UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

MISCELLANEOUS
PUBLICATION
No. 58

Systematics of Three Species of Woodrats (Genus Neotoma) in Central North America

By

Elmer C. Birney

UNIVERSITY OF KANSAS
LAWRENCE 1973

April 13, 1973

UNIVERSITY OF KANSAS PUBLICATIONS
MUSEUM OF NATURAL HISTORY

The University of Kansas Publications, Museum of Natural History, beginning with volume 1 in 1946, was discontinued with volume 20 in 1971. Shorter research papers formerly published in the above series are now published as Occasional Papers, Museum of Natural History. The Miscellaneous Publications, Museum of Natural History, began with number 1 in 1946. Longer research papers are published in that series. Monographs of the Museum of Natural History were initiated in 1970. All manuscripts are subjected to critical review by intra- and extramural specialists; final acceptance is at the discretion of the publications committee.

Institutional libraries interested in exchanging publications may obtain the Occasional Papers and Miscellaneous Publications by addressing the Exchange Librarian, University of Kansas Library, Lawrence, Kansas 66044. Individuals may purchase separate numbers of all series. Prices may be obtained upon request addressed to Publications Secretary, Museum of Natural History, University of Kansas, Lawrence, Kansas 66044.

University of Kansas
Museum of Natural History

Miscellaneous Publication No. 58

April 13, 1973

Systematics of Three Species of Woodrats (Genus *Neotoma*) in Central North America

By

Elmer C. Birney

James Ford Bell Museum of Natural History
University of Minnesota
Minneapolis, Minnesota

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The University of Kansas, 1970

University of Kansas
Lawrence
1973

University of Kansas Publications, Museum of Natural History

Editor: Linda Trueb
Managing Editor: William E. Duellman

Miscellaneous Publication No. 58
pp. 1-173; 44 figures
Published April 13, 1973

Museum of Natural History
University of Kansas
Lawrence, Kansas 66044
U.S.A.

Printed by
University of Kansas Printing Service
Lawrence, Kansas

CONTENTS

INTRODUCTION

Two species of woodrats, *Neotoma floridana* and *Neotoma micropus,* have allopatric, but adjacent, distributions on the Great Plains; the species inhabit distinctly different environments at most localities. Because *N. floridana* is brown and *N. micropus* is gray, the species are readily distinguishable. The geographic ranges of the two, as mapped by Hall and Kelson (1959:684), were known to abut in the central and southern Great Plains from southeastern Colorado and southwestern Kansas southward to the Gulf Coast of eastern Texas; but not a single locality of sympatry was known. However, it had been discovered (Dwight Spencer, pers. com.) that members of the two species would hybridize in the laboratory with the production of viable offspring.

The polytypic characteristics of both species in the zone of potential sympatry and the existence of a geographically isolated subspecies of *Neotoma floridana* make the problem even more interesting from an evolutionary point of view. *Neotoma floridana baileyi* is restricted to the region of the Niobrara River in north-central Nebraska. *Neotoma floridana campestris* is a large pallid subspecies that lives in eastern Colorado, southwestern Nebraska and northwestern Kansas. Rats of this race may have been isolated in post-Wisconsin times from presently contiguous populations of the species to the east (Jones, 1964:26). The eastern parts of Kansas, Oklahoma, and northern Texas were inhabited by a dark brown race known as *N. f. osagensis.* In southern Texas the range of *N. f. attwateri* abuts that of *N. micropus;* specimens of *floridana* from farther east in Texas have been referred to the subspecies *rubida.*

When this study was begun, *Neotoma micropus* was divided into five nominal subspecies. *Neotoma micropus micropus* occupied roughly the eastern half of the range of the species from Tamaulipas to southern Kansas. Much of the western part of the range reportedly was occupied by *N. m. canescens,* allegedly a smaller and more pallid race. Two other subspecies, *N. m. leucophea* and *N. m. planiceps,* were known only from their respective type localities in New Mexico and San Luis Potosí. The fifth recognized subspecies, *N. m. littoralis,* was known only from a few localities in southern Tamaulipas.

Initially, this study was centered in Nebraska, Colorado, Kansas, and Oklahoma, an area which includes the northern half of a zone in which the geographic range of *Neotoma floridana* approaches that of *N. micropus.* The study area was selected principally because three subspecies of *N. floridana* (*baileyi, campestris,* and *osagensis*) and two of *N. micropus* (*canescens* and *micropus*) occur within its boundaries. This facilitated comparison of a variety of parameters in order to determine relationships among these five taxa. Although it had been supposed that the ranges of *N. f. campestris* and *N. f. osagensis* met in north-central Kansas, the exact zone of contact and the nature of the interaction had not been documented. Moreover, *N. albigula* generally is considered to be closely related to both *N. floridana* and *N. micropus* (Burt, 1960; Hooper, 1960); this species occurs in southeastern Colorado and the western part of the Oklahoma panhandle. Finley (1958) suggested that *N. albigula* and *N. micropus* formed natural hybrids in this region. Finally, the area was selected because of its accessibility to Lawrence, Kansas. This facilitated both field and laboratory investigations.

Ultimately, all available specimens of both species from the initial region of study and from near the zone of potential contact in Texas were examined. All specimens of *N. micropus* in the Museum of Natural History of the University of Kansas were included, and selected specimens of *N. micropus* were examined in

other museums if it seemed likely that they might reveal information on the relationship of this species to *N. floridana*. Eastern subspecies of *N. floridana* were treated taxonomically by Schwartz and Odum (1957); with the exception of *N. f. rubida*, which occurs in extreme southeastern Texas, the eastern subspecies were not considered in my investigation.

One other species, *Neotoma angustipalata*, is considered herein. The affinities of this large woodrat, known only from Tamaulipas and San Luis Potosí, México, have remained enigmatic since it was described by Baker (1951) as a member of the *Neotoma mexicana* species-group. *Neotoma angustipalata* since has been considered by different authors to be closely related to *N. mexicana*, *N. micropus* or *N. albigula*.

Parameters studied in the field included habitat preference and utilization, exact distributional relationships in those areas where members of two taxa might come into contact, and seasonal reproductive patterns of natural populations. Parameters studied in the laboratory included data on the following: 1) control and experimental matings of members of each taxon to those of each other taxon; 2) mating success and fecundity of hybrids; 3) growth and development of hybrids and nonhybrids; 4) karyological analyses; 5) serological studies involving hemoglobin electrophoretic patterns (Birney and Perez, 1970) and immunoelectrophoretic reactions of esterases; 6) water balance physiology (Birney and Twomey, 1970); and 7) univariate and multivariate analyses of geographic variation of mensural and qualitative morphological characters.

The primary purposes of my research have been to elucidate the systematic and evolutionary relationships, assess the zoogeographic history and re-evaluate the nomenclatorial arrangement of the woodrats studied. A secondary purpose has been to compare so-called classical taxonomic procedures with some of the newer methods of systematics and thereby evaluate the applicability of the various methods to systematic studies of closely related mammalian taxa.

MATERIALS AND METHODS

The general materials and methods that pertain to several facets of the study are discussed below. Specific materials and methods are related in detail preceding results and discussion of the various topics covered.

Initial efforts to collect live woodrats for laboratory studies were undertaken in September 1966. The last animals of the colony were sacrificed in October 1969. Specimens studied in the laboratory were obtained either by dismantling active dens and capturing the rats by hand as they fled, or by trapping them in live-traps set near active dens. Havahart traps (18 by 5 by 5 inches) were found to be highly successful, easily transported, and relatively durable. Woodrats are not difficult to trap and can be taken in practically any device large enough to permit entry and constructed to prevent escape. In rocky habitats, usually it was necessary to use traps, but in other areas woodrats were captured more often by hand. To prevent undue destruction of available denning sites at two localities of special interest (Major County, Oklahoma, and Cherry County, Nebraska), woodrats were obtained only by trapping.

Animals used in laboratory experiments were obtained during the months indicated at the following localities (here specified only to county; see lists of specimens examined for exact localities of record within these counties): NEBRASKA: Cherry County (March and April 1967, August 1968); Rock County (August 1968). COLORADO: Baca County (April and May 1968); Prowers County (April 1968). KANSAS: Barber County (October 1966, March and July 1968); Douglas County (September, October, and November 1966, March 1967, February and March 1968, March 1969); Ellis County (December 1966); Ellsworth County (September 1967, October

and December 1968); Finney County (September and October 1968); Hamilton County (September 1968); Haskell County (September and November 1966, June 1967, February, May, and August 1968, April 1969); Hodgeman County (September and November 1968); Logan County (August 1967); Meade County (November 1966, June 1967); Ness County (September 1968); Russell County (December 1968); Stevens County (August 1968). OKLAHOMA: Dewey County (June 1968); Major County (June 1968, January 1969).

Woodrats were housed indoors and maintained on a daily regime of 14 hours of light and 10 hours of darkness from 1 February to 1 October. Illumination from several windows in the animal rooms was the only source of light during other months. An attempt was made to maintain a stable temperature of 20°C in the animal rooms, but temperatures ranged from as low as 13°C at times during winter to as high as 30°C on occasional summer afternoons. During one three-day period in June 1968, air conditioning failed and the temperature soared to at least 35°C and may have surpassed 38°C. No deaths were attributed to extremes in temperature, but consumption of water increased noticeably as temperature increased. Relative humidity was not measured in the animal rooms during the summer or winter, but was measured regularly from March to June, 1968, when it ranged from 15 to 45 percent.

Woodrats were caged individually except when two were placed together for breeding or when a female was rearing a litter. Litters were weaned at six weeks of age. Cages used to house woodrats were of three general types. One type was constructed of wood and ¾-inch mesh hardware cloth. Dimensions of these cages were 30 by 18 by 18 inches with 3.75 square feet of floor space. The other two types of cages used were all-metal commercially available cages with approximately four square feet of floor space. Both were satisfactory, but the type having a removable pan beneath a grated floor could be cleaned easily without disturbing the occupant. Females with unweaned litters were kept in special large metal cages that had eight square feet of floor space. Although woodrats can be maintained in smaller cages, I doubt that these would be satisfactory for maintenance of a breeding colony (see Wood, 1935:109). All cages were supplied with one gallon cardboard milk cartons or other disposable nest boxes of equivalent size. Cages having solid floors were covered with wood shavings; shredded newspaper for use as nesting material was available in all cages. Cages were cleaned at weekly intervals.

Purina Laboratory Chow and water were available to woodrats in the laboratory on an *ad libitum* regime. On occasion, especially in the early phases of the study, this diet was supplemented with lettuce leaves and whole-kernel corn; when it became evident that supplementary foods were unnecessary, this practice was discontinued. At times individual rats would severely reduce food intake and begin to lose weight, usually indicating that the incisors were broken or maloccluding; rats with such teeth were removed from the colony. Occasionally the teeth of rats that were not feeding properly appeared to be normal; on these occasions feeding of laboratory chow was discontinued and the animals were given rolled oats *ad libitum* for a few days, then gradually returned to a diet of laboratory chow. While conducting one experiment wherein it was necessary to limit protein intake, the experimental group was fed only corn (see Birney and Twomey, 1970).

Diseases and ectoparasites caused little problem in maintaining a thriving woodrat colony. In the spring of 1967 several rats died after having had diarrhea for two to five days, losing weight, and having an inactive, sickly appearance. Several sick rats and some that recently had died were taken to the Veterinary Diagnostic Laboratories affil-

iated with Kansas State University at Manhattan, Kansas. Although the disease was never diagnosed, the necropsy report (H. D. Anthony, pers. com.) stated that a "hemolytic *E.* [*scherichia*] *coli* was isolated from the spleen and intestine of one of the specimens." Anthony recommended immediate treatment of drinking water with nitrofurazone, followed by prophylactic doses every three months. This treatment prevented spread of the disease, and generally cured all but the sickest rats. On two later occasions when more than one rat evinced signs of the affliction, the entire colony was treated. Cages were cleaned after each occupancy and those that had housed sick woodrats were washed in a dilute lysol solution before being reused.

To prevent ectoparasites from becoming a problem, each woodrat was dusted with commercial "flea powder" before being placed in the animal house. On three separate occasions individual woodrats became infested with an unidentified species of mite; the entire colony subsequently was dusted and the infested animals were dusted on two or three successive days. Although each of the individuals survived, two females infested at the time of parturition abandoned their litters. Rats infested with mites tend to be lethargic, lose weight rapidly, and have matted, swollen eyes.

In addition to study of live animals, a total of 2163 museum specimens, including seven holotypes or lectotypes, was examined by me. Several hundred additional specimens were examined. These include more than 300 laboratory-reared individuals prepared as museum specimens and deposited in The Museum of Natural History of the University of Kansas, specimens of eastern subspecies of *Neotoma floridana* not treated herein, specimens of other species of *Neotoma* (especially *N. albigula* and *N. mexicana*) examined for comparative purposes, and woodrats examined incidentally while searching for misidentified specimens of the species studied.

ACKNOWLEDGMENTS

I thank the following agencies for financial support for this investigation: 1) National Science Foundation Grant GB-4446X administered by the Committee on Systematics and Evolutionary Biology at The University of Kansas, provided a Research Traineeship for my support from September 1966 until June 1969 and additional funds for cages and equipment to maintain woodrats in the laboratory; 2) Travel grants for field work and museum visitations were received from the Graduate School and the Museum of Natural History (Watkins Grant) at The University of Kansas; 3) Research grants from the Kansas Academy of Science supplied monies used to purchase Laboratory Chow; 4) Funds for computer time were provided by the Computation Center of The University of Kansas; 5) Partial support for July and August 1969 was made available through The University of Kansas General Research Fund (Biomedical Division), under grant no. 3453-5038; 6) Equipment and supplies for serological experiments and rabbits used for preparation of antisera were purchased with funds from the Public Health Service and research monies of the Department of Zoology at The University of Kansas.

I am indebted to each of the persons listed below for permission to examine specimens of woodrats in their charge, which included both arrangement of loans and provision of working space in their respective institutions (Museum abbreviations used in the accounts beyond are in parentheses): Sydney Anderson and Richard G. Van Gelder, American Museum of Natural History (AMNH); William J. Voss, Fort Worth Museum of Science and History (FWCM —formerly Fort Worth Children's Museum); John P. Farney, Kearney State College (KSC); Dwight L. Spencer, Kansas State Teachers College (KSTC); Robert S. Hoffmann and J. Knox Jones, Jr., Museum of Natural History of The University of Kansas (KU); George H.

Lowery, Jr., Museum of Natural Sciences of Louisiana State University (LSU); Eugene D. Fleharty, Museum of the High Plains of Fort Hays Kansas State College (MHP); Walter W. Dalquest, Midwestern University (MWU); Bryan P. Glass, Oklahoma State University (OSU); Edwin D. Michael, formerly at Stephen F. Austin State University (SFA); J. Keever Greer, Stovall Museum of Science and History of the University of Oklahoma (SM); Dilford C. Carter, formerly with the Texas Cooperative Wildlife Collection of Texas Agricultural and Mechanical University (TCWC); W. W. Newcomb, Texas Natural History Collection of the University of Texas (TNHC); Robert J. Baker and Robert L. Packard of Texas Tech University (TT); Bernardo Villa-R., Instituto de Biologia, Universidad Nacional Autónoma de México (UNAM); Charles O. Handley, Jr., and R. H. Manville, United States National Museum, including the Biological Surveys Collection (USNM).

Serological experiments were conducted in the Charles A. Leone Laboratories at The University of Kansas. Persons granting permission to use these facilities or who were especially helpful include Jay D. Gerber, Richard D. Koehn, Charles A. Leone, Robert B. Merritt, and Julio E. Perez. Karyological studies were conducted in the botany laboratories at The University of Kansas and in the cell biology laboratories at Texas Tech University. Raymond C. Jackson at Kansas and Robert J. Baker at Texas Tech were especially generous with their supplies, equipment, and time. James Fraine and Sievert A. Rohwer assisted in the use of numerical taxonomy programs and other analyses of data, all of which were conducted at the Computation Center of The University of Kansas.

I am especially indebted to J. Knox Jones, Jr., formerly of the Museum of Natural History and Department of Systematics and Ecology of The University of Kansas, for his excellent advice and general assistance throughout this study and for editorial advice in preparation of the manuscript. Frank B. Cross and Raymond C. Jackson also critically read the manuscript and provided sound editorial advice.

Persons deserving of special thanks for assistance in the field include David M. Armstrong, Russell H. Birney, Jay D. Gerber, Thomas H. Kunz, D. Michael Mortimer, Robert R. Patterson, Duane A. Schlitter, Ronald W. Turner, and Larry C. Watkins. Additionally, D. Michael Mortimer assisted by cleaning woodrat cages in the summer of 1968 and Hugh H. Genoways fed and watered the animals when it was necessary for me to be absent.

Several of my colleagues at The University of Kansas, especially David M. Armstrong, Hugh H. Genoways, Robert S. Hoffmann, and Carleton J. Phillips, were both stimulating and helpful by giving needed technical advice and willingly discussing topics germane to my research. Sydney Anderson, the American Museum of Natural History, assisted this study in a similar manner.

My wife, Marcia Birney, has been both helpful and patient throughout this study and my graduate career. She prepared most of the figures used herein, typed drafts of the manuscript, and provided much needed clerical assistance.

TAXONOMIC TREATMENT

HISTORICAL ACCOUNT

Although woodrats were observed in North America by early naturalists such as John Bartram, no species was treated taxonomically until early in the nineteenth century. Ord (1818:181) published a short description and figure of *Mus floridanus,* a woodrat from eastern Florida. Previously, Ord (1815:292) described the bushy-tailed woodrat as *Mus cinereus.* Having noted the distinctive dental characters of the New World

rats, Say and Ord (1825:345) diagnosed and named the genus *Neotoma* and designated *Mus floridanus* as the type species. Later Baird (1855:333) named *Neotoma micropus* from the type locality of Charco Escondido, Tamaulipas (see remarks following synonymy of *N. m. micropus*).

Baird (1858:487-490, 492-495) treated *Neotoma floridana* and *N. micropus* as separate species, although he repeatedly commented on the similarities between the two. Having only the type of *micropus* with which to compare specimens of *floridana*, Coues (1877:15) considered *micropus* a synonym of *floridana*, a conclusion based primarily on his interpretation of the gray pelage of *micropus* as being that of an immature animal. With additional specimens of *micropus* from Tamaulipas, southern Texas, and from "the northwestern corner of the Indian Territory" (now western Oklahoma), Allen (1891:282) recognized *micropus* as a species distinct from *floridana*. Allen (1891:285) applied a new subspecific name, *Neotoma micropus canescens*, to specimens from the Indian Territory primarily on the basis of their pallid coloration.

Woodrats from a population at Valentine, Nebraska, were collected in June of 1888 by Vernon Bailey and later named as a new species, *Neotoma baileyi*, by Merriam (1894a:123). Merriam (1894b) published a synopsis of the known members of the genus *Neotoma*, including fossil relatives, and diagnosed the subfamily Neotominae. Allen (1894b:322) described *Neotoma campestris*, the *floridana*-like woodrat of northwestern Kansas and northeastern Colorado, on the basis of specimens from Pendennis, Kansas (type locality), and Fort Lyons, Colorado. In the same publication, Allen (1894b:323) noted that he considered the woodrats which he previously had allocated to *Neotoma micropus canescens* to be "inseparable from *N. micropus*."

Neotoma attwateri was named on the basis of a sample of woodrats from just east of the Edwards Plateau, near Kerrville, Texas (Mearns, 1897:721). Mearns (1897:722) suggested that 'it is not improbable . . . [that *N. attwateri*, *N. baileyi*, and *N. campestris*] . . . may prove to be but geographic races of *N. floridana*." Prior to the turn of the century, only one other name was applied to the woodrats considered here. Elliot (1899:279) assigned the name *Neotoma macropus* [*sic*] *surberi* to specimens from the vicinity of Alva, Oklahoma. According to Elliot, *surberi* differed from both *micropus* and *canescens* in having a longer tail and darker pelage.

Neotoma micropus littoralis, from Altamira, Tamaulipas, and *Neotoma micropus planiceps*, based on a single specimen from Río Verde, San Luis Potosí, were the last names applied (Goldman, 1905:31 and 32, respectively) to the woodrats treated in this study prior to the revision of the genus *Neotoma* by Goldman in 1910. In the latter work, Goldman recognized three subgenera and 28 species. Only two species, *Neotoma (Homodontomys) fuscipes* and *Neotoma (Teonoma) cinerea*, were not considered members of the subgenus *Neotoma*. Woodrats presently included within the genus *Neotoma*, but which were considered as separate genera at that time are *Neotoma (Hodomys) alleni* and *Neotoma (Teanopus) phenax* (see Burt and Barkalow, 1942:296). Burt and Barkalow also placed *Homodontomys* in the synonymy of *Neotoma*.

Goldman (1910:14) considered *N. floridana* and *N. micropus* to be separate but closely related species comprising the *floridana* species-group. *Neotoma floridana baileyi* was thought to occur in South Dakota, most of Nebraska and Kansas, and in eastern Colorado. The name *campestris* was treated as a junior subjective synonym of *baileyi*. Woodrats of eastern Texas (except the extreme eastern part, where the name *N. f. rubida* Bangs was applied) and eastern Oklahoma, were assigned to *N. f. attwateri*. Goldman (1910:26-31) reinstated *N. micropus canescens* as the best name for western populations of that species,

placed *surberi* in the synonymy of *N. m. micropus,* and recognized both *N. m. littoralis* and *N. m. planiceps* as distinct subspecies.

