subsurface layer, the soil is full of stony chips which seem to act as a deterrent to pocket gophers.

Except in the four areas mentioned above, pocket gophers occur generally throughout the state. When the problem was undertaken it was hoped that clearly distinguishable physical barriers could be demonstrated as having affected differentiation between the various subspecies occurring in the state. Except for the isolated mountain masses previously mentioned, Oklahoma does not have striking physical features that could act as barriers. The general topography is rolling, and the wide meandering rivers have sandy flood plains that serve better as highways than as barriers to a fossorial animal such as the pocket gopher. It is amply clear that rivers have played no part in speciation in Oklahoma, for the large rivers flow mainly from west to east, while the lines separating subspecies of pocket gophers run north and south.

It is not possible to classify the choice of habitat of the pocket gophers over an area as large as Oklahoma, except in the most general terms. Many factors enter into the selection of a living site, and the absence of a species from one particular location is not necessarily

indicative that that place is unsuitable. Availability of food, and freedom from molestation are important factors in habitat preference. Indicative of this is the choice of alfalfa fields and cemeteries as preferred collecting sites. If pocket gophers are present in an area they may almost invariably be detected by examining the nearest alfalfa field or country burial ground. Only continued demonstration of their absence should be taken to indicate that the species does not occur over a considerable area.

The types of vegetational climaxes in Oklahoma affect occurrence, but apparently do not affect speciation. Pocket gophers for the most part prefer the grasslands or open woods where there is an abundance and variety of grass and herbaceous plants. Dense woods with few plants growing on the forest floor are not attractive to these animals. Consequently in eastern Oklahoma, where forest and prairie are intermingled, the range of pocket gophers is discontinuous. Nevertheless, there is but one subspecies of pocket gopher in eastern Oklahoma. The vegetation type map accompanying Duck and Fletcher's (1943) game survey of Oklahoma shows that the oak forests that characterize much of eastern Oklahoma encroach upon the western half of the state particularly along the Cimarron, North and South Canadian, and Washita Rivers. The eastern subspecies of pocket gopher does not follow these westward extensions of the eastern vegetation type. The western part of Oklahoma is covered with a varied assortment of vegetational climaxes, in addition to the oak intrusions from the east. Tall grass, short grass, and sagebrush are intermingled throughout the main part of the state, while the latter two are found in the Panhandle. Figure 9 shows that the distribution of the subspecies of Geomys is not limited by the boundaries of any of these vegetation types.