Since Goldman's revision, the nomenclature of woodrats has remained relatively stable. Kellogg (1914:5) removed *campestris* from the synonymy of *baileyi* and recognized both as subspecies of *floridana.* Goldman (1933:472) gave a slightly paler (as compared to *N. m. canescens*) population of *micropus* the name *Neotoma micropus leucophea.* Blair (1939a:5) described woodrats from eastern Oklahoma, eastern Kansas, and adjacent parts of Missouri, Arkansas, and Texas as *Neotoma floridana osagensis* (type locality in Osage County, Oklahoma). Recognition of *osagensis* limited the distribution of *baileyi* to the Noibrara Valley of northern Nebraska. Burt and Barkalow (1942:290) considered *N. micropus* to be intermediate between *N. floridana* and *N. albigula.* On that basis they created the *micropus* species-group thus removing *micropus* from the *floridana* group where it had been placed by Goldman (1910:14). *Neotoma floridana* and *N. micropus* were studied by Spencer (1968), who concluded that the two species are closely related and incompletely speciated.

On the basis of two specimens from the Sierra Madre Oriental of southern Tamaulipas, Baker (1951:217) named the species *Neotoma angustipalata.* Hooper (1953:10) suggested that *angustipalata* may represent no more than a deeply pigmented population of *micropus,* and Hall (1955:329) thought it should be placed in the *albigula* species-group.

ACCOUNTS OF SPECIES AND SUBSPECIES

I regard the biological species concept (Wilson and Brown, 1953:97-99; Mayr, 1963, 1965, and 1969) as the best presently available concept of the species both for evolutionists and taxonomists, and subscribe to Tilden's (1961:22) statement on the use of subspecies as follows: "In defense of the use of the subspecies concept, it may be mentioned that in our present system of classification the subspecies is the category expressly provided for the treatment of populations less than species. That this tool is imperfect must be admitted. But to admit imperfection is not necessarily to reject the tool entirely. The point of view is held here, that the good results outweigh the objections that have been brought forward." Because of the arbitrary nature of the subspecies, it is necessary to state what "kind" of subspecies is to be recognized. Lidicker (1962:169) stated that "a subspecies is a relatively homogeneous and genetically distinct portion of a species which represents a separately evolving, or recently evolved, lineage with its own evolutionary tendencies, inhabits a definite geographical area, is usually at least partially isolated, and may intergrade gradually, although over a fairly narrow zone, with adjacent subspecies." Further, it was noted by Lidicker *(loc. cit.)* that although most such subspecies will not become species, they are populations that have made initial steps toward species formation and could form species under suitable isolating conditions. This interpretation focuses on the evolutionary process of speciation rather than on individual geographically variable characters. It is this sort of subspecies that I have attempted to recognize.

Taxonomic decisions were made after intensive study and evaluation of the morphological, reproductive, serological, and karological data discussed beyond. Accounts of species and subspecies are presented first merely as a matter of convenience so that the nomenclatorial arrangement proposed herein will obtain throughout subsequent discussions.

Eight nominal taxa of woodrats, representing three species, are treated in the accounts that follow. The arrangement of species and that of subspecies within a species does not imply relationship or degree of specialization. Instead, taxa

are arranged with respect to geographic distribution, with more northern taxa treated before southern ones. Each account includes a basic synonymy, which is followed by a relatively brief section of remarks. Remarks include comments on type specimens if such are appropriate, general comments on the variation within and between subspecies, and other comments that may be germane to the taxonomic status of the taxon under consideration. Records of occurrence follow remarks and include both specimens examined and additional records.

The total number of specimens examined is given for each taxon. This is followed by exact localities from which the specimens originated, the number of specimens examined from each locality, and the abbreviated designation for the museum(s) in which specimens are housed. In the account of *N. m. canescens,* specimens from localities in the United States are listed before those from México. States and counties within the United States are arranged alphabetically. Localities within each county and Mexican state are arranged from north to south. If two localities are at the same latitude, the westernmost is given first. Locality data of some specimens examined were specific only to county; these are listed as "unspecified" after specific localities within the county. In a few instances, a group of specimens is from the same general locality with the exact localities of capture varying only slightly; these are totaled and listed collectively as within a certain radius of a single locality. Specimens judged to be "hybrids" of two species (see account of *N. m. canescens*) are listed with specimens of the taxon that they most resemble. Subspecific intergrades are included under the subspecies to which I consider them best assigned. Published citations to localities from which specimens have been collected but not examined by me are listed under "Additional records." Also included in this category are reliable, published observations of woodrats or their houses in areas known to be inhabited by a single species of *Neotoma.*

Following records of occurrence, the distribution and habitat of each taxon are discussed. The latter topics are treated in especial detail if they directly concern the relationships of two species or two subspecies. The general ranges of all three species (*floridana, micropus,* and *angustipalata*) are shown in figure 1. Most locality records are plotted on regional maps, but some were not plotted to prevent undue crowding of symbols. Unplotted localities are set in italic type in lists of specimens examined and of additional records. Localities specified only to county were plotted only in the absence of any other county record; symbols for such records are square and placed near the center of the county. Localities of specimens bearing questionable data are not plotted, but are discussed in the account of *N. m. canescens.*

Eastern subspecies of *Neotoma floridana* were reviewed by Schwartz and Odum (1957). With the exception of *N. f. rubida,* which I have treated only in eastern Texas, these races of the species are not considered here. Specimens of *Neotoma micropus* were studied throughout the range of the species. However, because New Mexico is well to the west of the range of *N. floridana* and to the north of that of *N. angustipalata,* no attempt was made to examine all specimens from that state. Specimens from there were studied primarily to determine the best taxonomic position of the subspecies *N. m. leucophea* and to determine if New Mexican woodrats fit the pattern of variation of the species in a general way. In the accounts that follow, therefore, records of *N. micropus* from New Mexico are not plotted on a regional map and records from the published literature are limited to those that are distributionally marginal.

Western Subspecies of *Neotoma floridana*

Neotoma floridana baileyi Merriam

Neotoma baileyi Merriam, 1894a:123 [Holotype

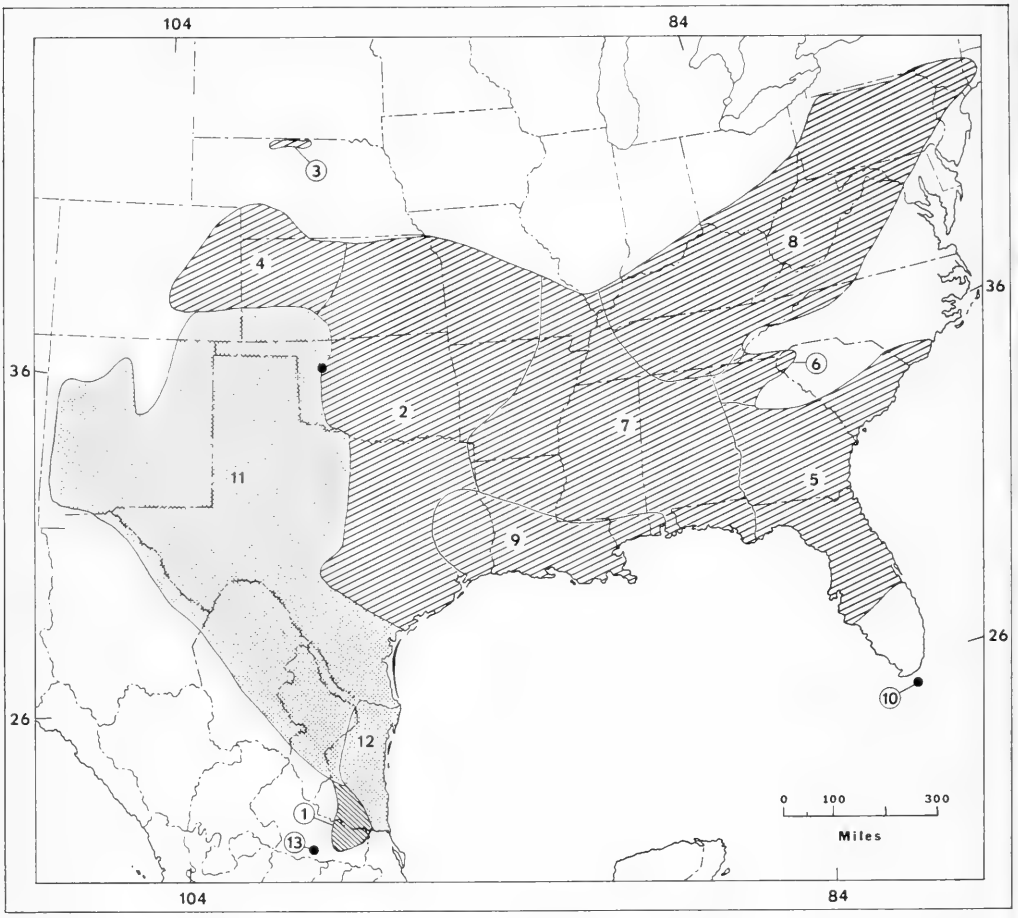

FIG. 1. Geographic distributions of *Neotoma angustipalata*, *N. floridana*, and *N. micropus*. Identification of species and subspecies is as follows: 1) *N. angustipalata;* 2) *N. f. attwateri;* 3) *N. f. baileyi;* 4) *N. f. campestris;* 5) *N. f. floridana;* 6) *N. f. haematoreia;* 7) *N. f. illinoensis;* 8) *N. f. magister;* 9) *N. f. rubida;* 10) *N. f. smalli;* 11) *N. m. canescens;* 12) *N. m. micropus;* and 13) *N. m. planiceps*. The symbol in Oklahoma denotes the single known locality of sympatric occurrence of *N. floridana* and *N. micropus*. Distribution of eastern races of *N. floridana* follows Hall and Kelson (1959:634).

—USNM 4311/5034 from Valentine, Cherry County, Nebraska].

Neotoma floridana baileyi—Bailey, 1905:109.

Remarks.—Because of its present geographic isolation, *Neotoma floridana baileyi* assumes certain characteristics of an "insular" subspecies. Although members of this subspecies are distinctive in at least minor characteristics of every parameter studied, no results obtained in this study indicate that *baileyi* has evolved to a level warranting specific status.

Records of occurrence.—Specimens examined (56).—NEBRASKA: *Cherry County:* Valentine, 6 (USNM); 4 mi E Valentine, 6 (KU); 6 mi E Valentine, 15 (KU); Clark's Canyon, near Valentine, 12 (USNM); 3 mi SSE Valentine, 1 (KU); 10 mi S Cody, 5 (USNM); 22 mi SW Valentine, 3 (KU). *Keya Paha County:* 6 mi S, 8 mi E Springview, 1 (KU). *Rock County:* 11.5 mi N, 7.5 mi W Bassett, 7 (KU).

Additional record.—NEBRASKA: *Brown County:* Long Pine (Jones, 1964:218).

Distribution and habitat.—Selected localities of recorded occurrence of *Neotoma floridana baileyi* are plotted in figure 2. Goldman (1910:25) reported as

this subspecies a woodrat from 18 mi SE Rapid City, South Dakota, but Jones (1964:217) stated that the individual recorded "is without question *Neotoma cinerea rupicola*." I have searched extensively for *Neotoma floridana* in Todd, Mellette, and Tripp counties, South Dakota, but found neither the woodrats nor their distinctive dwellings. Habitat that appeared suitable for woodrats was extensive along and near the Little White and Keya Paha rivers, and in the vicinity of Okreek, South Dakota. Although no specimens were taken in South Dakota, it seems likely that *N. f. baileyi* will be found there eventually. However, it is conceivable that dispersal farther northward is not possible even for a population long in the process of adapting to the inclement winters of northern Nebraska.

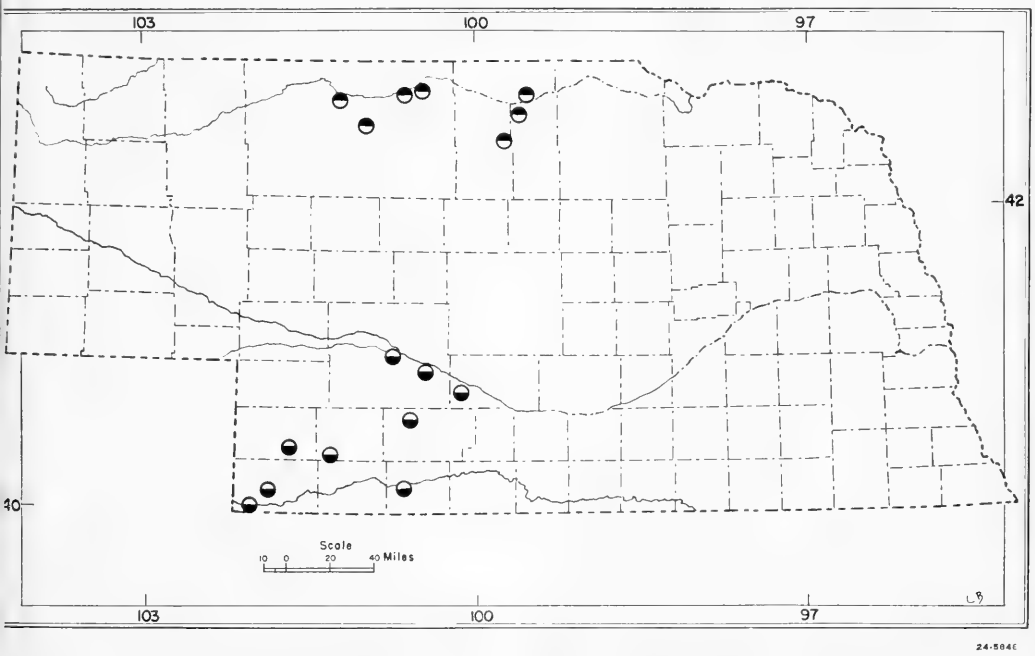

FIG. 2. Selected locality records for *Neotoma floridana baileyi* (symbols solid above) and *N. f. campestris* (symbols solid below) in Nebraska.

In Cherry, Keya Paha, and Rock counties, Nebraska, *N. f. baileyi* occurs in three more or less distinguishable habitat types. On the Fort Niobrara Wildlife Refuge these rats were abundant in the heavily wooded floodplain of the Niobrara River in March and April 1967 and August 1968. Nests were constructed in and around fallen trees, inside hollow upright trees, at the bases of upright trees, and in piles of brush and treelimbs. In April, the bark and cambium layers of woody twigs appeared to serve as a primary source of food. Just north of the Snake River Falls in Cherry County (22 mi SW Valentine), three specimens were taken from nests constructed in the steep, rocky, canyon walls bordering the Snake River. In Keya Paha County (6 mi S, 8 mi E Springview) a single specimen was trapped under a rocky ledge at the top of a deep canyon several miles north of the Niobrara River; no additional nests or signs of woodrat activity were located as a result of searching similar ledges in the immediate area and lower in the same and adjacent canyons. Habitat of this

type apparently is marginal and not frequently utilized.

Woodrats were common in abandoned and little-used buildings at a ranch near Long Pine Creek (11.5 mi N, 7.5 mi W Bassett) in Rock County in 1968. At this locality I found no evidence that "natural" nest-site types (e.g. rock outcrops, trees, logs, brushpiles) harbored woodrats, although these sites probably are utilized occasionally. Near Long Pine Creek at Long Pine, Brown County, where this woodrat has been reported to occur (Jones, 1964:218), I found the habitat even more extensive than at the locality discussed above. A superficial search there for woodrats was unsuccessful, but I am confident they occur in the area and probably are locally common along the creek from Long Pine to the place where it empties into the Niobrara River. I did not revisit the locality of record 10 mi S Cody nor have I searched for *N. f. baileyi* along the Niobrara or elsewhere to the west of that locality. To the east of the easternmost locality of record (southwest of Springview), I have searched for these woodrats as far as eastern Boyd and Holt counties. Apparent marginal habitat was found on Ponca Creek near Spencer (Boyd County) and at several localities along the Niobrara River. Another area worthy of further search was observed south of the Niobrara River just east of Midway in Holt County. I suspect that *N. f. baileyi* occurs farther to the east than present records indicate.

Neotoma floridana campestris J. A. Allen

Neotoma campestris J. A. Allen, 1894:322 [Holotype—AMNH 7765/6742 from Pendennis, Lane Co., Kansas].

Neotoma floridana campestris—Kellog, 1914:5.

Remarks.—Although not recognized by Goldman (1910:24), *Neotoma floridana campestris* is distinctly paler in color than adjacent populations of *N. f. attwateri,* occupies relatively distinct types of habitat in comparison with other populations of the species, and tends generally to be larger than rats to the east. Although relatively narrow, the area of contact between *campestris* and *attwateri* in eastern Ellsworth and western Russell counties, Kansas, forms an obvious zone of integradation. The arbitrary line dividing the ranges of the two taxa is drawn on a north-south axis generally corresponding to the county line separating Ellsworth and Russell counties. A specimen (KU 119700) assigned to *campestris* from only one mile west of that county line might be equally well assigned to *attwateri,* but two specimens (KU 14001-02) from one mile east of the line clearly are best assigned to *attwateri.* The county line serves as a convenient line of demarcation and is as accurate as any other would be.

Records of occurrence.—Specimens examined (221).—COLORADO: *Crowley County:* 3 mi N Fowler, 4400 ft, 7 (KU); Olney (= Olney Springs), 12 (USNM). *El Paso County:* 1.5 mi SW Fountain, 5700 ft, 2 (KU); *2.5 mi SW Fountain, 5700 ft,* 1 (KU); *3 mi S, 2 mi W Fountain, 5600 ft,* 1 (KU). *Kit Carson County:* Tuttle, 2 (USNM). *Yuma County:* Wray, 5 (1 USNM, 4 AMNH); *1 mi S Wray, 3550* ft, 3 (KU); 2 mi W Hale, 1 (KU); *1 mi S, 3 mi W Hale,* 1 (KU).

KANSAS: *Decatur County:* 5 mi S, 8 mi W Oberlin, 1 (KU). *Ellis County:* 16 mi N Hays, 13 (KU); 13 mi N, 1 mi W Hays, 1 (MHP); *SE ¼ sec. 28, T. 11 S, R. 18 W (13 mi N Hays),* 6 (MHP); *NW ¼ sec. 31, T. 13 S, R. 18 W (2 mi W Hays),* 3 (MHP); Hays, 7 (USNM); *0.5 mi S, 3.5 mi W Hays,* 1 (KU); *2 mi S Hays,* 1 (MHP); *7 mi S, 10 mi W Hays,* 3 (KU); NW ¼ sec. 11, T. 15 S, R. 20 W (8 mi S, 10 mi W Hays), 2 (MHP); *SW ¼ sec. 16, T. 15 S, R. 19 W (9 mi S, 6 mi W Hays),* 1 (MHP). *Finney County: 19 mi S Dighton,* 7 (KU); 23 mi S Dighton, 2 (KU). *Gove County:* Castle Rock, 9 (KU). *Hodgeman County:* 4 mi S, 0.5 mi W Jetmore, 2 (KU). *Lane County: 1 mi N Pendennis,* 10 (KU); Pendennis, 29 (6 AMNH, 23 USNM); 12 mi SW Pendennis, 2 (KU); *unspecified,* 2 (KU). *Logan County:* NE ¼ sec. 8, T. 13 S, R. 35 W (2.5 mi N, 2.5 mi W Russell Springs), 1 (MHP); *NE ¼ sec. 27, T. 13 S, R. 35 W (1 mi S, 1 mi W Russell Springs),* 1 (MHP); *1 mi S Russell Springs,* 6 (KU); *5 mi SE Elkader,* 2 (KSTC); 5 mi S Elkader, 4 (KU); *unspecified,* 4 (KU). *Ness County:* 1 mi S, 16 mi W Ness City, 4 (KU). *Rawlins County:* 7 mi N, 16.5 mi W Atwood, 1 (KU). *Rooks County:* 1.5 mi S, 1 mi W Stockton, 6 (MHP); *3 mi S, 3 mi W Stockton,* 1 (MHP); 6 mi SW Woodston, 3 (KU); 20 mi N Hays, 1 (MHP);

SW ¼ sec. 34, T. 10 S, R. 17 W (7 mi S, 4.5 mi E Plainville), 1 (MHP). *Russell County:* NE ¼ sec. 34, T. 12 S, R. 11 W (6 mi S, 1 mi E Lucas), 1 (MHP); *NW ¼ sec. 8, T. 13 S, R. 11 W (8 mi S, 2 mi W Lucas),* 1 (MHP); *NE ¼ sec. 17, T. 13 S, R. 11 W (9 mi S, 1 mi W Lucas),* 4 (MHP); *SE ¼ sec. 13, T. 13 S, R. 11 W (10 mi S, 3 mi E Lucas),* 1 (MHP); 0.5 mi W Russell, 1 (KSTC); *NW ¼ sec. 34, T. 13 S, R. 12 W (11 mi E Russell),* 1 (MHP); 2 mi W Wilson, 1 (KU); 6 mi S, 4 mi E Russell, 18 (KU). *Scott County: State Park,* 1 (KU); 12 mi N, 3 mi W Scott City, 2 (MHP). *Thomas County:* unspecified, 1 (MHP). *Trego County:* sec. 29, T. 13 S, R. 25 W (Banner), 6 (KU); *unspecified,* 1 (USNM). *Wallace County:* Lacey Ranch (9 mi S, 4.5 mi E Wallace), 1 (KU).

NEBRASKA: *Dundy County:* 5 mi N, 2 mi W Parks, 8 (KU); Haigler, 1 (USNM).

Additional records.—COLORADO (Finley, 1958:318, unless otherwise noted): *Bent County:* Fort Lyon. *Elbert County:* 8 mi NE Agate; Cedar Point, 6 mi NW Limon. *El Paso County: 7 mi SSE Colorado Springs, 5900 ft;* 10 mi S Colorado Springs; 16 mi W Wigwam (Armstrong, 1972). *Kit Carson County:* South Fork Republican River, near Flagler (Cary, 1911:114). *Lincoln County:* Big Sandy Creek, near Hugo (Cary, 1911:115). *Pueblo County:* N of Piñon (Warren, 1942:209); Chico Basin, 20 mi N Pueblo *(ibid.);* Pueblo. *Yuma County:* Dry Willow Creek, Boyce Ranch.

NEBRASKA (Jones, 1964:219): *Chase County:* 5 mi S Imperial. *Dawson County:* 10 mi S Gothenburg. *Frontier County:* vicinity Curtis. *Hays County:* 0.5 mi S Hamlet. *Lincoln County:* North Platte; sec. 10, T. 11 N, R. 27 W (5 mi S, 2.5 mi W Brady). *Red Willow County:* McCook.

Distribution and habitat.—Locality records for *Neotoma floridana campestris* are shown in figures 2, 3, and 4. Several localities listed by Finley (1958:318) and one reported by Jones (1964:219) are based on observations of dens by collectors and laymen. Of the undocumented reports I have traced, I accept the following: 5 mi S Imperial, Chase Co., Nebraska (Jones, 1964:215); near Flagler, Kit Carson Co., Colorado, and near Hugo, Lincoln Co., Colorado (Cary, 1911:114, 115); Chico Basin, 20 mi N Pueblo, Pueblo Co., Colorado, and N of Piñon, Pueblo Co., Colorado (Warren, 1942:209). I have disregarded the following records pending their documentation by specimens: 6 mi N, 12 mi W Pueblo, Pueblo Co., Colorado—this is a den record reported by Finley (1958:318) and, although the den most likely was constructed by *N. f. campestris,* it is conceivable that both *N. mexicana* (disregarded by Finley as constructing dens unlike the one he observed) and *N. albigula* occur at this locality; 10 mi N Arlington, Kiowa Co., Colorado—Cary (1911:114) entered this record on the strength of reports by "stockmen" that a few woodrats occurred in the area, which, if true, probably represented *N. f. campestris* but could have been *N. micropus;* along the Arkansas River, south of Chivington, in Prowers Co., Colorado—this is another "stockmen" report cited by Cary *(loc. cit.),* but because *micropus* now is known on the north side of the Arkansas River both east and west of this locality, it is more likely that the observed woodrat dens were those of that species; Arkansas River bottom, near Holly, Prowers Co., Colorado—originally reported by Warren (1910:112), this record of woodrat dens clearly should be removed from localities included in the distribution of *campestris* because *micropus* has been collected approximately six miles east in adjacent Kansas (Coolidge) and the general habitat near Holly is more like that of *micropus* than that of *campestris.*

One other locality of record for *campestris* is worthy of comment. Finley (1958:318) discussed a specimen represented only by a skull with incomplete data (USNM 6301) and Armstrong (1972) reported another (USNM 6320) of *N. floridana* from Denver, Colorado, both collected by E. Palmer. Both authors agree, as do I, that Denver is certainly not within the present distributional range of *campestris* and, although the identity of the skulls is not in question, they probably are from some locality(ies) to the east of Denver.

Considering only the records accepted, the distribution of *campestris* in Colorado extends from just north of the Arkansas River (Fort Lyon, 3 mi N Fowler, and Olney Springs) to the foothills of the Rockies (several localities

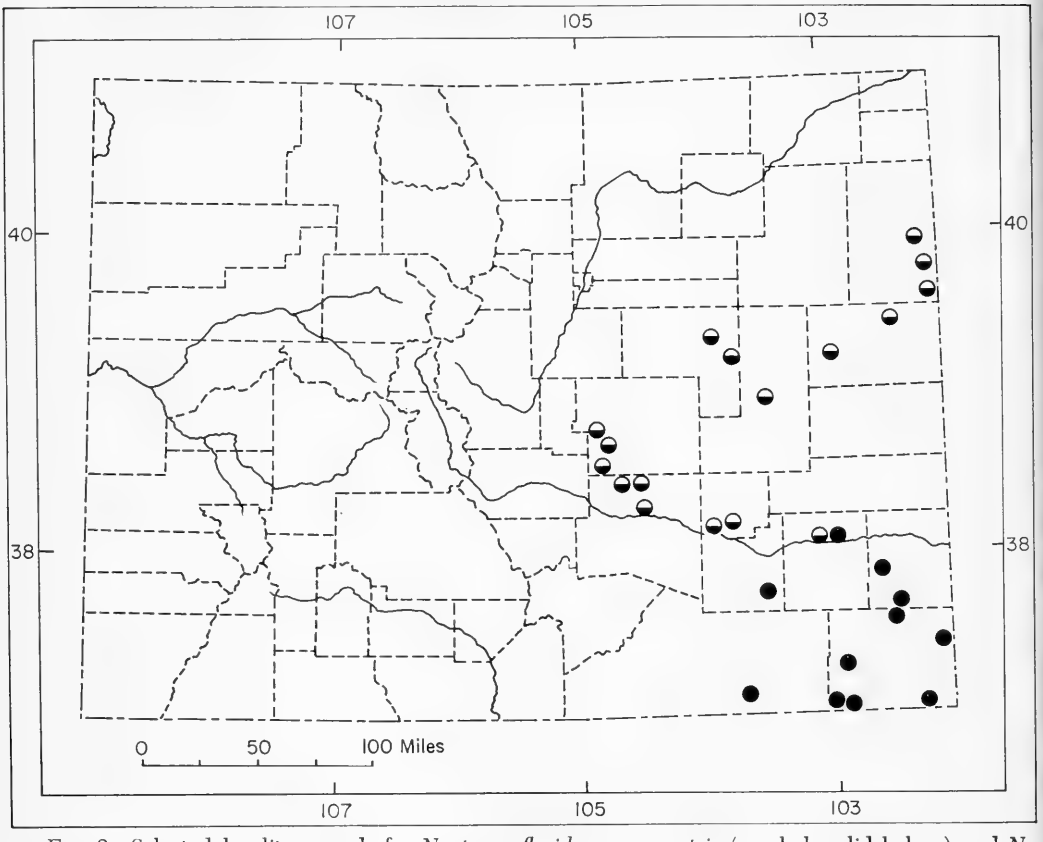

FIG. 3. Selected locality records for *Neotoma floridana campestris* (symbols solid below) and *N. micropus canescens* (solid symbols) in Colorado.

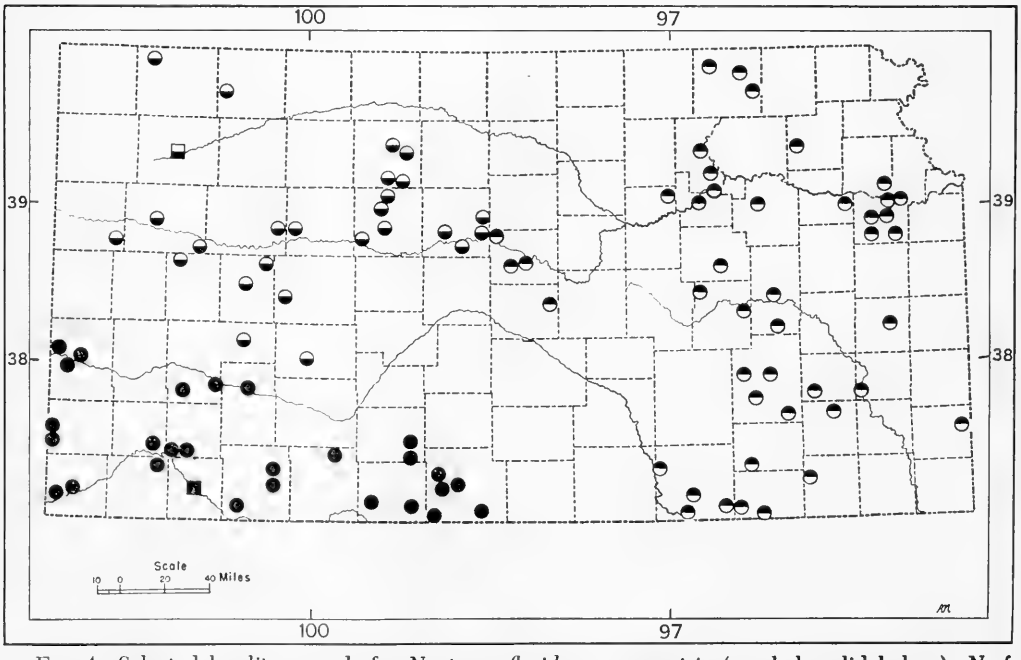

FIG. 4. Selected locality records for *Neotoma floridana campestris* (symbols solid below), *N. f. attwateri* (symbols solid above), and *N. micropus canescens* (solid symbols) in Kansas. Circles represent records accompanied by specific locality data; squares denote records specific only to county.

south and southeast of Colorado Springs), thence northeastward at least as far as Wray and in Nebraska as far as North Platte. In Kansas, the race occurs east to the line (discussed above) between Russell and Ellsworth counties, where *campestris* intergrades with *attwateri*. I have not attempted to determine the northern limit of range of *campestris* through field investigations, but Andersen and Fleharty (1967:39) did not find woodrats in Jewell County, Kansas, and neither Jones (1964) nor Choate and Genoways (1967) reported finding them in southern Nebraska east of Red Willow County. The first specimens to be associated with the name *campestris* in Nebraska were reported by Jones (1954: 485), although Goldman (1910:25) earlier listed a specimen from Haigler under the name *baileyi*.

The southern extension of the species in western Kansas seems to correlate well with the southern extent of the Ogallala limestone formations north of the Arkansas River. I have searched for woodrats throughout the area between the Arkansas River and the southernmost locality records for *campestris*. Specimens of *campestris* from the Pawnee River in northern Finney County are from only about 20 miles north of a locality (just north of the Arkansas River) where I have collected *Neotoma micropus*. The distributional status of *floridana* and *micropus* in those areas where the two might come into contact is discussed in the account of *N. m. canescens*.

A detailed and extensive ecological account of *N. f. campestris* in Colorado is given by Finley (1958:499-514). He found that this rat is one of the most versatile species of the genus in utilizing available materials, rocks, tree cactus, trees, or bushes for the construction of dens. Type of vegetation available is apparently of little importance, with the exception that unsculptured shortgrass prairie is insufficient for the fulfillment of denning requirements. In Kansas and Nebraska the situation is undoubtedly much the same. In Dundy County, Nebraska, I have seen houses of *campestris* constructed in sagebrush in a manner that rendered them indistinguishable from houses of *micropus* in southwestern Kansas. At several localities in Kansas (e.g. 19 mi S Dighton, Finney County, and 4 mi S and 0.5 mi W Jetmore, Hodgeman County) I have collected this woodrat from rock outcrops in otherwise open grasslands. In many cases the nearest outcrops or river systems were several miles distant. At two localities (16 mi N Hays, Ellis County, and 6 mi S and 4 mi E Russell, Russell County) large populations of *campestris* were observed in eastern red cedar windbreaks not far from major rivers (the Saline River and the Smoky Hill River, respectively). Most nests in the windbreaks were on the ground at the bases of trees, partially shielded by overhanging boughs. A few nests, however, were two to about 10 feet above the ground, supported solely by the trees. Along the Pawnee River in Finney County and the Smoky Hill River in Logan County, woodrats were living in piles of flood debris. In some cases the debris served as a skeleton upon which the rats had amassed large superstructures, but in others the only outward signs of the presence of woodrats were fecal droppings and faint runways.

Throughout the range of *N. f. campestris*, the distributional pattern is one of apparent disjunctness, with most populations almost certainly at least semi-isolated. Such a pattern probably results from inability of these woodrats to permanently occupy shortgrass prairie between river systems, rock outcrops, and stands of trees. A study of long-range dispersal habits of the race would be enlightening in revealing how isolated populations are founded and how much (if any) interpopulational gene flow takes place (see Wiley, 1971).

Neotoma floridana attwateri Mearns

Neotoma attwateri Mearns, 1897:721 [Holotype —USNM 11964/10402 from Lacey's Ranch, Turtle Creek, Kerr Co., Texas].

[*Neotoma floridana*] *attwateri*—Elliot, 1901: 157.

Neotoma floridana osagensis Blair, 1939:5 [Holotype—UNMZ 76070 from Okesa, Osage Co., Oklahoma].

Remarks.—Relegation of the name *Neotoma floridana osagensis* to the synonymy of *N. f. attwateri* extends the distribution of *attwateri* north to Kansas and Missouri. Total geographic variation within the subspecies is increased as a result of this change. As discussed beyond, the pattern of variation northward through Texas and in southern Oklahoma is clearly clinal, and lacking in abrupt changes that might indicate either restricted gene flow or secondary intergradation. I have not examined specimens from the area between Hill and Robertson counties, Texas, but according to Strecker (1924:16 and 1929:220) woodrats are common in that area, at least along the Brazos River, Tehuacana Creek, and White Rock Creek. These reports indicate that although documentary specimens may be lacking, woodrats are more or less continuously distributed throughout the area in which the ranges of *attwateri* and *osagensis* were alleged to meet; therefore, no reason exists to suspect reduced gene flow.

The pattern of variation at the zone of contact between *attwateri* and *campestris* is discussed in the remarks of the previous account. On the east, the range of *attwateri* meets that of *N. f. illinoensis* in Missouri and Arkansas and that of *N. f. rubida* in southeastern Texas. I have only superficially studied woodrats from Missouri and Arkansas, and cannot comment in detail on the relationships of *illinoensis* to *attwateri*. These two races seemingly resemble each other to a greater degree than either resembles *rubida*, but detailed study might not support this supposition. I have examined specimens of *rubida* from Texas and found woodrats assignable to that name relatively distinct from those representing *attwateri*. One specimen from Harris County, Texas (SFA 2312), appears to be an intergrade between the two subspecies, but herein is assigned to *attwateri* on the basis of its comparatively small size and the absence of reddish coloration typical of *rubida*.

Records of occurrence.—Specimens examined (680).—KANSAS: *Allen County:* 2 mi N, 0.5 mi W Neosho River Bridge, Humbolt, 2 (KU). *Anderson County:* 3.7 mi S Garnett, 1 (KU); *4.5 mi NNE Welda,* 1 (KU). *Chase County:* 9 mi E Lincolnville, 1 (KU); 1.5 mi S Saffordville, 1 (KSTC). *Chautauqua County:* Cedar Vale, 8 (USNM); 1 mi N, 2.5 mi W Elgin, 1 (KU). *Cowley County:* 3.75 mi S, 1.5 mi W Udall, 1 (KU); 6 mi N, 12 mi E Arkansas City, 2 (KU); 3 mi W Cedar Vale, 1 (KU); 8.6 mi E Arkansas City, 2 (KU); *3 mi SE Arkansas City,* 2 (KU). *Crawford County:* Mulberry, 1 (KU). *Douglas County:* 7 mi N Lawrence, 1 (KU); *5 mi N, 2 mi W Lawrence,* 1 (KU); *6 mi NW Lawrence,* 1 (KU); *1 mi N Midland,* 2 (KU); *1 mi NW Midland,* 5 (KU); *1 mi W Midland,* 2 (KU); within 3 mi radius of Lawrence, 17 (KU); *1 mi N, 5 mi W Lawrence,* 1 (KU); 7 mi W Lawrence, 2 (SM); *8 mi SW Lawrence,* 1 (KU); *8.5 mi SW Lawrence,* 2 (KU); *10 mi SW Lawrence,* 3 (KU); Lone Star Lake, 6 (KU); *9 mi S, 9 mi W Lawrence,* 1 (KU); *10 mi S, 9 mi W Lawrence,* 1 (KU); 2 mi S, 2 mi W Pleasant Grove, 1 (KU); *unspecified,* 1 (KU). *Elk County:* 1.12 mi S, 1.75 mi W Moline, 1 (KU). *Ellsworth County:* 3 mi S Wilson, 2 (KU); 3.5 mi SE Ellsworth, 8 (KU); 5 mi SW Ellsworth, 3 (KU). *Geary County:* Fort Riley, 2 (USNM). *Greenwood County:* within 5 mi radius of Hamilton, 32 (KU); 15 mi W Hamilton, 9 (1 AMNH, 8 KU); *12 mi W Hamilton,* 1 (AMNH); *4 mi S, 17 mi W Hamilton,* 3 (1 AMNH, 2 KU); *4 mi S, 14 mi W Hamilton,* 1 (KU); *12 mi SW Hamilton,* 4 (KU); 8 mi SW Toronto, 7 (KU); *8.5 mi SW Toronto,* 17 (KU); *unspecified,* 1 (AMNH). *Jackson County:* 6 mi S, 10 mi W Holton, 1 (KU). *Jefferson County:* 13 mi NE Lawrence, 2 (KU). *Leavenworth County:* 5 mi NE Lawrence, 1 (KSTC); *unspecified,* 10 (KU). *Lyon County: Ross Natural History Reservation,* 2 (KSTC); Emporia, 1 (KSTC); *unspecified,* 1 (KSTC). *Marshall County:* 1 mi W Vermillion, 2 (KU). *Montgomery County:* 17 mi NNE Sedan, 1 (KU). *Morris County:* 4.12 mi S, 6 mi W Council Grove, 1 (KU). *Rice County:* 2 mi N, 2 mi E Little River, 1 (KSTC). *Riley County:* 3.25 mi S, 2 mi E Randolph, 1 (MHP); Manhattan, 9 (4 AMNH, 5 USNM). *Shawnee County:* 1 mi N, 1 mi W Big Springs, 1 (KU). *Wabaunsee County:* 1 mi N Alma, 4 (KU). *Wilson County:* 2 mi N, 3 mi E Benedict, 1 (KSTC). *Woodson County:* State Lake, 2 (KSTC).

OKLAHOMA: *Adair County:* 5 mi SE Flint, 1 (OSU); *3 mi NNE Chewey,* 5 (SM); 7 mi W Stilwell, 1 (KU); Stilwell, 8 (USNM). *Blaine County:* Canton Public Hunting Area and Lake—vicinity of Longdale, 17 (1 FWCM,