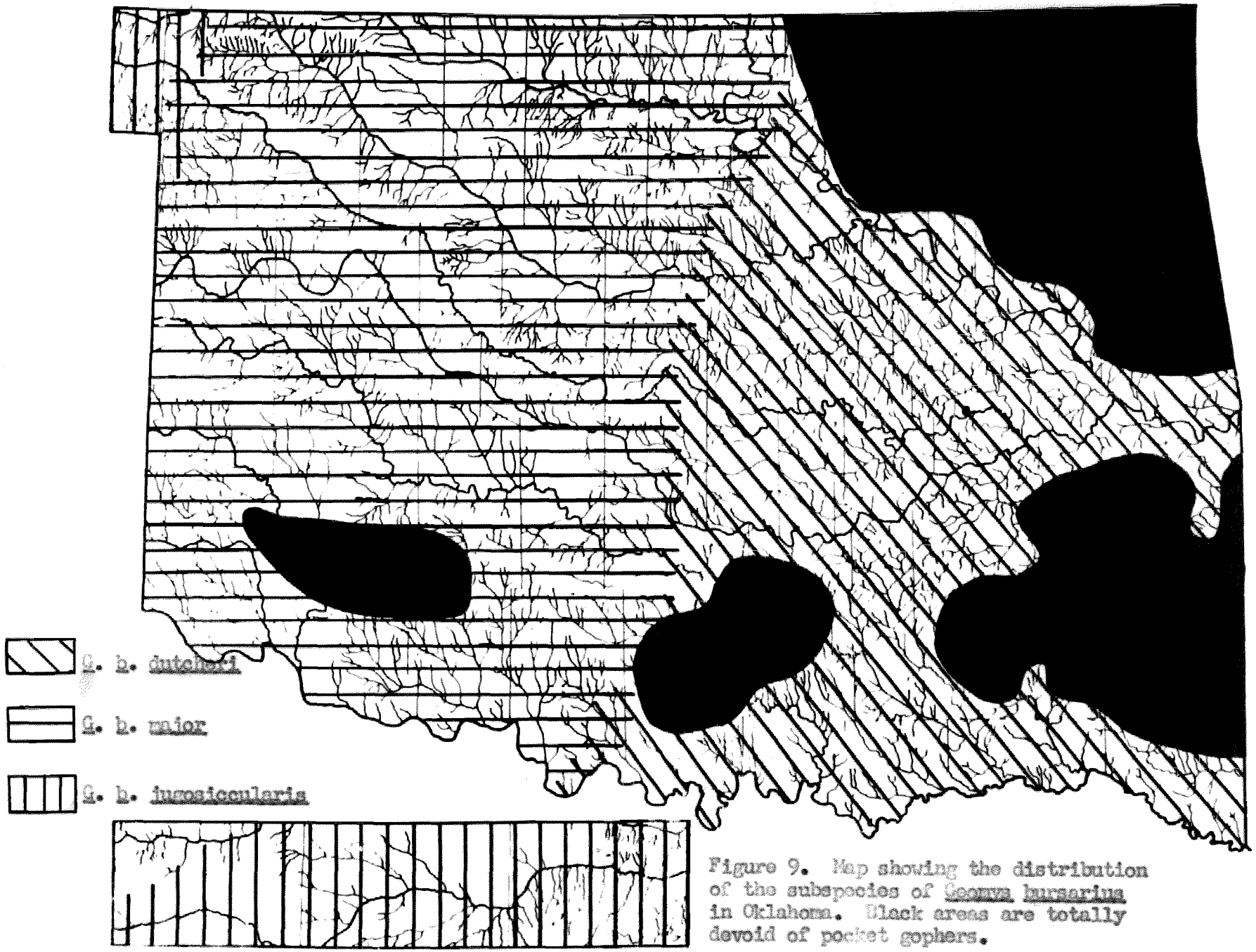

Figure 9. Map showing the distribution of the subspecies of Geomys bursarius in Oklahoma. Black areas are totally devoid of pocket gophers.

The composition of the topsoil determines to a great extent the occurrence and abundance of pocket gophers. Sandy soil favors them, for they are most numerous in the dune areas in the western part of the state. However, gophers are not by any means limited to soils of a sandy nature. In many places in the western half of the state they are found in areas of pure clay. They do not occur in the scattered regions of the southwest, mainly in the vicinity of Mangum, Hollis, and Altus, where the clay is very heavy, or is mixed with gravel, but in contiguous areas of lighter clay or more sandy soils they are always found. The presence of a thick layer of gypsum does not deter pocket gophers from occupying an area. In the gypsum hills region of western Oklahoma (see Fig. 10) there is a layer of this rock approximately 30 feet in thickness, covered by a thin layer of topsoil, overlying a deep deposit of red Permian clay. Pocket gophers are abundant both on top of the gypsum, where the soil is mixed with decomposed gypsum, and below the rock layer in eroded areas. In the latter situation the clay is frequently mixed with considerable sand.

In the Panhandle the soil is generally sandy. In places the sand is deep, while in others the top layer is shallow, and overlies a gravelly substratum. The genus Geomys has been taken in both situations, but occurs in greater abundance in deep sand. Cratogeomys has not been taken in deep sand, but has been found in the gravelly soils and also in the rocky canyon region of northwestern Cimarron County, where Geomys has never been taken. In the latter region Cratogeomys has been found both in the deep alluvium of the creek bottoms and in the gravelly canyon soils.