11 OSU, 5 USNM); *Salt Creek Canyon,* 2 (KU); *2 mi N, 9 mi W Okeene,* 1 (KSTC); 2 mi N, 2 mi W Okeene, 1 (KSTC); Roman Nose State Park, 9 (OSU); 2 mi W Watonga, 3 (OSU). *Bryan County:* 10 mi SE Bennington, 1 (TNHC); *5 mi N Colbert,* 2 (TNHC); 0.5 mi NW Colbert, 3 (TNHC). *Caddo County:* 5 mi W Cogar, 3 (SM); Fort Cobb, 2 (USNM). *Canadian County: Methodist Church Camp, sec. 18, T. 11 N, R. 10 W,* 1 (SM); 5.5 mi SE Hinton, 1500 ft, 1 (KU). *Carter County:* 3 mi N Springer, 3 (USNM). *Cherokee County:* 2.5 mi NW Chewey, 2 (SM). *Choctaw County:* 1.5 mi N Hugo, 1 (OSU); *1 mi N, 3 mi E Hugo,* 1 (OSU). *Cleveland County:* 9 mi N, 2 mi E Norman, 2 (SM); within 5 mi radius of Norman, 18 (6 SM, 1 USNM, 11 KU); 1 mi N, 9 mi E Norman, 1 (SM); *0.5 mi N, 6 mi E Norman,* 1 (SM); *6 mi E Norman,* 1 (SM); *8 mi E Norman,* 1 (SM); *9 mi E Norman,* 1 (SM); *3 mi NE Noble,* 1 (SM); 1 mi N, 3 mi E Lexington, 1 (OSU); *4 mi SE Lexington,* 1 (OSU); *unspecified,* 2 (SM). *Comanche County:* Wichita Mountains Wildlife Refuge, 24 (10 OSU, 6 SM, 8 USNM); *19 mi NW Cache,* 1 (SM); Mt. Scott, 7 (USNM); *9 mi NW Cache,* 1 (SM); Chattanooga, 1 (USNM); *unspecified,* 1 (SM). *Cotton County:* 5 mi SE Taylor, 3 (SM). *Creek County:* Sapulpa, 4 (KU). *Dewey County:* 2 mi N, 6 mi W Longdale, 4 (KSTC); *NE corner Canton Public Hunting Area,* 1 (OSU); 2 mi S, 2 mi W Seiling, 1 (KU); *6 mi S, 2 mi W Seiling,* 2 (KU); 5 mi W Canton, 2 (KU); 6.5 mi S, 3 mi W Seiling, 2 (KU); *7 mi S, 2.5 mi W Seiling,* 3 (KU); 8 mi S, 5 mi W Seiling, 2 (KU). *Garfield County:* 1 mi S, 2 mi E Enid, 1 (OSU). *Haskell County:* 8.5 mi S Stigler, 1 (SM). *Johnston County:* Tishomingo National Wildlife Refuge, 1 (USNM). *Kay County:* 1 mi S, 7 mi E Ponca City, 1 (OSU); *Ponca Agency,* 1 (USNM). *Latimer County:* 5 mi N Wilburton, 1 (KU); *3.5 mi N Wilburton,* 8 (SM); Red Oak, 1 (USNM); Wilburton, 2 (OSU). *Le Flore County:* 5 mi S Wister, 1 (SM); 2 mi NE Zoe, 2 (SM); *0.75 mi N Zoe,* 4 (SM). *Lincoln County:* 3.5 mi S Perkins, 1 (OSU); 5 mi W Stroud, 1 (OSU). *Major County: 15 mi S Waynoka* (see remarks in account of *N. m. canescens*), 1 (OSU); 1.5 mi N, 0.25 mi W Cleo Springs, 8 (KSTC); 5 mi S, 2.5 mi E Cleo Springs, 2 (KSTC); 3 mi S Chester [=1.5 mi N Seiling] (see remarks in account of *N. m. canescens*), 16 (8 KSTC, 8 KU); *3 mi S, 0.5 mi E Chester,* 4 (KU); 3 mi S, 1 mi E Chester, 1 (KU). *Marshall County:* 6 mi N Willis, 1 (SM); *5 mi S, 1 mi W Shay,* 1 (OSU); *0.5 mi E Willis,* 1 (SM); 2 mi E Willis, 4 (MWU); *1 mi S, 2 mi W Willis,* 1 (SM); *University of Oklahoma Biological Station, including Engineering Tract and Paul's Landing,* 19 (2 OSU, 17 SM); *unspecified,* 4 (1 MWU, 2 OSU, 1 SM). *Mayes County:* 1 mi S Spavinaw, 6 (KU). *McCurtain County:* 2 mi N Smithville, 1 (SM); 2.5 mi W Smithville, 3 (SM); *2 mi W Smithville,* 2 (SM); Beavers Bend State Park, 4 (2 SM, 2 KU); 15 mi SE Broken Bow, 1 (SM). *Murray County:* Sulphur, 1 (OSU); 1.5 mi S Dougherty, 1 (MWU); *unspecified,* 1 (OSU). *Muskogee County:* 4 mi below [=SW] Fort Gibson Dam, 1 (OSU); 6 mi SE Fort Gibson, 1 (OSU). *Okmulgee County:* 3 mi S Okmulgee, 1 (OSU). *Osage County:* 10 mi NE Pawhuska, 1 (TNHC); *Osage Hills State Park,* 6 (OSU); 10 mi WSW Fairfax, 3 (SM); *McClintock Boy Scout Camp,* 1 (USNM); *Heartwood Mountain,* 1 (OSU). *Pawnee County:* 7.5 mi N, 2.75 mi W Pawnee, 1 (KU). *Payne County:* 2 mi N, 15 mi W Stillwater, 1 (OSU); *1 mi N, 9 mi W Stillwater,* 2 (OSU); vicinity of Lake Carl Blackwell, 36 (34 OSU, 2 USNM); *11 mi W Stillwater,* 1 (OSU); *10 mi W Stillwater,* 8 (2 OSU, 6 TT); *8 mi W Stillwater,* 1 (OSU); *5.5 mi W Stillwater,* 1 (OSU); *4 mi W Stillwater,* 1 (OSU); Stillwater, 1 (OSU); *2 mi E Stillwater,* 1 (OSU); *4 mi E Stillwater,* 1 (OSU); 5 mi E Stillwater, 1 (OSU); *1 mi S, 3 mi W Stillwater,* 2 (OSU); *4.25 mi SW Stillwater,* 1 (OSU); *2.5 mi S, 0.25 mi W Stillwater,* 1 (OSU); *1 mi S, 3 mi W Mehan,* 1 (OSU); 10.5 mi S Stillwater, 2 (OSU); *unspecified,* 7 (OSU). *Pittsburg County:* 4 mi NW McAlester, 1 (OSU); *2 mi E McAlester,* 1 (OSU); Savanna, 1 (USNM). *Pontotoc County:* 4 mi S Ada, 1 (OSU); *unspecified,* 2 (OSU). *Pottawatomie County:* 1 mi W Pink, 3 (SM); 7 mi SE Tecumseh, 2 (KU). *Pushmataha County:* 4 mi SE Clayton, 1 (SM); 1 mi S Nashoba, 4 (TNHC). *Rogers County:* 0.5 mi E Chelsea, 1 (OSU). *Stephens County:* unspecified, 1 (SM). *Tulsa County:* 8 mi W Red Fork, 2 (USNM); Red Fork, 2 (USNM); *unspecified,* 1 (SM). *Woodward County: unspecified* (see remarks in account of *N. m. canescens*), 2 (SM).

TEXAS: *Brazos County:* 3 mi W Bryan, 1 (TCWC); *7 mi W College Station,* 1 (TCWC); *within 5 mi radius of College Station,* 19 (TCWC); 7 mi SW College Station, 1 (TCWC); 10 mi SE College Station, 1 (TCWC). *Collins County:* 1 mi NE Wylie, 2 (MWU). *Colorado County:* Eagle Lake, 1 (TCWC). *Cooke County:* Marysville, 2 (USNM); *2 mi S Marysville,* 2 (TCWC); *8 mi W Gainsville,* 2 (MWU); Gainsville, 1 (USNM); *unspecified,* 2 (USNM). *Gonzales County:* Palmetto State Park, 1 (TNHC). *Gregg County:* 3.2 mi E Gladewater, 1 (TT). *Grimes County:* Navasota, 3 (USNM). *Harris County:* 22 mi N Houston, 1 (SFA). *Henderson County:* 2 mi NE Malakoff, 1 (SFA); 12 mi SE Athens, 1 (SFA). *Hill County:* 4 mi N Blum, 2 (KU). *Jack County:* 7 mi SE Jacksboro, 1 (MWU). *Kaufman County:* 19 mi SE Dallas, 2 (TT). *Kerr County:* Lacey's Ranch, Turtle Creek, 11 (5 AMNH, 1 TNHC,

5 USNM); *Ingram,* 9 (USNM). *Lavaca County:* 3 mi W Hallettsville, 1 (TCWC); *0.5 mi W Hallettsville,* 1 (TCWC); 14 mi WSW Hallettsville, 1 (TCWC). *Montague County: 2 mi W Nocona,* 1 (MWU); 3 mi E Nocona, 1 (MWU); 4 mi E Stoneburg, 1 (MWU). *Navarro County:* Barry, 1 (SFA). *Parker County:* 8.9 mi S Aledo, 13 (FWCM). *Robertson County:* 2 mi W Hearne, 2 (TCWC). *Tarrant County: Lake Worth Area,* 1 (FWCM); Fort Worth, 1 (FWCM); 6.5 mi S, 4 mi W Benbrook, 2 (FWCM). *Victoria County:* Victoria, 1 (USNM); *unspecified,* 1 (USNM). *Williamson County:* 3 mi N McNeil, 1 (TNHC).

Additional records: KANSAS (Rainey, 1956): *Dickinson County:* 15 mi E Talmage (Pl. 9). *Greenwood County: 7 mi E Eureka* (Pl. 2, Fig. 2). *Lyon County:* 6 mi N Madison (Pl. 3, Fig. 1). *Marshall County* (p. 634): 2 mi S Marysville; 5.5 mi S Beattie. *Riley County:* 7 mi S Manhattan (p. 551).

OKLAHOMA (Blair, 1939b:124, unless otherwise noted): *Adair County: 5 mi S Kansas. Bryan County:* 5 mi SW Colbert (McCarley, 1952:108). *Cleveland County: Noble. McClain County: 7 mi SW Norman* (Hays, 1958:235, 238). *Murray County: Dougherty. Osage County: Conway Springs;* Okesa (Blair, 1939a:7); *2 mi SW Okesa. Rogers County* (Blair, 1939a:7): 3 mi W Catoosa; *Garnett.*

TEXAS: *Cooke County* (Russell, 1953: 461): *13 mi NE Gainsville; 7 mi N Gainsville; 4 mi NNE Myra;* 4 mi NE Rosston; *3 mi NE Leo. Hunt County:* 5 mi N Greenville (Baker, 1942:343). *McLennan County:* vicinity of Waco (Strecker, 1929:220).

Distribution and habitat.—Figures 4, 5, and 6 show localities of occurrence of *Neotoma floridana attwateri* in Kansas, Oklahoma, and Texas, respectively. This subspecies also is known from adjacent parts of Missouri and Arkansas. The distribution of *attwateri* extends from north-central and northeastern Kansas and central Missouri southward through Oklahoma, western Arkansas, and eastern Texas to the Gulf of Mexico. In extreme southeastern Texas it is replaced by the larger, reddish-colored *N. f. rubida.* Goldman (1910:26) listed two specimens as *attwateri* from the Edwards Plateau at Rocksprings, Kerr Co., Texas. I examined two specimens (USNM 117552-53) from 7 mi S Rocksprings that were collected in 1902; I do not doubt that they are the same specimens studied by Goldman. The identity of these and other woodrats, and resultant ramifications as regards distribution of several species will be discussed elsewhere; it is only necessary to indicate here that both specimens are best referred to *Neotoma albigula. Neotoma floridana,* therefore, is not known to have occurred on the Edwards Plateau in Recent times (see Dalquest *et al.,* 1969:250). The southwesternmost locality of record for the species is Ingram, Kerr County.

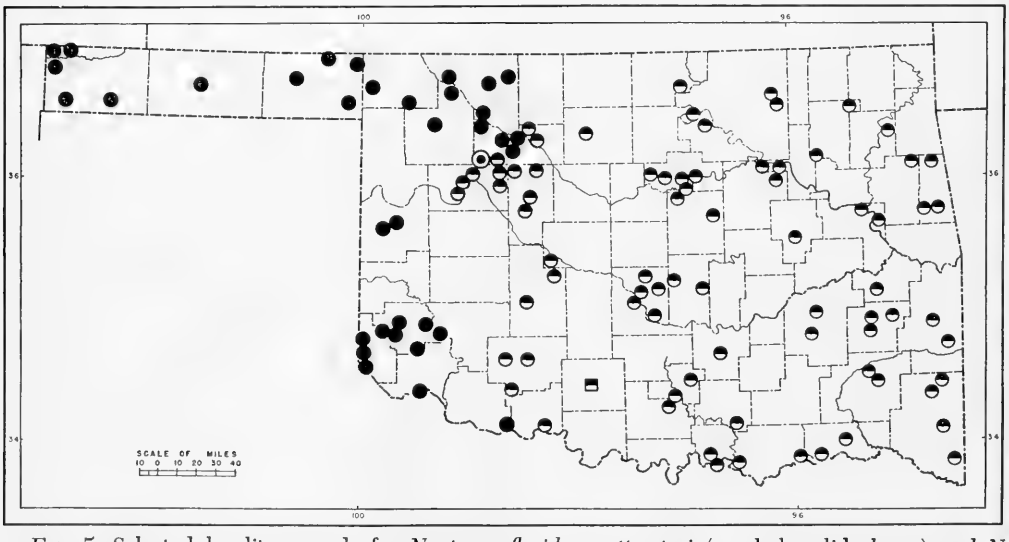

FIG. 5. Selected locality records for *Neotoma floridana attwateri* (symbols solid above) and *N. micropus canescens* (solid symbols) in Oklahoma. The encircled symbol denotes the single known locality of sympatric occurrence of the two species; for explanation of symbols see figure 4.

Distributional relationships of *N. f. attwateri* at the western limit of its range, where it abuts the range of *N. m. canescens*, will be discussed in the account of the latter. *Neotoma floridana attwateri* has not been found in Nebraska; factors possibly limiting its range to the north are discussed by Rainey (1956:632-637) and Jones (1964:218).

The literature is replete with ecological accounts of *N. f. attwateri* in Kansas and northern Oklahoma but the habits of this rat in southern Oklahoma and Texas are not well known. Rainey (1956: 549), in one of the better ecological studies of the species, summarized the habitat in eastern Kansas as follows: "habitat of the woodrat in eastern Kansas is divisible into two principal types; the osage orange, *Maclura pomifera* (Raf.), hedge-row habitat type, which is the more widespread, and the rock outcrop type of habitat. Stone fences, upland woods, wooded stream-courses, shrubby hillsides, and uninhabited buildings constitute habitat types of less importance." Fitch and Rainey (1956) contributed significantly to a general understanding of the ecology of woodrats in eastern Kansas, but found them only in the habitats reported by Rainey *(loc. cit.)*. My observations of *attwateri* in eastern Kansas also fit the pattern outlined by Rainey. In Ellsworth County, this woodrat was trapped in two markedly different habitats. At a locality 3.5 mi SE Ellsworth, woodrats were living in crevices and around large boulders of a steep rocky hillside just south of the Smoky Hill River, but 5.5 mi SW Ellsworth I found a sparsely distributed, and apparently small, population of woodrats occupying what appeared to be marginal habitat along the banks of a dry creek. Most houses were in small piles of flood debris, but one small, active nest was on the ground partially concealed by the dead stems of annual weeds in the corner of a recently harvested milo field. A few scattered trees near the creek may have afforded some cover and building materials, but no dens were observed directly associated with the trees.

Murphy (1952:205) concluded that woodrats in north-central Oklahoma prefer postoak-blackjack oak ravines and fringed forest ravines. Goertz (1970:96-98) studied *attwateri* in the same area and found them in various types of woodlands, brushy areas, riparian associations along stream banks, and to a lesser extent in small rock outcrops in relatively open prairie. Spencer (1968: 38) reported collecting *attwateri* in a mesquite-prickly pear cactus association in gypsum rock outcrops near the western edge of the range in Oklahoma.

A colony of woodrats in thick woodland along the banks of a sandy gully in Brazos County, Texas, was studied by Lay and Baker (1938). Rats variously occupied surface dens in the wooded area, burrows and root crevices in the gully bank, and an underground burrow in a nearby pasture. Farther north in Texas, Strecker (1929:220) reported *attwateri* common along rocky and wooded river banks. Bailey (1905:110) stated that "near Ingram, in the valley of the Guadalupe River, a few of these wood rats were caught in the cliffs and rocks bordering the river valley, but they were more common under the great heaps of driftwood and rubbish along the river bottoms."

As expressed or implied by most of the authors cited and as observed by me, the most important factor of the habitat of *Neotoma floridana* (including this subspecies and the two previously discussed) is the availability of cover together with materials and structural elements for construction of dwellings. *Neotoma floridana* seems to be extremely versatile as regards food requirements and relatively opportunistic in terms of habitat selection so long as minimal requirements for cover and nesting materials are available.

Neotoma floridana rubida Bangs

Neotoma floridana rubida Bangs, 1898:185 [Holotype—collection of E. A. and O. Bangs

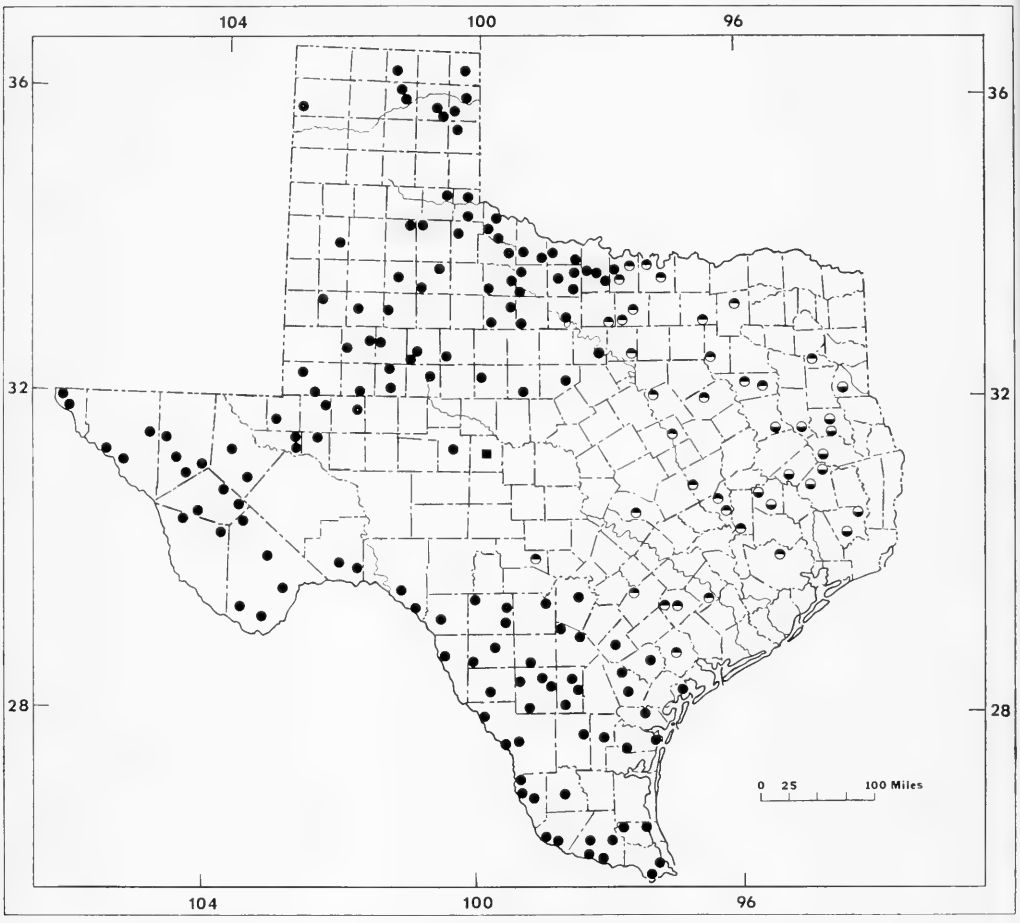

Fig. 6. Selected locality records for *Neotoma floridana attwateri* (symbols solid above), *N. f. rubida* (symbols solid below), and *N. micropus canescens* (solid symbols) in Texas. For explanation of symbols see figure 4.

2872 from Gibson, Terrebonne Parish, Louisiana].

Remarks.—The systematic status of *Neotoma floridana rubida* was not a primary concern of this study, but was considered to determine the eastern extent of the distribution of *N. f. attwateri* in southern Texas. My findings agree with those of McCarley (1959:411), except that specimens from Nacogdoches and Panola counties (although herein assigned to *rubida*) are much less reddish than specimens of *rubida* from farther south in Texas and those (LSU) examined from Louisiana. This may be an area of intergradation between *N. f. rubida* and *N. f. attwateri* or *N. f. illinoensis* (or among all three). Kelson (1952:236) referred a specimen, previously assigned to *rubida* (Goldman, 1910:23), from Texarkana, Bowie County, to *N. f. illinoensis,* but indicated it resembled *N. f. osagensis* (= *N. f. attwateri*) in certain characters. I have not seen the specimen in question and therefore follow Kelson. Goldman (1910: 26) assigned two specimens from Kountze, Hardin County, to *attwateri* and 22 specimens from nearby Sourlake, Hardin County, to *rubida* (p. 23). That portion of Texas was mapped by him as within the range of *rubida* (p. 21). I regard the specimens from Kountze as *rubida* on geographic grounds.

Records of occurrence.—Specimens examined (25).—TEXAS: *Anderson County:* 5.5 mi SE Slocum, 1 (SFA). *Angelina County:* Diboll, 1 (SFA). *Cherokee County: 0.5 mi N Forest,* 1 (SFA); 3 mi W Forest, 1 (SFA). *Nacogdoches County:* 1 mi N Nacogdoches, 2 (TT); *Nacogdoches,* 3 (SFA); *5 mi S Nacogdoches,* 1 (SFA); 8 mi S Nacogdoches, 1 (SFA). *Panola County:* 2 mi S, 5 mi W Carthage, 1 (SFA). *Polk County:* 14 mi N Camden, 4 (TCWC); 12 mi W Camden, 1 (TCWC). *Trinity County:* 1 mi E Trinity, 1 (TCWC). *Walker County:* 17 mi WNW Huntsville, 1 (TCWC); Huntsville, 2 (TCWC); *4 mi E Huntsville,* 1 (TCWC); *2 mi SW Huntsville,* 1 (TCWC); *6 mi S Huntsville,* 1 (TCWC); *11 mi NW New Waverly,* 1 (TNHC).

Additional records: TEXAS: *Hardin County:* Kountze (Goldman, 1910:26); Sourlake (Goldman, 1910:23).

Distribution and habitat.—The distribution of *N. f. rubida* in Texas is shown in figure 6. I have not studied woodrats of this subspecies in the field, but McCarley (1959:411) indicated that their habits are not markedly different from those of *N. f. attwateri* in Texas. Davis (1960:192) reported that in some areas of eastern Texas woodrats live in burrows and do not construct surface nests. If true, this would be a departure from the usual habits of *N. floridana* in northern and western portions of the range.

Neotoma micropus

Three nominal subspecies of *Neotoma micropus* are recognized herein; this is a reduction by two in the number heretofore regarded as valid. In comparison with most other species of woodrats, the biological attributes (including geographic variation and taxonomy) of *micropus* have received relatively little attention from mammalogists. As indicated previously, I studied *micropus* throughout its geographic range, but less intensively in New Mexico than in other areas.

Recent studies have shown that *Neotoma micropus* and *Neotoma albigula* are more closely related than previously was thought. The two species have been found together at many localities and at some of these they apparently hybridize. Finley (1958) first reported specimens from Colorado that appeared to be possible hybrids and Anderson (1969) researched this problem in Chihuahua and Coahuila. I have examined the material studied by Finley as well as additional material from Texas and New Mexico. Elucidation of the *micropus-albigula* problem eventually will affect the total understanding of the systematics of the woodrats of both of these species and of *Neotoma floridana.* In this report, however, I have concentrated on *micropus* and *floridana.*

The patterns of geographic variation in *micropus* are such that I considered three alternative schemes with regard to the assignment of subspecific names. Irrespective of the alternatives, it seems clear that the woodrats from White Sands, New Mexico, are only slightly more pallid ecomorphs of populations of the species in adjacent areas and do not warrant recognition at the subspecific level. However, one of the alternatives discussed and rejected below would require use of the name *leucophea* for all populations of the species in western Texas, New Mexico and adjacent Chihuahua, Coahuila, and Nuevo León.