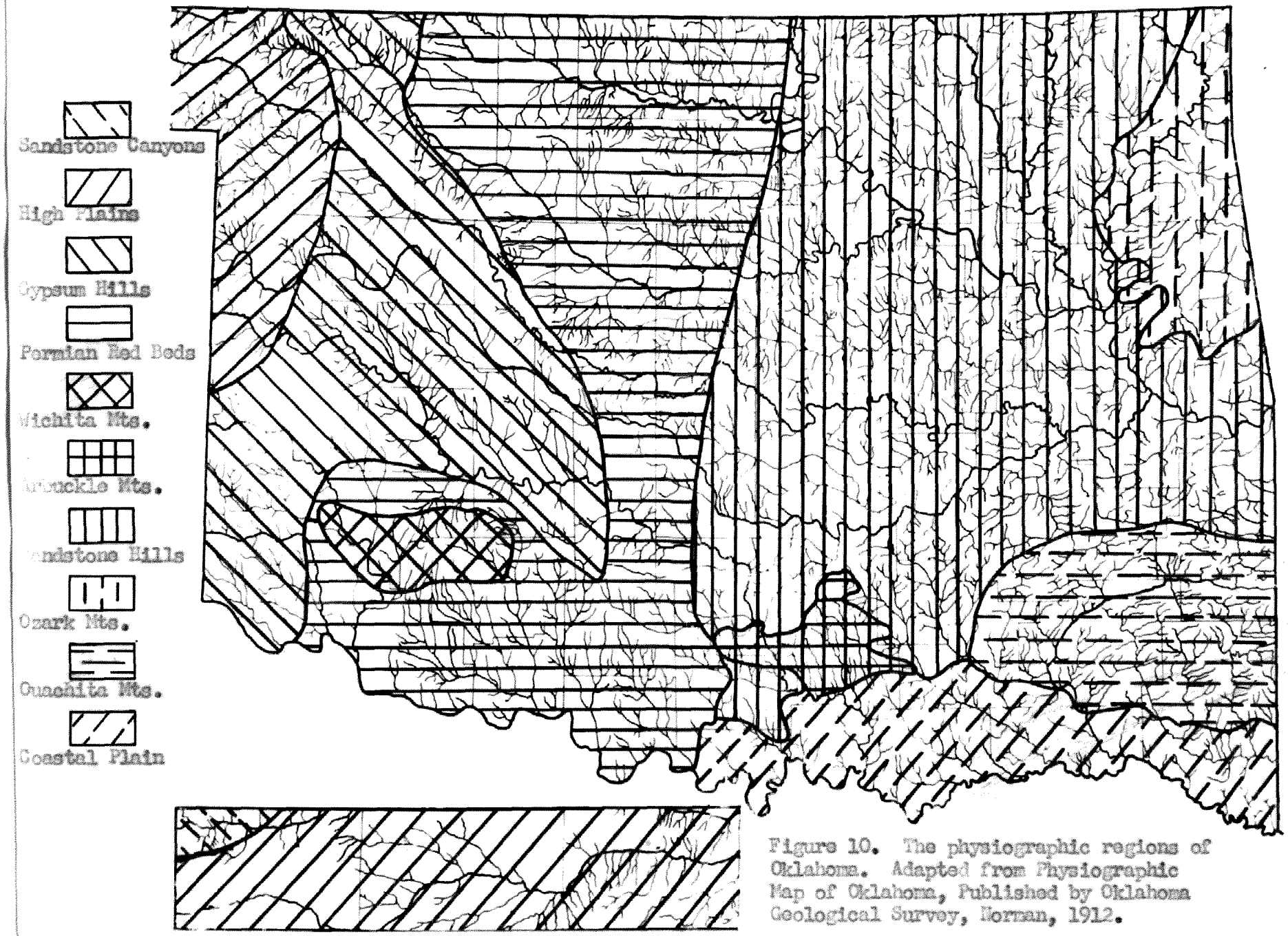

Figure 10. The physiographic regions of Oklahoma. Adapted from Physiographic Map of Oklahoma, Published by Oklahoma Geological Survey, Norman, 1912.

Comparison of the ranges of the various species and subspecies of pocket gophers as depicted in Figures 4 and 9 with the physiographic data in Figure 10 reveals the accuracy with which speciation has followed physiographic boundaries. The two subspecies of Cratogeomys castanops occupy distinct physiographic areas, castanops being confined to the Mesozoic sandstone region in the northwest corner of Cimarron County, while perplanus is found in the later Tertiary deposits of the High Plains. As noted earlier, the gophers of this species occupy the gravelly plains, and are absent from areas of deep sand. This preference does not provide absolute ecological separation from the genus Geomys, however, for both were taken at the same locality along the Rock Island Railroad tracks at Hooker, in Texas County.

The limits of the range of each of the three subspecies of Geomys bursarius follow equally well the limits of certain physiographic regions. Geomys bursarius lutescicularis is characteristic of the High Plains region, intergrading with Geomys bursarius major where the Tertiary deposits of the plains give way to the rolling red lands of the Permian Red Beds. The subspecies occupies all of the Permian region, whether it is red plains, overlaid with gypsum, or covered with sand dunes. Where the Permian gives way to the eastern sandstone hills, which are largely of Pennsylvanian age, intergradation occurs with Geomys bursarius dutcheri, which occupies the Sandstone Hills and Gulf Coastal Plains regions. Both of these regions are of predominantly sandy soil, although in the Coastal Plain there are limestone outcrops and a few areas of blackland soil where pocket gophers do not occur.