The first alternative was to leave existing names (with the exception of *leucophea*) unchanged and simply describe geographic variation within that system. The only advantage seemed to be that of nomenclatural stability. Recognition of a darker eastern subspecies *(micropus)* and a generally paler western subspecies *(canescens)* would obscure some trends in variation in color and in external and cranial sizes. This alternative also would result in continued recognition of the name *N. m. littoralis,* even though woodrats previously assigned to that name differ appreciably from specimens of *N. m. micropus* from farther north in Tamaulipas only in being somewhat more brownish.

The second alternative involved recognition of seven subspecies to denote each general kind of variant seen. *Neotoma micropus littoralis* and *N. m.*

planiceps would continue to be recognized. *Neotoma micropus micropus* would be restricted to the small, dark, coastal woodrats of central and northern Tamaulipas. A new name would be proposed for the large, intermediate-colored woodrats of the Texas Coast and adjacent inland areas. The available name *N. m. surberi* would be applied to the large, dark woodrats of south-central Kansas and western Oklahoma (not including the panhandle of that state). The name *canescens* would be restricted to the large, pale-colored woodrats of the Oklahoma Panhandle, southwestern Kansas, and southeastern Colorado; and the name *leucophea* would be applied to the small, pallid woodrats of New Mexico, western Texas, and México, exclusive of coastal Tamaulipas and the vicinity of Río Verde, San Luis Potosí.

The third alternative, and the one adopted, involves provisional retention of the name *N. m. planiceps* (pending acquisition of specimens that elucidate the distributional and morphological relationships of this woodrat, which presently is known only by the holotype). The name *N. m. littoralis* is placed in the synonymy of *N. m. micropus*, a subspecies of small, dark-colored (often brownish) woodrats of coastal Tamaulipas. All other populations of the species, including those previously known as *N. m. micropus* from localities other than coastal Tamaulipas, are referred to a single subspecies, *N. m. canescens*. Because variation both in size and color is gradually clinal throughout the distribution of *canescens*, no clearcut areas of demarcation separate local populations. However, to recognize only a single taxon results in assignment of woodrats that are quite different (especially from the extremes of the clines) to the same subspecies. Total geographic variation within the subspecies *N. m. canescens* as thus conceived exceeds that in any of the other races considered in this study.

Neotoma micropus canescens J. A. Allen

Neotoma micropus canescens J. A. Allen, 1891: 285 [Lectotype—AMNH 3030/2350 from North Beaver (=North Canadian River), Indian Territory (Cimarron Co., Oklahoma), near the boundary line between the Indian Territory and New Mexico].

Neotoma macropus [*sic*] *surberi* Elliot, 1899: 279 [Holotype—Field Mus. Nat. Hist. 6755 from 3 mi W Alva, Oklahoma Territory (Woods Co., Oklahoma)].

Neotoma micropus leucophea Goldman, 1933: 472 [Holotype—USNM 251057 from White Sands, 10 mi W Point of Sands, White Sands National Monument, Otero Co., New Mexico].

Remarks.—Confusion exists concerning the proper lectotype of *Neotoma micropus canescens*. Although I would have resolved this question differently, I follow Finley (1958:310-312) in the above synonymy to avoid belaboring a controversial point. Considerations germane to the taxonomic status of this subspecies are discussed above, including nomenclatorial alternatives that might be used to reflect patterns of geographic variation within the samples of woodrats here treated as *N. m. canescens*.

Records of occurrence.—Specimens examined (1102).—COLORADO: *Baca County:* 14 mi N, 4 mi E Springfield (Two Buttes Reservoir), 2 (KU); 5 mi S, 2 mi W Pritchett, 22 (KU); 2 mi N, 7 mi W Regnier, 4 (KU). *Bent County:* 2 mi S, 2 mi E Hasty, 11 (KU). *Las Animas County:* 11 mi N, 8 mi E Branson, 5600 ft, 4 (KU). *Prowers County:* 16 mi N, 1 mi E Springfield, 1 (KU); *1 mi N Two Buttes Reservoir, 4350 ft*, 1 (KU).

KANSAS: *Barber County: 5 mi S Sun City*, 1 (KU); 15 mi W Medicine Lodge, 1 (KSTC); 10 mi W Medicine Lodge, 16 (KU); *8 mi SW Medicine Lodge*, 2 (KU); *6 mi N Aetna*, 1 (KU); *7 mi N, 7 mi W Kiowa*, 2 (KSC); 7 mi N, 6 mi W Kiowa, 1 (KSC); *1 mi N Aetna*, 1 (KSC); *1 mi SW Aetna*, 1 (KU); 3 mi S Aetna, 1 (KU); *3.5 mi S Aetna*, 1 (KU); *Marty Ranch*, 5 (KU); *unspecified*, 2 (SM). *Clark County:* 7 mi S Kingsdown, 3 (KU); *11 mi S, 1 mi W Kingsdown*, 3 (KU). *Comanche County:* 7 mi S Coldwater, 3 (KSTC); 11.5 mi S, 16 mi E Coldwater, 6 (KU); *Cave Creek*, 1 (KU). *Finney County:* 1 mi S Pierceville, 2 (KU); 15 mi S, 4 mi W Garden City, 1 (KU). *Gray County:* 2 mi NW Ingalls, 1 (KU). *Hamilton County:* Coolidge, 1 (KU); State Lake, 5 (2 MHP, 3 KU); *2.5 mi N Syracuse*, 1 (KU); *1 mi N, 3 mi W Syracuse*, 4 (KSTC); 1 mi S, 6 mi W Syracuse, 1 (MHP). *Haskell County: 2 mi S, 4 mi W Satanta*, 30 (KU); 3 mi S, 1 mi W Satanta, 11 (KU); 5 mi S, 4 mi W

Satanta, 8 (KU). *Kiowa County:* 5 mi N Belvidere, 31 (17 AMNH, 14 KU); Rezeau Ranch, N of Belvidere, 1 (KU). *Meade County:* 0.5 mi S, 4 mi E Fowler, 7 (KU); 11.5 mi E Meade, 2 (KU); *11 mi SW Meade,* 2 (AMNH); vicinity of State Park (12-17 mi SW Meade), 67 (21 AMNH, 3 MHP, 43 KU); *unspecified,* 1 (KU). *Morton County:* 9 mi N, 3 mi E Elkhart, 13 (KU); *8 mi N Elkhart,* 3 (KSTC); *7 mi N, 2 mi W Elkhart,* 2 (KU); 7 mi N Elkhart, 2 (MHP); *unspecified,* 4 (3 KU, 1 UNAM). *Seward County:* unspecified, 1 (KSTC). *Stanton County:* 1 mi N, 8 mi W Manter, 5 (KU); *1 mi N, 7.5 mi W Manter,* 2 (KU); *1 mi N, 6 mi W Manter,* 2 (KU); 3 mi S, 14 mi W Johnson, 7 (MHP). *Stevens County:* 4 mi E Moscow, 4 (KU).

NEW MEXICO: *Eddy County:* 3.25 mi NE Carlsbad, 2 (LSU); 24 mi E Carlsbad, 3500 ft, 1 (KU); 5 mi SW Carlsbad, 1 (KU); 2 mi NE Black River Village, 1 (KU); Carlsbad Cavern, 1 (KU); Rattlesnake Spring, 30 mi SW Carlsbad, 1 (KU). *Hidalgo County:* 6 mi SSE Lordsburg, 4200 ft, 1 (KU). *Luna County:* 3 mi N Deming, 4300 ft, 2 (KU). *Otero County:* 13 mi W Tularosa, 1 (TNHC); 3 mi SW Alamogordo, 2 (TNHC); 3 mi S Alamogordo, 3 (TNHC); 10 mi W Point of Sands, White Sands National Monument, 3 (USNM). *San Miguel County:* 1 mi S, 2 mi W Conchas Dam, 2 (KU). *Santa Fe County:* 0.5 mi NW Santa Fe Municipal Airport, 1 (KU); 1 mi W Santa Fe Municipal Airport, 1 (KU); 8 mi SW Santa Fe, 4 (KU); Santa Fe Field Station, 1 (KU).

OKLAHOMA: *Beaver County:* 21 mi S Meade, Kansas, 1 (KU); 8 mi NE Gate, 1 (KU); 1.5 mi NE Beaver, 2 (KU); 3 mi NE Slapout, 1 (SM). *Blaine County: Canton Reservoir* (see remarks below), 1 (OSU). *Cimarron County:* Regnier, 4375 ft, 1 (KU); *3 mi SE Regnier, 4350 ft,* 1 (KU); 6 mi N Kenton, 3 (OSU); *4 mi N Kenton,* 1 (OSU); *1 mi S, 2 mi E Kenton,* 1 (SM); 3 mi S, 2 mi E Kenton, 1 (OSU); 7.5 mi S, 10 mi W Boise City, 3 (KU); 9 mi W Griggs, 3900 ft, 1 (KU). *Greer County:* Granite, 1 (OSU); 5 mi NE Reed, 1700 ft, 1 (SM); 1 mi S, 1 mi W Reed, 1 (SM); 10 mi SE Mangrum, 1 (MWU). *Harmon County:* 3 mi W Reed, 6 (SM); *1 mi S, 6 mi E Vinson, 1700 ft,* 9 (SM); 1 mi S, 2 mi W Madge, 1 (SM); *6.5 mi SE Vinson,* 1 (SM); *13 mi N Hollis,* 1 (OSU); *11 mi N Hollis,* 2 (FWCM); *6 mi N, 2 mi W Hollis,* 2 (OSU); 6 mi N Hollis, 13 (FWCM); 5.5 mi S Hollis, 5 (FWCM). *Harper County: Beaver River, Southern Great Plains Experiment Range,* 15 (OSU); *3.4 mi N Fort Supply,* 2 (USNM); 3 mi N Fort Supply, 43 (USNM). *Jackson County:* 14 mi S Olustree, 4 (TNHC). *Kiowa County:* 2 mi S Lugert, 1 (OSU). *Major County:* 5.5 mi S Waynoka, 2 (SM); *6 mi S, 3 mi E Waynoka,* 1 (OSU); *16 mi NW Orienta,* 1 (OSU); *1 mi N, 7 mi W Orienta,* 3 (KSTC); 16 mi W Orienta, 8 (OSU); *5 mi W Orienta,* 4 (2 SM, 2 USNM); 3 mi W Orienta, 1 (OSU); 3 mi N, 9 mi W Fairview, 1 (OSU); 3 mi S Chester [=1.5 mi N Seiling]—(see remarks below), 37 (8 KSTC, 29 KU); *3 mi S, 0.5 mi E Chester,* 2 (KU); *unspecified,* 2 (OSU). *Roger Mills County:* 7 mi N Cheyenne, 2000 ft, 2 (SM). *Texas County:* 5.5 mi N Guymon, 3100 ft, 1 (SM); *4.5 mi N Guymon, 3100 ft,* 3 (SM); *2 mi N Guymon, 3000 ft,* 3 (SM). *Tillman County:* 5.5 mi S Grandfield, 1 (SM). *Woods County:* Alva, 7 (USNM); 2 mi W Edith, 6 (5 SM, 1 USNM); 4 mi S, 12 mi W Alva, 3 (KU); *Waynoka Dunes,* 1 (OSU); 3 mi S Waynoka, 2 (SM); *5 mi S Waynoka, 1400 ft,* 6 (SM). *Woodward County:* Alabaster Caverns, 4 (3 OSU, 1 SM); Boiling Springs State Park, 6 (1 KSTC, 5 SM); 2 mi NNW Woodward, 1900 ft, 4 (SM); *Woodward,* 3 (USNM); *unspecified,* 3 (SM).

TEXAS: *Andrews County:* 10 mi NW Andrews, 1 (TCWC); 14 mi S Andrews, 1 (OSU). *Aransas County:* Aransas National Wildlife Refuge, 3 (TCWC); *4.6 mi NE Rockport,* 3 (TNHC); *6 mi W Rockport,* 1 (TNHC); *Rockport,* 1 (TNHC). *Archer County: 20 mi N Archer City,* 1 (MWU); *6 mi W Holliday,* 1 (MWU); *within 5 mi radius of Holliday,* 4 (MWU); *within 4 mi radius of Mankins,* 17 (MWU); 7 mi SW Wichita Falls, 1 (MWU); 6 mi S Wichita Falls, 1 (MWU); *11 mi SW Wichita Falls,* 1 (MWU); *vicinity of Lake Kickapoo,* 9 (MWU); 1 mi W Scotland, 2 (MWU); *12 mi N Archer City,* 1 (MWU); *9 mi N Archer City,* 1 (MWU); *14 mi S Holliday,* 2 (MWU); *4 mi W Archer City,* 1 (MWU); *4 mi S Archer City,* 1 (MWU); *5 mi S Archer City,* 1 (MWU); *7 mi S Archer City,* 1 (MWU); 7 mi NE Olney, 1 (MWU). *Atascosa County:* 7 mi SE Lytle, 1 (TNHC); *7 mi SW Somerset,* 1 (TNHC); *8 mi SW Somerset,* 1 (TNHC); 12 mi W Floresville, 1 (TNHC). *Baylor County:* 12 mi NW Seymour, 1 (MWU); Bomarton, 1 (MWU). *Bee County:* 12.5 mi N Beeville, 2 (TNHC). *Bexar County:* San Antonio, 2 (TNHC); *unspecified,* 1 (KU). *Borden County:* 16 mi W Gail, 1 (MWU). *Brewster County:* 11 mi N Alpine, 1 (MWU); *2 mi W Alpine,* 2 (AMNH); 7.4 mi S Marathon, 1 (AMNH); 5 mi S Terlingua, 2 (KU); Tornillo Creek, 12 mi N Government Springs, 2700 ft, 1 (AMNH); *Government Springs, 3950 ft, Chisos Mountains,* 2 (AMNH); *East base Chisos Mountains,* 2 (USNM); *Burnham Ranch, 3950 ft,* 2 (AMNH). *Callahan County:* 30 mi SE Abilene, 1 (SFA). *Cameron County:* 10 mi E Río Hondo, 4 (LSU); *8 mi NW Bayside,* 1 (LSU); *2 mi W Port Isabel,* 1 (TNHC); Brownsville, 5 (2 KU, 1 TNHC, 2 USNM); *14.7 mi E Brownsville,* 5 (KU). *Childress County:* 18 mi N Childress, 1 (MWU); *15 mi N Childress,* 1 (MWU); *5 mi N Childress,*

1 (TNHC); 5 mi S Childress, 1 (TNHC). *Clay County:* 7 mi SE Wichita Falls, 2 (MWU); 2 mi NE Bellevue, 1 (MWU). *Cottle County:* 13 mi N Paducah, 3 (TNHC). *Crane County:* 20 mi NNW Crane, 1 (MWU). *Crosby County:* Home Creek Canyon, 1 (AMNH); *unspecified,* 2 (AMNH). *Culberson County:* 25 mi N Van Horn, 1 (MWU); 16 mi E Van Horn, 5 (TCWC); 16 mi SE Van Horn, 8 (TCWC). *Dawson County:* 10 mi E Lamesa, 4 (TNHC); 12 mi NW Patricia, 1 (TNHC). *Dickens County:* 7 mi NE Dickens, 1 (MWU); 5 mi NW Spur, 2 (MWU). *Eastland County:* 9 mi S Ranger, 2 (TNHC). *El Paso County:* 15 mi N El Paso, 2 (USNM); *10 mi N El Paso,* 7 (USNM); *East El Paso,* 1 (USNM); near El Paso, 3 (USNM). *Fisher County:* 12 mi E Hermleigh, 6 (TNHC). *Floyd County:* 6 mi S, 2 mi W Quitaque, 1 (OSU). *Foard County:* 1 mi N, 12 mi E Crowell, 1 (MWU). *Frio County:* 2 mi N Dilley, 1 (TNHC). *Garza County:* 4 mi W Post, 1 (OSU). *Goliad County:* 3.5 mi N Goliad, 2 (TCWC). *Hansford County:* 6 mi S, 3 mi W Gruver, 1 (KU); *6 mi S, 2 mi W Gruver,* 1 (KU). *Hardeman County:* 3 mi N Quanah, 1 (MWU); 3 mi SE Lazare, 1 (MWU); *7 mi SW Quanah,* 2 (MWU); 13.5 mi S Quanah, 1 (MWU). *Hartley County:* Romero, 5 (AMNH). *Haskell County:* 6 mi N, 11 mi E Haskell, 3 (MWU); 12 mi SW Haskell, 1 (MWU). *Hemphill County:* 6 mi E Canadian, 4 (TCWC); 9 mi NNE Miami, 1 (MWU). *Hidalgo County:* 4 mi WSW Hargill, 1 (LSU); 17 mi NW Edinburg, 3 (TNHC); Alamo, 1 (LSU); 5 mi S Mission, 1 (LSU); *6 mi S McAllen,* 7 (TNHC). *Howard County:* 7 mi E Vealmoor, 2 (TNHC); Big Spring, 1 (USNM). *Hudspeth County:* Fort Hancock, 2 (1 AMNH, 1 USNM); W slope Sierra Diablo, 1 (FWCM). *Hutchinson County:* 1 mi S, 10 mi E Pringle, 2 (KU); 9 mi E Stinnett, 14 (TNHC). *Jeff Davis County:* 7 mi NW Toyahvale, 2 (MWU); 16 mi NE Fort Davis, 3 (TCWC); *Mouth of Madera Canyon,* 1 (TCWC). *Jim Hogg County:* 20 mi S Hebbronville, 9 (TNHC). *Jim Wells County:* Alice, 1 (LSU). *Karnes County:* 2 mi SW Kenedy, 2 (TNHC). *Knox County:* 4 mi SE Vera, 1 (MWU); 5 mi NW Knox City, 1 (MWU). *La Salle County:* 2 mi S Woodward, 1 (TCWC); 8 mi NE Los Angeles, 5 (TCWC); *3 mi NE Los Angeles,* 1 (TCWC); *8 mi W Cotulla,* 2 (TCWC); 25 mi E Cotulla, 1 (KU); 8 mi E Encinal, 3 (TCWC). *Lynn County:* 2 mi W Tahoka, 1 (MWU). *Martin County:* Stanton, 4 (USNM). *Maverick County:* Eagle Pass, 1 (TCWC). *McMullen County:* 21 mi W Three Rivers, 3 (TNHC); *20 mi W Three Rivers,* 1 (TNHC); 10 mi W Simmons, 2 (TNHC); 18 mi SE Tilden, 1 (LSU); *21 mi SW Three Rivers,* 1 (TNHC). *Medina County:* 7 mi N Castorville, 3 (KU). *Midland County:* 9 mi S Stanton, 1 (TCWC). *Mitchell County:* Colorado City, 2 (USNM). *Montague County: 5 mi S Ringgold,* 1 (MWU); *3 mi N Stoneburg,* 1 (MWU); 2 mi N Stoneburg, 1 (MWU). *Motley County:* 6 mi N Flomot, 2 (MWU). *Nueces County:* 1 mi S Bishop, 2 (TNHC). *Palo Pinto County:* Brazos, 1 (USNM). *Presidio County:* 7 mi W Valentine, 7 (TNHC); *1.5 mi SE Buford Well, Miller Ranch,* 1 (TNHC); *unspecified,* 1 (USNM). *Reeves County:* 20 mi S Pecos, 4 (KU). *Roberts County:* 6 mi N Miami, 4 (MWU). *San Patricio County:* 8 mi NE Sinton, 4 (LSU). *Scurry County:* 4 mi SW Synder, 1 (MWU); 20 mi NW Colorado City, 1 (USNM). *Starr County:* Garciaville, 2 (MWU). *Taylor County:* 6 mi W View, 4 (MWU). *Terrell County:* Lozier, 1 (USNM). *Terry County:* 8 mi N Tokio, 1 (TNHC). *Throckmorton County:* 18 mi SW Throckmorton, 2 (TNHC); *20 mi SW Throckmorton* [= *Lambshead Ranch*], 2 (TNHC). *Uvalde County:* Montell, 2 (KU); 3 mi N Sabinal, 2 (TNHC); 20 mi E Uvalde, 1 (TCWC). *Val Verde County:* Comstock, 1 (USNM); Del Rio, 2 (USNM). *Ward County:* 4 mi NW Royalty, 3 (TNHC). *Webb County:* 45 mi NW Laredo, 10 (KU); *40 mi NW Laredo,* 1 (TNHC); *40 mi SW Catarina,* 3 (TNHC); *15 mi NE Laredo,* 1 (TNHC); Islitas, 10 mi NNW Laredo, 3 (KU). *Wichita County:* 4 mi SE Electra, 2 (MWU); *within 6 mi radius of Iowa Park,* 25 (MWU); within 2 mi radius of Wichita Falls, 11 (MWU); *5 mi NNW Wichita Falls,* 1 (MWU); *6 mi E Wichita Falls,* 1 (MWU); *1.5 mi N Oliversion Lake,* 1 (MWU); *0.5 mi W Lake Wells,* 1 (MWU). *Wilbarger County:* 8 mi S, 2 mi W Vernon, 1 (MWU); *9 mi S Vernon,* 1 (MWU); *15 mi S Vernon,* 2 (TNHC); 7 mi S Harrold, 2 (MWU); *unspecified,* 2 (MWU). *Willacy County:* 10 mi NW Raymondville, 1 (TNHC); 28 mi E Raymondville, 3 (1 KU, 2 TCWC). *Young County:* 7 mi SW Graham, 1 (MWU). *Zapata County:* 16 mi N San Ygnacio (=1.8 mi from Webb County line on highway 83), 3 (TNHC); 6 mi NW San Ygnacio, 1 (TCWC); *5 mi N Zapata,* 1 (TNHC); *3.5 mi NE Zapata,* 2 (TNHC); 5 mi E Zapata, 6 (TNHC). *Zavala County:* 29 mi S Uvalde, 4 (TNHC); 14 mi W Crystal City, 1 (KU); *unspecified,* 3 (TNHC).

CHIHUAHUA: San Isidro, 10 mi SE Zabagoza, 2 (KU); 7 mi W Porvenir, 1 (KU); 3.5 mi ESE Los Lamentos, 420 m, 1 (KU).

COAHUILA: 1 mi S, 9 mi W Villa Acuña, 8 (6 KU, 2 UNAM); 10 mi SE Villa Acuña, 1 (TNHC); Cañon del Cochino, 3200 ft, 16 mi N, 21 mi E Piedra Blanca, 1 (KU); 11 mi S Hacienda San Miguel, 2200 ft, 1 (KU); 15 mi N, 8 mi W Piedras Negras, 5 (KU); 2 mi S, 11 mi E Nava, 810 ft, 4 (KU); Ciudad Allende, 1 (TNHC); 10 mi SE Guerrero, 7 (TNHC); 29 mi N, 6 mi E Sabinas, 10 (KU); 10 mi E Hacienda La Mariposa, 3000 ft, 1 (KU); Mariposa Ranch, 1 mi E Nacimiento, 27 mi

NE Ciudad Múzquiz, 1 (TNHC); La Gacha [=La Concha], 1600 ft, 1 (KU); La Lajita, Rancho de la Golondrina, 13 mi NE Ciudad Múzquiz, 1 (TNHC); *10 mi N Ciudad Múzquiz,* 2 (TNHC); 2 mi S, 3 mi E San Juan de Sabinas, 1160 ft, 1 (KU); Sabinas, 4 (TNHC); 10 mi ESE Sabinas, 2 (KU); 9 mi NW Don Martín, 2 (KU); Don Martín, 800 ft, 2 (KU); *Base of Don Martín Dam,* 2 (KU); 8 mi N Hermanas, 1500 ft, 2 (KU); Hermanas, 1205 ft, 2 (KU); *1 mi S Hermanas, 1200 ft,* 1 (KU); Cuatrociénegas, 1 (TNHC); 5 mi N, 2 mi W Monclova, 1 (KU); 0.5 mi E San Antonio de Jaral, 4400 ft, 1 (UNAM); 3 mi N, 5 mi W La Rosa, 3600 ft, 3 (KU).

NUEVO LEON: 15 mi N, 2 mi W Anáhuac [=Rodríguez], 1 (KU); 5 mi N, 3 mi W La Gloria, 1 (KU); 5 mi WSW [General] Zuazua, 1 (UNAM); Rancho 14 de Mayo, 1 km E Casa Principal, 1 (UNAM); 7 mi NW Providensia, 1 (KU).

TAMAULIPAS: 4 mi SW Nuevo Laredo, 900 ft, 14 (KU); *4.5 mi S Nuevo Laredo,* 1 (KU).

Additional records: COLORADO (Finley, 1958:315, unless otherwise noted): *Baca County:* Monon, Bear Creek; Furnish Canyon; Craugh Ranch, Cimarron River. *Otero County:* 18 mi S La Junta. *Prowers County:* 15 mi S Lamar (Armstrong, 1972).

KANSAS: *Barber County:* Sun [City] (Goldman, 1910:28). *Grant County:* 10 mi S, 8 mi E Ulysses (record of unoccupied woodrat dwellings, see text beyond in this account).

NEW MEXICO (marginal records only): *Luna County:* 8 mi E Deming (Goldman, 1910:29). *Rio Arriba County:* Rinconada (Goldman, 1910:29). *Valencia County:* 8 mi SE Grants (Hooper, 1941:32).

OKLAHOMA (Blair, 1939b:125): *Harper County:* 4 mi N Laverne. *Woods County: 3 mi W Alva; White Horse Spring; Waynoka.*

TEXAS (Goldman, 1910:28, unless otherwise noted): *Bee County:* Beeville. *Bexar County: Adams. Brewster County: Alpine;* Altuda; *Marathon. Cameron County: 11 mi E Brownsville* (Baker and Mascarello, 1969:196). *Clay County:* Henrietta. *Concho County:* unspecified. *Culberson County:* Kent. *Dimmit County:* Blocker Ranch. *Duval County:* San Diego. *Ector County:* 9 mi N Odessa (Baker and Mascarello, 1969:196). *Garza County: Post* (Baker and Mascarello, 1969:196). *Hall County:* Newlin. *Hudspeth County:* Sierra Blanca. *Jeff Davis County:* Valentine. *Kinney County:* Fort Clark. *Lamb County:* 3 mi N Fieldton. *La Salle County: Cotulla. Lipscomb County:* Lipscomb. *Lynn County: 2.5 mi S, 1 mi W Tahoka. Maverick County: Moras Creek; Pinto Creek. Nueces County:* Corpus Christi; *Nueces Bay. Presidio County:* 7 mi NE Marfa, 4900 ft (Blair, 1940:32). *Reeves County:* Toyah; *Toyahvale. Roberts County:* Miami. *San Patricio County:* 7 mi NE Sinton (Raun, 1966:2). *Starr County:* Roma; *Río Grande City. Taylor County: Tebo. Terrell County:* Dryden. *Tom Green County:* San Angelo. *Ward County:* Monohans. *Webb County: Dos Hermanos;* Laredo; *Santo Tomas. Wheeler County: Mobeetie;* 5.5 mi S, 2.5 mi W Old Mobeetie (Stickel and Stickel, 1948: 292). *Wilbarger County: Vernon. Winkler County* (Baker and Mascarello, 1969:196): *2 mi N Wink;* 8 mi SSE Kermit.

CHIHUAHUA: Monument 15, Boundary Line (Anderson, 1969:29).

COAHUILA (Goldman, 1910:21, 29, unless otherwise noted): 3 mi NW Cuatrociénegas (Baker, 1953:253); *7 mi E Las Vacas;* Sabinas; *Monclova* (also see Anderson, 1969:43); *Saltillo* (probably *N. albigula,* see Anderson, 1969:43).

NUEVO LEON (Goldman, 1910:28, unless otherwise noted): *Rodríguez;* 70 mi S Nuevo Laredo (Booth, 1957:15); Doctor Cos; 16 mi S China; Allende (Jiménez—G., 1966:187); Linares.

TAMAULIPAS (Goldman, 1910:28, unless otherwise noted): *Nuevo Laredo; 10 mi S Nuevo Laredo* (Booth, 1957:15); Camargo.

Distribution and habitat.—Locality records for *Neotoma micropus canescens* are shown in figures 3, 4, 5, 6, and 7. On the west, the range of this primarily Lower Sonoran subspecies corresponds roughly with the foothills of the Rocky Mountain-Sierra Madre Oriental Cordillera and associated extensions. The Rio Grande and Canadian rivers have served as corridors into the Rio Grande and Pecos valleys of New Mexico (see Bailey, 1932:171) as far north as Rinconada and possibly as far as the San Jose River Valley near Grants. A single juvenile tentatively identified as this subspecies by Hooper (1941:32) extends the distribution to the latter valley. In northern México, *N. m. canescens* extends into the lower mountainous areas in the natural breaks between various mountain ranges (Baker, 1956:129). In the watershed of the Río Saládo, for example, *canescens* is known to occur as far west as Cuatrociénegas. Distributional relationships of *N. m. canescens* and the geographically contiguous subspecies, *N. m. micropus,* are discussed beyond in the account of that subspecies.

In southeastern Colorado, southwestern Kansas, western Oklahoma, and east-central Texas, the range of *N. micropus*

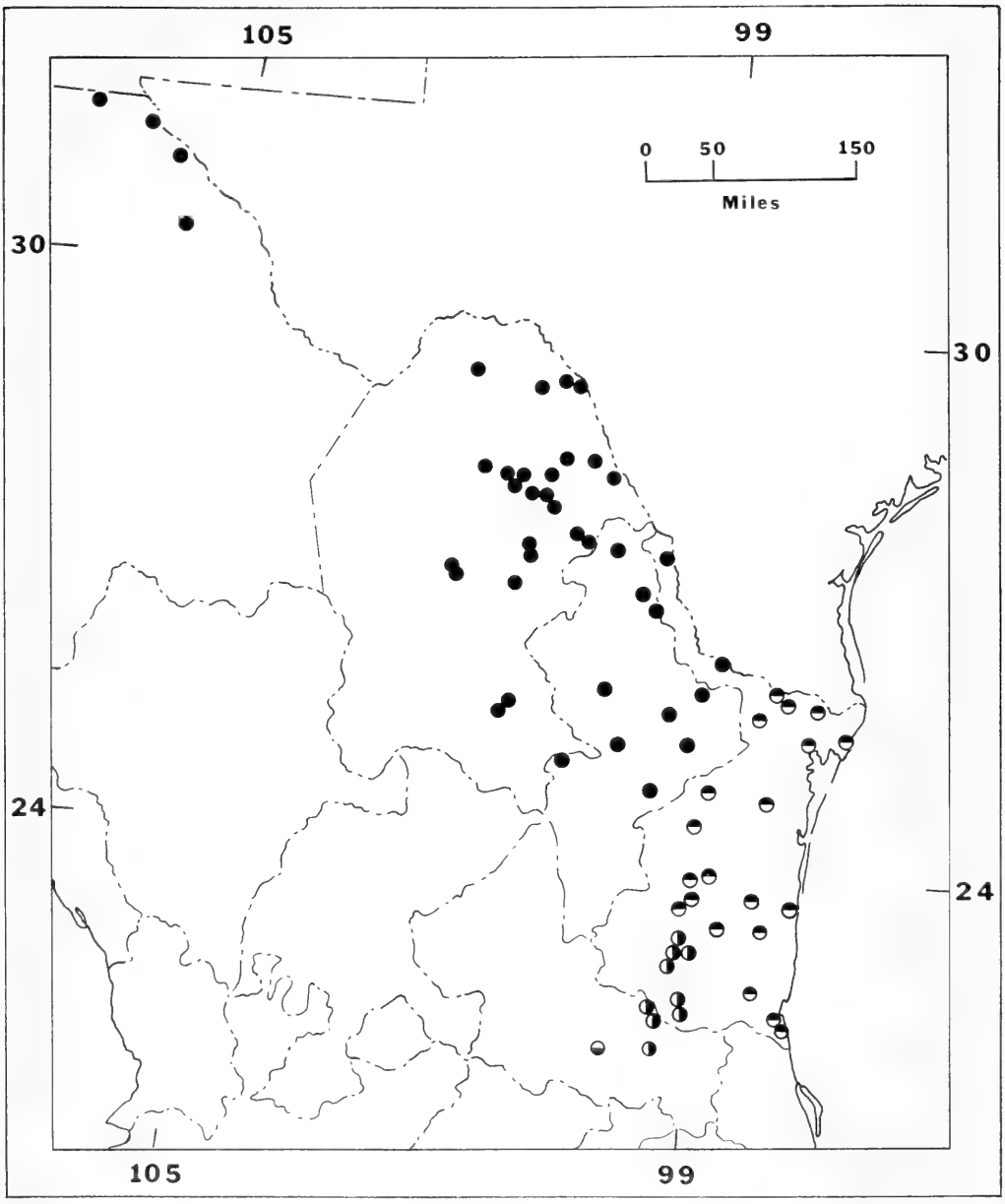

FIG. 7. Selected locality records in México for *Neotoma angustipalata* (symbols solid right), *N. micropus canescens* (solid symbols), *N. m. micropus* (symbols solid above), and *N. m. planiceps* (symbol solid below).

abuts that of *N. floridana*. Spencer (1968) reported the single locality of known sympatry, which is on the North Canadian River in extreme southwestern Major County, Oklahoma (Figs. 1 and 5). The distributional relationships of the two species along the zone of potential abutment, with special emphasis on the area of sympatry, is considered below following a review of habitat types used by *N. m. canescens*.

In comparison with *Neotoma flori-*

dana, N. micropus occurs in more xeric habitats, is associated less often with either trees or rocks, and usually occurs in areas marked by a high incidence of one or more species of cactus (genus *Opuntia*). In western Kansas (Haskell County), I have found *canescens* common in overgrazed shortgrass pastures, especially where prickly pear cactus *(O. polyacantha)* is locally abundant. In pastures that also have soapweed *(Yucca)* or sagebrush *(Artemisia)*, large dens of cactus stems and cow dung are constructed in and around these plants. However, in pastures having abundant cactus and lacking soapweed and sagebrush, dens are built over clumps of cactus, and are characterized by an extensive underground system of tunnels and usually a low superstructure of cactus and cow dung. In this situation the woodrat dwellings appear to be small dome-shaped protrusions in an otherwise gently rolling sea of buffalo grass and cactus. On August 11, 1968, approximately 30 houses of this type were examined in a pasture 10 mi S and 8 mi E Ulysses in Grant County. The dwellings were in good repair, some even contained green cactus stems and well-formed grass nests, but none was occupied at that time.

Farther east in Kansas (Barber County), this woodrat utilizes the crevices and caves formed by gypsum outcrops and often constructs dens around trees and brush in wooded draws. In such habitats the dwellings are not unlike those of *floridana;* in fact, much of the habitat in southern Barber County seems to me more like that normally occupied by *floridana* than by *micropus.*

In Baca and Prowers counties, Colorado, dens of *N. m. canescens* often are constructed in tree cactus *(Opuntia arborescens).* Finley (1958:494) reports that tree cactus also is the most important food plant of the species in Colorado, but where other species of cactus and *Yucca* are available, tree cactus is not essential.

In New Mexico the habitat of this woodrat is apparently similar to that in Colorado. Bailey (1932:171) stated that these rats "are abundant in open arid valleys where cactus abounds and are usually found associated with either cactus or some of the thorny desert shrubs. Their favorite location for a house is in the midst of a bed of large prickly-pears or thorny bushes . . . where an abundance of cactus can be found for building material." Blair (1943a, 1943b) studied *canescens* in the Tularosa basin near Alamogordo, New Mexico, where it was common in a mesquite association in which cactus apparently was either absent or scarce.

Published reports of the habits of *N. m. canescens* in Oklahoma and northern and western Texas are scarce. Glass (1949:29) found these rats nesting in canyons along with *N. mexicana* and *N. albigula* in the Black Mesa region of extreme western Oklahoma. Blair (1939b: 125) stated that "its bulky nests of sticks, liberally augmented by the remains of prickly pear plants, often are built around mesquite or other thorny shrubs." In Major County, Oklahoma, I have collected this rat along the North Canadian River where it comes into contact with *Neotoma floridana.* This unique area is discussed in more detail below. Blair (1954:252) studied *canescens* in northern Texas and adjacent Oklahoma, and reported that "these rats show a remarkable amount of variation in their ecological preference . . . at some stations they are found only on rock bluffs; at other stations they live on the level plains and away from rocks." In the Davis Mountains of southwestern Texas, Blair (1940: 32) collected woodrats of this subspecies from nests constructed in the bases of thorny shrubs in shortgrass-yucca, mesquite-cholla, and shortgrass-mesquite associations. In similar habitat in southwestern Texas, Blair and Miller (1949: 18) noted that in some cases old dens of *Dipodomys spectabilus* were utilized. In one of the more complete ecological studies of *Neotoma micropus,* Raun (1966) reported the species common in

a shortgrass-cactus-mesquite association in San Patricio County, Texas. Blair (1952:224) characterized *micropus* as one of the commonest and widely distributed mammals in the southern part of Texas.

In Coahuila, *N. m. canescens* has been reported (Baker, 1956:285) to avoid rocky areas and densely vegetated arroyos. Houses are constructed most commonly in prickly pear cactus. At one locality (vicinity of Nava) rats lived in oak thickets, and at another (La Rosa) near houses constructed in short vegetation on desert flats.

In the summer of 1969, *N. m. canescens* first was collected from north of the Arkansas River in Colorado. This locality, near Hasty in Bent County, is only about 10 miles from the nearest locality record, (Fort Lyon) for *N. floridana*. (The single specimen from Fort Lyon was collected about 80 years ago and the species probably does not occur at that locality today.) Southeastern Colorado, especially in the area of the Arkansas River, is undoubtedly one of the critical areas in which members of the two species are likely to come into contact. If they are in contact at this time or should come together at some future time, study of the two together would be most interesting because sympatry of *N. f. campestris* and *N. m. canescens* is not known now.

Neotoma micropus canescens is known from four localities north of the Arkansas River in western Kansas (Fig. 4), but *floridana* is known from no nearer than 20 miles to any of these record stations. I have searched the intervening areas intensively; most are presently either cultivated or shortgrass patsureland devoid of habitat likely to support either species. Farther east in Kansas, the hiatus between the ranges of the two species widens appreciably and in the south-central portion of that state is roughly 80 miles in width. In the upland areas of much of the hiatus, land utilization is primarily for cultivation of grain and the fields are not habitable for woodrats. Intervening lowland areas, however, are often at least sparsely wooded, planted hedgerows are common but discontinuous, and several small tributaries of the Arkansas River extend riparian communities into the zone. The watershed of the Arkansas River is heavily wooded along most of its course. In September of 1967, I searched for several days, walking long sections of the Arkansas River and many likely-looking hedgerows, but neither woodrats nor any evience of their presence was seen. I am not convinced that this area is devoid of woodrats, but, if present, they are uncommon; thus, the chance of the two species occurring together in south-central Kansas seems negligible.

In northern Oklahoma, the haitus between the ranges of the two species narrows rapidly and specimens of both species are known from localities separated by less than three miles along the Cimarron River just west of Orienta. South and west of Orienta on the north side of the North Canadian River on either side of U.S. Highway 281, *micropus* and *floridana* occur together. This unique area of sympatry was reported by Spencer (1968) and subsequently was visited by me in June, 1968, and January, 1969. Specimens from this area in the collection at Kansas State Teachers College (collected by Spencer) are labeled 1.5 mi N Seiling, in Major Co., Oklahoma, whereas those collected by me (all KU) are labeled 3 mi S Chester, Major Co., Oklahoma.

West of highway 281, woodrats occur in two distinct areas. Immediately adjacent to the river, vegetation is dense and shrubby with occasional trees and fallen trees in an area varying in width from 30 to 80 feet. Superficially this appears to be habitat typical of *floridana*. A cultivated field approximately an eighth to a quarter of a mile in width separates the river-edge habitat from an area roughly an eighth of a mile wide where yucca, cactus, sparse grass, and scattered large trees grow on semi-stabilized sand dunes. This area is super-

ficially like that often inhabited by *micropus*. East of the highway, the river edge (50 to 100 feet wide) was densely wooded in 1968 with a dense layer of leaf-litter and a canopy that permitted little ground vegetation. Woodrats were not found in this habitat. Bordering the dense trees to the south was a pasture of relatively stable, vegetated sand dunes. Small stands of large trees were scattered throughout the pasture, primarily at the bases of the dunes. Vegetation on the sides and tops of the dunes consisted of grass and cactus. The area extended approximately three-eighths of a mile north and half a mile east. Farther to the east, the density and sizes of trees increased, density of cactus decreased, and the area became more typical of the habitat of *floridana*. In 1969, the dense woods bordering the river east of the highway were uprooted and piled in a huge windrow bordering the sand dunes on the south. At that time the windrow already harbored several woodrat dens.

Of eighteen woodrats collected at this locality in 1965 and 1966 by Spencer (1968), six were identified as *N. floridana*, three as *N. micropus*, and nine as probable hybrids or intergrades. I have examined 16 of these specimens and identified seven as *floridana*, three as *micropus*, and six as being of mixed parentage. Using my identifications, six *floridana*, one *micropus*, and four "hybrids" were collected east of the highway and one *floridana*, two *micropus*, and two "hybrids" were obtained west of the highway. Four of seven animals trapped west of the highway in 1968 were identified as *micropus* and three were considered to be of mixed parentage; of 16 specimens taken at that time from the east side, six were identified as *micropus*, three as *floridana*, and seven as "hybrids." No traps were set west of the highway in 1969, but traps set within half a mile east of the highway yielded four *micropus* and eight "hybrids." No woodrats identified as *N. floridana* were taken from the place defined by Spencer (1968) as the area of sympatry. However, another series of traps set in an area 100 to 200 yards farther east caught one *floridana*, one *micropus*, and four "hybrids." Although these findings are inconclusive, it appears that the hybrid zone may have shifted eastward at least a quarter of a mile between 1965 and 1969, although remaining about three fourths of a mile in length. The destruction of trees and formation of the windrow may have significantly altered the ecological balance of the two species in the area of sympatry; if so, the alteration likely will favor *N. floridana*. A single specimen trapped one mile east of the highway in 1968 was clearly referable to *floridana;* it showed no characteristics of *micropus* or of hybrids.