It is interesting to note that the distribution of the subspecies of

Geomys bursarius follows closely the outline of the Biotic Districts as given by Blair (1939). The range of G. b. dutcheri corresponds in most particulars with the extent of the Osage Savanna district, G. b. major corresponds in extent with the Mixed-grass Plains, Mesquite Plains, and Sand Dune areas, and G. b. jugosiccularis corresponds in extent with the Short-grass Plains. Blair (ibid.) also noted that the reddish color of the western pocket gopher, which he called G. brevicens llanensis, was apparently correlated with the red Permian soil in which it lives. This phenomenon has been even more forcibly impressed upon the author in the present study. Color is the most constant criterion for determining subspecies, and the change from one color pattern to another coincides exactly with the change from one physiographic region to another. The conclusion seems inescapable that the limits of each physiographic region constitute the necessary barriers for speciation. The pale-colored subspecies jugosiccularis is characteristic of the pale-colored soils of the Panhandle. The reddish-colored subspecies major is characteristic of the reddish Permian soils of the western part of the state. The dark subspecies dutcheri is characteristic of the varicolored sandy soils of the eastern part of the state. Further evidence that the physiographic boundary is one that actually limits interbreeding of the two populations is provided by the fact that large areas in eastern Oklahoma where the sandstone is red, and the soil is correspondingly red, the pocket gophers are just as dark as the ones from areas where the soil is brown or blackish. On the other hand, within the range of major where there are outcrops of sandstone, such as are found in the vicinity of Hinton, Caddo County, the pocket gophers are just as red as in other parts of

the range of that subspecies. This seems to indicate that interbreeding between populations within the limits of each of these physiographic boundaries is much more common than interbreeding between populations across these same boundaries.

The author feels that two further observations should be made, although there are no data to support them. It has long been observed by ecologists that mammals in southern regions tend to be smaller, and their color darker, than their close relatives in more boreal climates. Geomys bursarius dutcheri, whose affinities lie with the pocket gophers of Texas and Louisiana, is small and darker in color than the subspecies to the west and north. The subspecies major seems to represent an intergradient population whose size is very variable, while lutescicularis, whose affinities are with the northern forms, is consistently large. Both of the latter subspecies are lighter in color, with less black, than dutcheri.

Secondly, the size gradient exhibited by the three subspecies of Geomys bursarius may be a result of the mineral content of the soil. Albrecht (1944) has shown definite correlations between bone structure, bone strength, and mineral content of the diet in rabbits in Missouri. It is well known that the High Plains region of Oklahoma is an area of high mineral content in the soil. By contrast the high rainfall and sandy soil structure in the eastern part of the state have contributed to the leaching of the soil, so that the area in general is deficient in these substances. The intermediate area, constituting roughly the western half of the main part of the state, lies somewhere between these two extremes. The overall size of the three subspecies of pocket gophers

correlates very well with these facts. In the Panhandle *jugosicularis* is consistently large. In eastern Oklahoma *dutcheri* is consistently small. In between, *major* shows an inconsistency with regard to size, some localities producing specimens that are uniformly large, while other localities produce specimens of much smaller average size.

SUMMARY

1. The known fossil history of the family Geomyidae is summarized.

2. A complete review of the taxonomy of the genera Geomys and Cratogeomys is included.

3. All published records for Geomys and Cratogeomys in the central region of the United States are plotted on maps.

4. A total of 591 specimens of pocket gophers from Oklahoma were examined, 463 from the Oklahoma A & M collections, and 128 were borrowed. The latter constituted the majority of specimens known from Oklahoma prior to the present study.

5. Cratogeomys castanops perplanus Nelson and Goldman, and Geomys bursarius jugosiccularis Hooper, are recorded from Oklahoma for the first time.

6. Two subspecies of Cratogeomys castanops and three of Geomys bursarius were found in Oklahoma. C. c. castanops was found in northwestern Cimarron County, while C. c. perplanus was found on the plains in the eastern part of the Panhandle. The ranges of the two forms apparently do not meet in Oklahoma. G. b. jugosiccularis was found in the Panhandle, intergrading with G. b. major where the Panhandle joins the rest of the state. G. b. major intergrades with G. b. dutcheri along a line that crosses from north to south near the middle of the state.

7. Pocket gophers were not found in the Wichita Mountains, the Arbuckle Mountains, the Ouachita Mountains, nor in an area in northeastern Oklahoma lying north and east of the Arkansas River, containing the sandstone hills of Osage County, the northern part of the Cherokee Prairie, and the Ozark Mountains.

8. The cranial features separating G. g. castanops and G. g. perplanus are very slight, and the two races are difficult to distinguish.

9. Pelage color provides the most satisfactory means of separating the three subspecies of G. bursarius. There is a correlation between pelage color and soil color in each subspecies. Cranial and morphological characters are not as satisfactory as color in separating the three subspecies.

10. Intergradation occurs along physiographic boundaries. G. g. castanops inhabits the sandstone canyons of northwestern Cimarron County. G. g. perplanus and G. b. jugosicularis inhabit light colored soils overlying late tertiary deposits of the High Plains. G. b. major inhabits the red soils of the Permian region of western Oklahoma. G. b. dutcheri inhabits the parts of eastern Oklahoma where soils are formed from decomposed sandstone, mainly of Pennsylvanian age, and the Coastal Plain along the Red River in southeastern Oklahoma.

11. A bibliography of references to Geomys and Cratogeomys in the United States is included.

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