Four specimens from Major and Woodward counties are worthy of special comment with respect to the distributional relationship of the two species. The first (OSU 3891), is a skin and skull that is referable to *floridana* on the bases of pelage (color) and cranial characters. This specimen bears the following information on the data label: "15 miles south of Waynoka, Okla., southside of Cimmarron [*sic*] River, Major Co." Fifteen miles south of Waynoka is no closer than nine miles to the Cimarron River and all other specimens examined by me from within 15 miles of Waynoka, in any direction, are *N. micropus*. Because these two species hybridize at the one known locality of sympatry, and because the locality in question here clearly is in error as stated above, I have not plotted this specimen on figure 5; I suspect it is from some locality east of Waynoka. Another specimen, OSU 4063, also is not plotted because of probable error in locality data; a skin alone, it is from "Canton Res. Blaine Co., Okla." Canton Reservoir is approximately 15 miles east along the North Canadian River from the locality of sympatry and hybridization. This rat is gray in color like *micropus*, but slightly atypical in being buffy on the shoulders and sides. However, the color variation is so slight that if this specimen was not otherwise

in question, it readily would be identified as *micropus*. I have examined several specimens from near the Canton Reservoir and all seem to be typical representatives of *floridana*. Three explanations seem possible: (1) both species occur at this locality, but *floridana* is commoner than *micropus;* (2) this is a hybrid population most like *floridana*, but occasional genetic combinations result in individuals colored as in *micropus;* (3) the locality data are incorrect and the specimen is from some more western locality. I regard the last alternative as the most plausible and the first as the least plausible. Both specimens apparently were collected by beginning students (field catalog numbers of both are below 10). OSU 3891 bears a collection date of 26 October 1958 and OSU 4063 is dated 28 October 1958. Although not prepared by the same student, it is possible that the labels were somehow switched in preparation. The other two noteworthy specimens are SM 4980 and 4981, preserved only as skins. Both specimens clearly were prepared some years ago (date of collection not on specimen labels) and are typical dark brown representatives of *floridana*. The specimen labels read "Woodward Co., Oklahoma." The southeastern corner of Woodward County is two miles west of the area of sympatry and all other specimens examined from that county are *micropus*. If the zone of contact is shifting gradually eastward and has been doing so for many years, it is possible that *floridana* may have occurred in Woodward County in the not too distant past. It also is possible that these specimens were not from the North Canadian River, but are from some locality elsewhere in Woodward County that once supported or still supports a population of *N. floridana*.

Farther south in Oklahoma, specimens of the two species are known from localities at a minimum of 20 miles from each other. The Red River, 5.5 mi S Grandfield, Tillman, Co., Oklahoma, is the locality of capture for SM 3602, a *N. m. canescens*. This locality is nearly straight south of Chattagnooga, Comanche County, where *N. f. attwateri* has been taken. It is west along the Red River from another *floridana* locality, 5 mi SE Taylor, Cotton County. South of Taylor, in adjacent Clay and Wichita counties, Texas, *micropus* is known from several localities.

Dalquest (1968:19) stated that "the ranges of *N. floridana* and *N. micropus* meet in Clay and Montague counties [Texas] but the two species do not interbreed." In actuality, *floridana* is not known from Clay County and *micropus* is known only from the extreme western edge of Montague County. *Neotoma micropus canescens* has been collected 2 mi N Stoneburg and *N. f. attwateri* is known from a locality 4 mi E Stoneburg, a distance of 4.47 miles. Continued field work in northern Texas and along the Red River likely will result in the location of a zone of contact between the two species, but none presently is known in northern Texas.

A specimen of *attwateri* (MWU 5256) obtained 7 mi SE Jacksboro, Jack County, is from west of known *micropus* localities both to the north and to the south, but *N. m. canescens* has not been taken at any nearby localities. Another area in Texas that would be worthy of additional field work is along the Brazos River in Parker and Hood counties. *Neotoma micropus canescens* is known from the Brazos River just west of Parker County in Palo Pinto County. A series of 13 *N. f. attwateri* from 8.9 mi S Aledo, Parker County, is suspiciously grayish-brown in color, but cranially members of the series are more or less typical of *floridana*. Possibly this population contains some introgressed genetic material derived from *micropus*, but more likely the color is the result of adaptation to the local environment on the western edge of the range of the species.

There are few records of museum specimens of woodrats from the central portion of Texas. Strecker (1929:220) reported *N. f. attwateri* from near Waco. West of Waco, the nearest locality of

record for *N. m. canescens* is approximately 175 miles distant in Concho County. On a north-south axis there is an apparent hiatus of some 200 miles in the distribution of *micropus* along the eastern edge of the range of the species in central Texas. The Colorado River and many smaller waterways traverse this area. Insofar as I am aware, there are no physiographic factors that would be expected to prevent woodrats from inhabiting this sizable portion of central Texas, which is surrounded by areas known to support *floridana* on the east and *micropus* on the north, west, and south.

Museum specimens indicate that the two species are in close proximity in southeastern Texas adjacent to the Gulf Coast. However, no localities of sympatry are known; the nearest localities are in Victoria County *(N. f. attwateri)* and Goliad County *(N. m. canescens).*

Neotoma micropus micropus Baird

Neotoma micropus Baird, 1855:333 [Lectotype —USNM 1676/554 from Charco Escondido, Tamaulipas].

Neotoma micropus littoralis Goldman, 1905:31 [Holotype—USNM 92952 from Altamira, Tamaulipas].

Remarks.—When Baird named *Neotoma micropus* he had specimens from both Charco Escondido, Tamaulipas, and Santa Rosalía (=Ciudad Camargo), Chihuahua. Unfortunately no holotype was designated by Baird. Merriam (1894b: 244) pointed out that the specimen from Santa Rosalía is "somewhat aberrant" and that because "the original description is based wholly on the Charco Escondido specimen . . . [it] must be taken as the type of this species." The specimen from Santa Rosalía, not seen by me, is assignable on geographic grounds to *Neotoma albigula* (see Anderson, 1969), but Merriam's designation of the Charco Escondido specimen as a lectotype firmly reserved the name for the woodrats to which it is applied.

The decision to consider the name *N. m. littoralis* as a junior synonym of *N. m. micropus* was not an easy one. However, when analyzed by both univariate and multivariate statistics, the samples of woodrats from northern and southern Tamaulipas are consistently more alike than either is to any other sample of the species. From north to south in Tamaulipas, these rats tend to become less grayish and more brownish. One extreme in this trend is reached in southern Tamaulipas to the south of the Sierra de Tamaulipas; it is the woodrats at this end of the range that formerly were recognized as *littoralis.* Alvarez (1963) studied *micropus* in Tamaulipas and chose to recognize two subspecies within the state. He (p. 453) concluded that *micropus* and *littoralis* intergraded in the vicinity of Soto la Marina, and assigned specimens from that locality to *N. m. micropus* and those from localities farther south in Tamaulipas to *N. m. littoralis.*

Woodrats throughout the coastal plain of Tamaulipas have relatively longer tails than specimens of *micropus* from other localities and tend to be somewhat brownish in coloration (rather than grayish), especially on the hind legs where the dorsal coloration meets the "white" of the feet. Although specimens of *micropus* from southern Texas are appreciably larger than those from Tamaulipas and are assignable to *N. m. canescens,* an occasional specimen from the general area of Brownsville resembles *N. m. micropus.*

Woodrats from just south of the Rio Grande near Nuevo Laredo, Tamaulipas, are somewhat intermediate between *micropus* and *canescens* but have been assigned to the latter. Conversely, specimens from Matamoros, Tamaulipas, have some characteristics of woodrats from farther north and west, but I have included these with *N. m. micropus.*

Specimens from the type locality of *N. m. micropus,* Charco Escondido, probably are intergrades between the small, brownish, long-tailed coastal woodrats and the equally small, but grayish short-tailed woodrats in Nuevo León and Coahuila. It is always somewhat incon-

venient when specimens from a type locality appear to be intergrades. To consider specimens from Charco Escondido to be of the same subspecies as those from Nuevo León and Coahuila would result in all the woodrats herein referred to as *N. m. canescens* being arranged as *N. m. micropus,* and those from coastal Tamaulipas being regarded as *N. m. littoralis.* Although specimens from Charco Escondido and adjacent localities in northwestern Tamaulipas could be placed about equally well with either the coastal population or with the inland and northern populations, I concluded that they best represent those nearer the coast. Specimens from Tamaulipas north to approximately Reynosa and south to the vicinities of Ciudad Victoria (on the southwest) and Altamira (on the coast) are here assigned to the subspecies *N. m. micropus,* with the type locality being Charco Escondido, Tamaulipas; the name *N. m. littoralis* thus becomes a subjective junior synonym of *N. m. micropus.*

Records of occurrence.—Specimens examined (66).—TAMAULIPAS: 3 mi SE Reynosa, 1 (KU); 3 mi S Matamoros, 2 (KU); Charco Escondido, 2 (1 UNAM, 1 USNM); 33 mi S Washington Beach, 1 (KU); San Fernando, 180 ft, 3 (KU); *7 km S, 2 km W San Fernando,* 2 (KU); 12 mi NW San Carlos, 1300 ft, 4 (KU); 9.5 mi SW Padilla, 800 ft, 3 (KU); 3 mi NE Guemes, 1 (KU); *3 mi N Soto la Marina,* 3 (KU); Soto la Marina, 500 ft, 13 (12 KU, 1 LSU); *4 mi N La Pesca,* 3 (KU); La Pesca, 2 (KU); *1 mi E La Pesca,* 1 (KU); 7 mi NE Ciudad Victoria, 1 (KU); Ciudad Victoria, 6 (KU); Sierra de Tamaulipas, 2 mi S, 10 mi W Piedra, 1200 ft, 6 (KU); Manuel, 1 (AMNH); 6 mi W Altamira, 8 (KU); Altamira, 100 ft, 5 (USNM).

Additional records: TAMAULIPAS (Goldman, 1910:28, unless otherwise noted): *Matamoros;* Bagdad; 40 mi S Matamoros (Hooper, 1953:9); Sierra San Carlos [=El Malato, Tamaulipeca] (Dice, 1937:254); 16 km N Ciudad Victoria (Hsu and Benirschke, 1968); Forlón.

Distribution and habitat.—The distribution of *N. m. micropus* is essentially the coastal plain of Tamaulipas, extending north to the Río Grande River and south to Altamira, Tamaulipas (Fig. 7). Possibly the subspecies occurs in northern coastal Veracruz, but specimens from that state are not presently available (see Hall and Dalquest. 1963). Distributional relationships of *N. m. micropus* and *N. m. canescens* in western Tamaulipas, eastern Nuevo León, and across the lower Rio Grande are discussed in remarks above.

With respect to ecological habits, *N. m. micropus* probably differs little from *N. m. canescens.* According to Alvarez (1963:453), the subspecies occurs throughout the Tamaulipas Biotic Province and is most common in brushy areas. Specimens have been obtained from the beach near La Pesca and in rocky areas on the Sierra de Tamaulipas.

Neotoma micropus planiceps Goldman

Neotoma micropus planiceps Goldman, 1905:32 [Holotype—USNM 82105 from Río Verde, San Luis Potosí].

Remarks.—Dalquest (1953:158) reported that no specimens of this woodrat were collected during his investigation of the mammals of San Luis Potosí, but did not indicate if specimens were sought near Río Verde. He suggested *(loc. cit.)* that the holotype of *N. m. planiceps* might be "an aberrant specimen, not fully adult, of *Neotoma albigula leucodon.*" I have examined the holotype and concur that it is not fully adult but concluded unequivocally that it is not a *Neotoma albigula.* I think it possible that *Neotoma angustipalata,* discussed in the following account, may be the same taxon as *N. m. planiceps;* however, specimens are not presently available to resolve this problem.

Record of occurrence.—Specimen examined (1).—SAN LUIS POTOSÍ: Río Verde, 1 (USNM).

Distribution and habitat.—This subspecies is known only from the type locality, which is shown in figure 7. Goldman (1905:32) did not contribute ecological comments in the original description of *N. m. planiceps,* but presumably it is an inhabitant of the plains immediately west of the Sierra Madre Oriental.

Neotoma angustipalata

Neotoma angustipalata is one of the least well-known members of the genus. The species was described in 1951, long after most species of *Neotoma* were at least moderately well studied. The distributional relationship of *N. angustipalata* and *N. micropus* might appear to be that of two subspecies; Hooper (1953) and Alvarez (1963) both suggested that *angustipalata* is probably no more than a subspecies of *micropus*. However, results of analyses presented beyond indicate that *angustipalata* is best regarded as a distinct species, albeit in the same species-group as *floridana* and *micropus*.

Neotoma angustiplata Baker

Neotoma angustipalata Baker, 1951:217 [Holotype—KU 36976 from 70 km (by highway) S Ciudad Victoria and 6 km W of the (Pan-American) highway (at El Carrizo), Tamaulipas].

Remarks.—As pointed out previously, the systematic affinities of this woodrat are poorly known. They have been considered to be with *Neotoma mexicana* (Baker, 1951:217), *N. albigula* (Hall, 1955:329), and *N. micropus* (Hooper, 1953:10; Alvarez, 1963:453). I suggested in the previous account that *N. angustipalata* may be identical to the rat that bears the name *N. micropus planiceps*. Had I synonymized the two, the name *angustipalata* would have been placed as a junior synonym of *planiceps*, and the latter would have been elevated to specific status.

I agree with Hooper and Alvarez that *N. angustipalata* is much like *N. micropus*, but have found that it shares a nearly equal number of characters with *N. floridana* in addition to having some characters unique unto itself. These characteristics are treated in detail in the discussion of quantitative and qualitative morphological comparisons beyond.

The three specimens from San Luis Potosí to which Dalquest (1951:363) gave the name *Neotoma ferruginea griseoventer* (placed in the species *mexicana* by Hall, 1955:330) were examined to determine if this woodrat and *N. angustipalata* also might represent the same taxon. The type locality of *N. mexicana griseoventer* is Xilitla, San Luis Potosí; two of the specimens (LSU 3193, 3194) are from the type locality and one (LSU 3191) is from El Salto, San Luis Potosí. The two specimens from Xilitla appear to be referable to *N. mexicana*, but LSU 3191 is indistinguishable from *N. angustipalata* and is best assigned to that species. The similarities between *N. angustipalata* and *N. m. griseoventer* are many and the two may yet prove to be synonymous. However, in all specimens of *N. angustipalata* (including LSU 3191), the vomer is solid beyond the leading edge of the palate, whereas all *N. mexicana* examined by me have a deep notch in the vomer anterior and dorsal to the palate; the vomers of the two specimens from Xilitla are distinctly notched. Specimens of both species have a deep anteroreentrant angle on M1, the character long used to distinguish *N. mexicana* from other species of *Neotoma*, but several authors have commented on the variability in depth of this angle both in *N. mexicana* and *N. micropus* (see especially Hooper, 1953:10).

Records of occurrence.—Specimens examined (12).—TAMAULIPAS: 70 km [by highway] S Ciudad Victoria, 6 km W [Pan-American] highway [at El Carrizo], 2 (KU); 10 km N, 8 km W El Encino, 400 ft, 1 (KU); 12 km S Ciudad Mante, 1 (UNAM); 2 km S Quintero, 250 m, 2 (UNAM); *4 km SSE Quintero*, 2 (UNAM). SAN LUIS POTOSI: El Salto, 1 (LSU); 5 mi W El Naranjo, 1 (TT); 30 km W Valles, edge of plateau, 1 (MWU).

Additional records.—TAMAULIPAS: Rancho del Cielo, 1050 m [6 km NW Gómez Farías] (Hooper, 1953:9; Goodwin, 1954:14; Koopman and Martin, 1959:7); *Infernillo (= Inferno), 1320 m* [7 km W Gómez Farías] (Koopman and Martin, 1959:6); Paraiso, 420 m [13 km SW Gómez Farías] *(ibid.);* El Pachón (Hooper, *loc. cit.;* Goodwin, *loc. cit.*).

Distribution and habitat.—Booth (1957:15) first reported *Neotoma angustiplata* from San Luis Potosí; reassignment of a specimen previously assigned to the species *N. mexicana* (see remarks) and assignment of TT 9769

and MWU 3055 to this species further elucidate the known geographic range of *angustiplata* in the state.

All locality records for *N. angustiplata* are either in or near the eastern slopes of the Sierra Madre Oriental (Fig. 7). Koopman and Miller (1959:2-3) described the localities from whence their material (owl pellets) probably originated as Tropical Evergreen Forest and Cloud Forest. Goodwin (1954:2) described Rancho del Cielo as being "on the first ridge of the Sierra Madre Oriental at 1150 meters. Humid, oak and sweet gum, cloud forest (humid upper tropical life zone) surrounding the ranch has been thoroughly lumbered since 1952." The specimens on which the name originally was based were trapped "in rocks and crevices at the base of a small hill in thick vegetation growing in deep humus" (Baker, 1951:218). All specimens reported by Hooper (1953:9) were collected in limestone caves.

COMPARATIVE MORPHOLOGICAL ANALYSES

In view of the ubiquity of woodrats in the United States and México, it is interesting that relatively little attention has been devoted to generic variation in *Neotoma* as compared with that given other cricetine genera such as *Peromyscus* (King, 1968). Hooper (1938 and 1940) studied geographic variation in *N. fuscipes* and *N. cinerea*. Hoffmeister and de la Torre (1960) assessed variation in *N. stephensi*, comparing it to *N. lepida*. The systematics of *N. goldmani* were considered by Rainey and Baker (1955). Size and physiological attributes of several species of *Neotoma* (not including *N. floridana* or *N. micropus*) were correlated with selected environmental factors by Brown and Lee (1969).

Geographic variation in six eastern subspecies of *Neotoma floridana* was studied by Schwartz and Odum (1957), but it has not been assessed in western races of the species or in *N. micropus*. Cockrum (1952:188) shifted the subspecies boundary between *N. m. micropus* (herein restricted to coastal Tamaulipas) and *N. m. canescens* eastward in Kansas from that proposed by Goldman (1910:27), but Cockrum did not study patterns of variation in *micropus* outside of Kansas. Baker (1956: 286) regarded all specimens of the species from Coahuila as *N. m. micropus*, whereas Goldman *(loc. cit.)* considered those from western localities in the state as *N. m. canescens*.

Although the above studies either lacked statistical treatment of data or were limited to univariate analyses of morphological characters, Anderson (1969) employed multivariate statistics in comparisons of *Neotoma micropus* with *N. albigula* from Chihuahua and Coahuila. Multivariate statistics have been used widely in studies of members of the genus *Canis* (Jolicoeur, 1959; Lawrence Bossert, 1967, 1969) and recently have been employed in studies of geographic variation in bats (Smith, 1972), shrews (Choate, 1970), and spiny mice (Genoways, 1971). Geographic variation in western subspecies of *N. floridana* and all subspecies of *N. micropus* is considered here by means of a combination of univariate and multivariate analyses.

MATERIALS AND METHODS

Age determination.—Age of specimens examined was determined by use of a modification of the scheme devised by Hoffmeister and de la Torre (1960: 479) for *Neotoma stephensi*. They recognized four age-groups based on degree of eruption of upper molars and subsequent wear on these teeth. The oldest and youngest categories in my arrangement correspond in a general way to those two groups as defined by Hoffmeister and de la Torre. However, preliminary calculations indicated that variance of mensural characters of rats in the intermediate groups exceeded that expected. Age groups then were reconsidered and eight age classes were rec-

ognized as follow: Group I.—immature rats in which M3 is not occlusal and often not erupted. Group II.—immature rats in which M3 is occlusal, but with the posterior loph of the tooth still isolated. Group III.—rats with the dentine of the posterior loph on M3 continuous with that of the anterior loph and with the labial reentrant angles of M2 and M3 continuing out of view into the alveolus; the proximal termination of the labial reentrant angles of M1 often is visible. Group IV.—rats characterized by visible, proximal terminations of reentrant angles on all upper molars; the reentrant angles of M1 are more than three-fourths as long as the exposed portion of that tooth. Group V.—young adults in which the reentrant angles of M1 are shorter than defined for group IV, but less than half as long as the height of M1. Group VI. —adults with the reentrant angles of M1 between a third and a half as long as the height of the tooth. Group VII.— rats with visible reentrant angles on M1 that are less than a third as long as the height of the tooth. Group VIII.—old adults with no visible reentrant angles on M1 but often with short reentrant angles on M2 and M3. For reasons discussed beyond (see variation with age), only specimens of age groups VI, VII, and VIII were included in studies of geographic variation when such specimens were available, and males and females were treated separately (see secondary sexual variation). In two instances it was necessary to include specimens of age group V (the holotypes of *N. m. planiceps* and *N. m. leucophea* both are males of this age and older individuals were not available).

Molars of woodrats that had been reared or maintained in the laboratory were less worn than those of woodrats that had not been in captivity. As a result, aging criteria described above were not applicable in separating laboratory animals into age groups comparable to those of non-laboratory rats. Laboratory specimens known to be more than two years of age frequently were placed in groups IV and V. Results of growth and development studies, which will be published elsewhere, indicated that laboratory woodrats essentially had ceased growth by 30 weeks of age; this age then was used as the critical age and only laboratory woodrats more than 30 weeks old were used in comparisons or treated statistically. As discussed beyond, it was found that laboratory woodrats were larger in some measurements than their non-laboratory counterparts from the same localities. Thus, woodrats that had been maintained in the laboratory in excess of one month were not included in studies of geographic variation employing univariate analyses or in multivariate analyses using CLSNT; a few were included in MULDIS when other specimens from critical areas were not available.

Pelage variation.—A Photovolt Photoelectric Reflection meter (Model 610), which yields values that are percentages of reflection of pure white, was employed to quantify color variation of woodrats. Readings made for each of three reflections (red, green, and blue) were taken from the lumbar region of museum specimens of age groups VI-VIII characterized by unworn or relatively unworn pelage. Analyses of adult molts and pelages were made on museum skins. The number and sequence of maturational molts were studied on live woodrats in the laboratory; these data will be included elsewhere in a discussion of growth and development.

Qualitative cranial characters.—Three cranial characters (Fig. 10) that have been used as "taxonomic characters" (Finley, 1958:248) were found to be more variable than previously recorded. The anterior palatal spine may be pointed and nonbifurcate or distally bifurcate. The presence and size of the bifurcation was scored from one to five, with "one" denoting absence of the fork. The posterior margin of the hard palate varies from having a relatively well-defined medial indentation to having a well-developed projecting medial con-

vexity. Variation in this character was scored one to eight, with one being assigned to specimens with the deepest indentation and eight to those with the largest convexity. Size of sphenopalatine vacuities was found to vary from nearly closed in a few individuals to a large opening extending anterior beyond the posterior edge of the hard palate in others; variation in this character was scored one to six, from smallest to largest. None of these characters lends itself to precise measurements without more sophisticated equipment than usually is available. To insure consistency in scoring, exemplary skulls were selected and used for comparison in scoring other specimens.

Bacular variation.—Bacula of selected adult male woodrats in the Museum of Natural History of The University of Kansas were prepared and stained according to the method described by Lidicker (1960:496), and subsequently removed from phalli. Measurements of bacula were taken to the nearest tenth of a millimeter with the aid of a Wild Heerbrugg Stereomicroscope, graph paper, and dial calipers.

External and cranial size variation.—External measurements (total length, length of the tail, length of the hind foot, and length of the ear from the notch) were recorded from data on specimen labels. These data were omitted if obviously erroneous as recorded. Ten cranial measurements were taken to the nearest tenth of a millimeter. Seven of the measurements were taken as illustrated and described by Hooper (1952: 9-11); these include greatest length of skull, zygomatic breadth, least interorbital constriction (interorbital breadth), length of rostrum, breadth of rostrum, alveolar length of maxillary toothrow (length of molar row), and length of palatal bridge (length of palate). The remaining three measurements were taken as follow: condylobasilar length—midline length of the skull from anteriormost extensions of the premaxillae to the posterior surface of the condyles; breadth at mastoids—the distance, perpendicular to the longitudinal axis of the skull, from the most lateral extension on one mastoid to the same point of the other; and length of nasals—the distance from the anterior edge of the longest nasal to the most posterior extension of either nasal.

Selection of samples.—Because there were so few adults of each sex for statistical treatment of specimens from individual localities it was necessary to include those from adjacent localities in pooled samples. Decisions for grouping specific localities and establishing size of geographic areas to include in each sample were based on several criteria. In no case were specimens of different nominal taxa, as recognized at the onset of the study, included together in a single sample. In areas of suspected intergradation or possible contact between species and subspecies, an attempt was made to keep size of geographic areas as small as possible. Whenever practical, localities were grouped so that at least three and preferably no fewer than five adults of each sex were available. Whenever the above criteria could be met and there was no cause to suspect biologically-based reasons for doing otherwise, locality groupings often were made with consideration to political boundaries merely to facilitate menial tasks such as sorting of original data.

The thirty-two aggregate localities (samples) and their identifying symbols are shown in figure 8 and briefly outlined below. When all available specimens of a species or subspecies are included in a single sample, the geographic area is not described (exact localities were listed previously under specimens examined). Grouped localities of *Neotoma floridana* were coded with numeric symbols and those of *N. micropus* and the single sample of *N. angustipalata* were given alpha symbols. Names given below in parentheses are those by which the woodrats previously were recognized.

Sample 1.—*Neotoma floridana baileyi.*

Sample 2.—*N. f. campestris* from all

localities in Colorado and Nebraska.

Sample 3.—*N. f. campestris* from all localities in Kansas west of a north-south line extended from the boundary between Trego and Ellis counties.

Sample 4.—*N. f. campestris* from all localities in Kansas east of the line described for sample 3 and west of a parallel line extended from the boundary between Russell and Ellsworth counties.

Sample 5.—*N. f. attwateri (N. f. osagensis)* from all localities in Kansas east of the line described for sample 4 and west of a parallel line extended from the boundary between Saline and Dickinson counties.

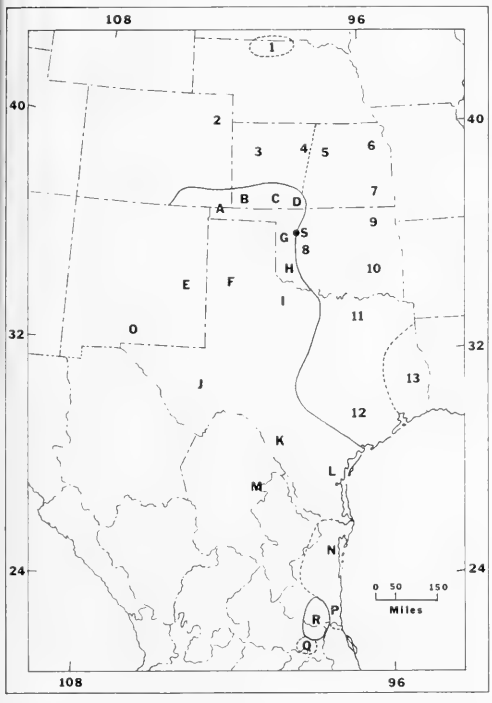

FIG. 8. Sketch map of region in which woodrats were studied showing general geographic areas of grouped localities, indicated by identifying code symbols. All samples of *Neotoma floridana* (1-13) are represented by numeric symbols and those of *N. micropus* (A-P) and *N. angustipalata* (R) are represented by alpha symbols. Solid lines separate the distributions of species and dashed lines the distributions of subspecies. The solid dot labeled S in Oklahoma marks the single known locality of sympatry between two of the species. See text for precise definitions of the area included in each grouped locality.

Sample 6.—*N. f. attwateri (N. f. osagensis)* from all localities in Kansas east of the line described for sample 5 and north of a perpendicular line extended from the boundary between Lyon and Greenwood counties.

Sample 7.—*N. f. attwateri (N. f. osagensis)* from all localities in Kansas south of the line described for sample 6.

Sample 8.—*N. f. attwateri (N. f. osagensis)* from all localities in Oklahoma west of a line extended from the boundary between Major and Garfield counties.

Sample 9.—*N. f. attwateri (N. f. osagensis)* from all localities in Oklahoma east of the line described for sample 8 and north of a perpendicular line extended from the boundary between Lincoln and Pottawatomie counties.

Sample 10.—*N. f. attwateri (N. f. osagensis)* from all localities in Oklahoma east of the line described for sample 8 and south of the line described for sample 9.

Sample 11.—*N. f. attwateri (N. f. osagensis)* from all localities in Texas north of a line extended from the boundary between Navarro and Limestone counties and west of a perpendicular line extended from the boundary between Harrison and Gregg counties.

Sample 12.—*N. f. attwateri* from all localities in Texas south of the east-west line described for sample 11 and southwest of a line extended from the southwestern border of Walker County where it abuts Montgomery County.

Sample 13.—*N. f. rubida* from all localities in Texas.

Sample A.—*N. micropus canescens* from all localities in Colorado, and in Cimarron County, Oklahoma.

Sample B.—*N. m. canescens* from all localities in Kansas northwest of U.S. highway 54, and in Beaver and Texas counties, Oklahoma.

Sample C.—*N. m. canescens* from all localities in Meade and Clark counties,

Kansas, and in Harper County, Oklahoma.

Sample D.—*N. m. canescens (N. m. micropus)* from all localities in Barber, Comanche, and Kiowa counties, Kansas.

Sample E.—*N. m. canescens* from all localities in New Mexico except the White Sands National Monument.

Sample F.—*N. m. canescens* from all localities in Texas north of a line extended from the boundary between Anderson and Winkler counties and west of a perpendicular line extended from the boundary between Fisher and Curry counties.

Sample G.—*N. m. canescens (N. m. micropus)* from all localities in Oklahoma north of the South Canadian River, exclusive of localities in samples A, B, and C.

Sample H.—*N. m. canescens (N. m. micropus)* from all localities in Oklahoma south of the South Canadian River.

Sample I.—*N. m. canescens (N. m. micropus)* from all localities in Texas north of the east-west line described for sample F, and east of the north-south line described for that sample.

Sample J.—*N. m. canescens* from all localities in Chihuahua and those in Texas south of the east-west line described for sample F and west of a line extended from the boundary between Reagan and Irion counties.

Sample K.—*N. m. canescens (N. m. micropus)* from all localities in Texas east of the line described for sample J, south of the east-west line described for sample F, west of a line extended from the boundary between Medina and Bexar counties, and north of the Webb-Zapata County boundary.

Sample L.—*N. m. canescens (N. m. micropus)* from all localities in Texas south of the east-west line described for sample F and the Webb-Zapata County boundary, and east of a north-south line extended south to the southern Webb County boundary from the boundary between Medina and Bexar counties.

Sample M.—*N. m. canescens (N. m. micropus)* from all localities in Coahuila and Nuevo León and those in Tamaulipas north of an east-west line passing through Reynosa.

Sample N.—*N. m. micropus* from all localities in Tamaulipas south of the line described for sample M and north of 23° 30′ N latitude.

Sample O.—*N. m. canescens (N. m. leucophea)* from White Sands National Monument in New Mexico.

Sample P.—*N. m. micropus (N. m. littoralis)* from all localities in Tamaulipas south of 23° 30′ N latitude.

Sample Q.—*N. m. planiceps.*

Sample R.—*N. angustipalata.*

Sample S.—*Neotoma floridana, N. micropus,* and their natural hybrids from 3 mi S Chester, Major Co., Oklahoma.

Statistical analyses.—Statistical analyses were selected for their appropriateness, ease of interpretation, and availability at The University of Kansas Computation Center. Standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) were calculated, after which group-means were simultaneously tested for significant differences at the 0.95 level of confidence (0.05 level of significance) by single classification analysis of variance (univariate ANOVA). If significant variation was present among the group-means and if more than two samples were being compared, the Sums of Squares Simultaneous Testing Procedure (SS-STP) described by Gabriel (1964) was employed to determine maximal non-significant subsets. Calculations involved in the SS-STP were outlined by Sokal and Rohlf (1969:582), and use of the procedure in studies of geographic variation was considered by Gabriel and Sokal (1969). All of the above calculations were computed by Power's UNIVAR program (Power, 1970).

Univariate analyses first were conducted to compare males and females by selecting samples of woodrats considered to be adults that were from the same geographic areas (ideally, animals from a single locality would be used, but no sufficiently large samples were available).

When it was clear that significant sexual dimorphism existed, samples of the previously described age groups were compared separately within each sex. Results indicated that animals of age groups V and younger frequently were significantly smaller than those in groups VI or older. Although animals in group VI occasionally were significantly smaller than those of groups VII and VIII, these three age groups were considered together with sexes being treated separately in analysis of geographic variation. So-called Dice-grams (Dice and Leraas, 1936) have been employed frequently to illustrate a general array of variation. For reasons discussed by Sokal and Rinkel (1963), Dice-grams are not appropriate for determination of statistical significance when more than two samples are being compared; therefore, all determinations of significance or the absence thereof were based on SS-STP tests.

Because the sample of specimens from each locality usually exhibited various subset relationships with samples from other localities when different characters were considered, it was necessary to use multivariate analyses to determine relationships based on all characters examined. This was accomplished by means of two programs (CLSNT-Version 2, and MULDIS) available in the Numerical Taxonomy System at the Computation Center of The University of Kansas. CLSNT was used to compare samples of populations for geographic variation by considering the sample of specimens from each aggregate locality as an Operational Taxonomic Unit (OTU) and sample means as characters. When only a single individual was available, as for *Neotoma micropus planiceps,* the characters of that specimen were treated as means. Discriminant function analysis (MULDIS) was employed to compare individuals from various samples and to analyze for hybridization and intergradation.

Among other sets of values, CLSNT and optional subroutines as employed by me computed matrices of Pearson's product moment correlations and matrices of taxonomic distance coefficients (see Sokal, 1961, and Sokal and Sneath, 1963). Each matrix was then subjected to cluster analyses using UPGMA (unweighted pair group method using arithmetic averages), and a two-dimensional phenogram was generated from each. A coefficient of cophenetic correlation (Sokal and Sneath, 1963) was computed to express the reliability of the phenogram based on comparisons with the respective matrices. Moss (1968) discussed relationships of the two phenograms and experimentally studied general types of variation affecting each. I have considered both matrices and both phenograms in all analyses, but because coefficients of cophenetic correlation usually were higher between the distance matrix and phenogram, these have been given greatest consideration. All computations for CLSNT were conducted on standardized data, which was derived by converting the mean for each character to zero and the variance and standard deviation to one so that the value for each character was expressed in terms of standardized deviates (see Sokal and Rohlf, 1969:109).

A principal components analysis also was conducted on the among-characters correlation matrix to "condense" or "compress" the variation in the characters considered into a smaller number of "new" characters, the first few principal components. At least the first three components were extracted in all cases and the first five components frequently were considered, especially when the number of characters for each OTU was large. The percentage of the total variation accounted for by each principal component also was calculated. OTU's were projected onto the principal components, and bivariate scatter diagrams were made by plotting projections of OTU's on all combinations of components. Projection of OTU's into three-dimensional drawings was accomplished with a PROJ-3D program whereby the first three principal component scores of each OTU

were transferred to a magnetic tape from which a Benson-Lehner incremental plotter made the perspective drawings. The shortest minimally connected network between OTU's was computed from the matrix of distance coefficients and included on the three-dimensional models.

Discriminant function analysis (MULDIS) employs variance-covariance mathematics to differentially weight each character relative to the variance within and between groups of that character when two reference samples are considered. A discriminant multiplier (discriminant function) was calculated for each variable; then each discriminant multiplier was multiplied by the value of its respective variable and summed for all variables to yield a discriminant score for each OTU. The discriminant scores then were plotted on a frequency histogram to compare the individuals of two populations, with or without additional comparisons of a test sample of geographic intermediates or suspected and known (laboratory-bred) hybrids.

NON-GEOGRAPHIC VARIATION

In order to undertake a meaningful assessment of geographic variation, it is necessary to understand the non-geographic variation that exists in populations of the organisms to be compared. I have analyzed variation with respect to age, secondary sexual characteristics, individual differences, and effects of having been held in captivity. Variation in pelages resulting from age and molts was considered and was found to vary seasonally. Because seasonal timing of molt and certain characteristics of pelage in woodrats vary geographically, these aspects are considered beyond with discussion of geographic variation in color.

Variation with Age

Variation in size correlated with age differences was analyzed for samples of *Neotoma floridana campestris* (Table 1), *N. f. baileyi*, *N. f. attwateri*, and *N. micropus canescens* (Birney, 1970). Because age-groups and sexes were separated sample size frequently was small, especially for *baileyi*. As a result, some age-groups were strikingly different in size, but the differences were not always statistically significant.

Dimensions of two external characters (length of hind foot and length of ear) and those of two cranial characters (least interorbital constriction and alveolar length of the maxillary toothrow) were influenced less by age than were those of other characters. Growth and development studies of laboratory woodrats demonstrate that the hind foot and ear grow at a disproportionately faster rate than the body and tail. Also, variation in external measurements of museum specimens is high (see discussion of individual variation) because of inconsistencies in techniques used to measure these characters by various collectors.

Alveolar length of the maxillary toothrow does not increase with age after the molars have become occlusal, because individual teeth of woodrats do not increase in diameter after eruption. There is a tendency for the molar row to be slightly longer in rats of age-groups III and IV than in older animals. The alveolar tissue in cleaned skulls of older woodrats usually is separated slightly from the base of the teeth and in some senile rats the molar roots extend to the alveolus. These factors tend to result in smaller measurements, and a decrease in accuracy of the measurement. Least interorbital constriction shows a general increase in size up to age-groups III and IV. Sequence of means varied noticeably in the older age-groups, indicating that the constriction changes little with age after the early period of rapid growth.

Dimensions of other cranial characters indicated that animals in age-groups VII and VIII do not differ significantly in size. Although the mean of a sample in age-group VI frequently was less than that of older woodrats, this difference seldom was significant. Highest F_s values and the greatest number of non-significant subsets frequently were com-

TABLE 1. Variation with age in 14 external and cranial measurements of *Neotoma floridana campestris*. F_s was calculated by single classification analysis of variance. Tabular F values are at the P 0.05 level of significance; ns indicates no significant difference within a group of means. Nonsignificant subsets (as calculated by the Sums of Squares Simultaneous Testing Procedure) of significantly different groups of means are shown in the last column.

Measurement, sex, and age class	N	Mean	± 2SE	Range	CV	F_s F	SS-STP
Total length							
Females							
VIII	15	370.8	8.70	(340.0-402.0)	4.54	22.88	I
VI	16	369.6	8.88	(340.0-409.0)	4.81	2.21	I
VII	10	268.7	11.39	(344.0-395.0)	4.88		I
V	20	353.5	6.72	(325.0-377.0)	4.25		I I
IV	14	337.0	8.91	(303.0-365.0)	4.94		I I
III	13	314.2	13.15	(291.0-374.0)	7.55		I I
II	2	284.0	24.00	(272.0-296.0)	5.98		I
Males							
VIII	7	399.7	15.56	(371.0-434.0)	5.15	30.90	I
VI	11	382.8	9.84	(350.0-408.0)	4.26	2.15	I
V	17	377.6	13.19	(325.0-424.0)	7.20		I I
VII	9	373.9	10.30	(341.0-395.0)	4.13		I I I
IV	13	347.8	12.54	(307.0-383.0)	6.50		I I
III	7	332.3	21.00	(288.0-365.0)	8.38		I
I	3	264.7	33.17	(232.0-286.0)	10.85		I
II	6	264.3	17.82	(240.0-287.0)	8.26		I
Length of tail vertebrae							
Females							
VI	16	156.6	4.54	(144.0-172.0)	5.80	13.65	I
VIII	15	154.5	4.85	(136.0-175.0)	6.07	2.21	I
VII	10	154.5	7.46	(138.0-172.0)	7.63		I I
V	20	148.4	4.86	(131.0-167.0)	7.33		I I
IV	14	142.2	3.35	(133.0-152.0)	4.41		I I
III	13	130.8	5.48	(115.0-154.0)	7.56		I I
II	2	122.5	25.00	(110.0-135.0)	14.43		I
Males							
VIII	7	164.4	6.38	(151.0-175.0)	5.13	17.39	I
VI	11	161.0	8.33	(130.0-178.0)	8.58	2.15	I
V	17	155.9	6.53	(132.0-177.0)	8.64		I
VII	9	151.6	9.17	(120.0-164.0)	9.07		I I
IV	13	146.8	6.08	(129.0-168.0)	7.47		I I
III	7	132.7	9.77	(107.0-147.0)	9.73		I I
I	3	113.0	21.94	(92.0-129.0)	16.81		I
II	6	108.5	8.53	(98.0-124.0)	9.63		I
Length of hindfoot							
Females							
IV	14	39.9	1.10	(36.0-43.0)	5.15	<1.00	ns
VI	16	39.7	0.60	(38.0-42.0)	3.01	2.21	
V	20	39.4	0.69	(36.0-41.0)	3.90		
VIII	16	39.2	0.71	(36.0-41.0)	3.64		
VII	10	39.1	1.28	(36.0-42.0)	5.18		
III	13	38.8	1.13	(35.0-41.0)	5.24		
II	2	38.0	4.00	(36.0-40.0)	7.44		

TABLE 1.—Continued.

Measurement, sex, and age class	*N*	Mean	± 2SE	Range	CV	F_s *F*	SS-STP
Males							
VII	4	40.8	0.88	(39.0-43.0)	3.43	4.84	I
VIII	8	40.8	1.50	(36.0-44.0)	6.38	2.14	I
V	10	40.6	0.90	(36.0-44.0)	4.73		I
VI	5	40.4	1.24	(37.0-44.0)	5.11		I
IV	7	40.0	1.01	(35.0-42.0)	4.56		I I
III	5	38.9	1.34	(37.0-41.0)	4.56		I I
II	5	36.7	1.52	(35.0-40.0)	5.08		I
I	3	36.7	0.67	(36.0-37.0)	1.57		I
Length of ear							
Females							
VIII	8	28.0	1.07	(26.0-30.0)	5.40	1.36	ns
VI	12	27.8	1.18	(25.0-32.0)	7.32	2.31	
VII	5	27.2	1.47	(25.0-29.0)	6.04		
IV	9	27.2	1.19	(25.0-30.0)	6.57		
V	6	27.0	0.89	(25.0-28.0)	4.06		
III	9	26.4	1.11	(25.0-30.0)	6.30		
II	2	25.0	4.00	(23.0-27.0)	11.31		
Males							
VI	5	29.0	2.28	(26.0-33.0)	8.79	1.70	ns
IV	7	28.9	1.60	(26.0-32.0)	7.33	2.26	
VIII	8	28.6	2.28	(26.0-33.0)	8.79		
VII	4	28.5	0.58	(28.0-29.0)	2.03		
V	8	28.5	1.00	(26.0-30.0)	4.96		
III	5	26.0	1.41	(24.0-28.0)	6.08		
II	5	25.6	1.36	(24.0-28.0)	5.92		
I	3	25.0	1.15	(24.0-26.0)	4.00		
Greatest length of skull							
Females							
VIII	14	49.9	0.69	(48.3-52.1)	2.57	24.01	I
VI	13	49.4	0.87	(47.0-53.3)	3.18	2.23	I
VII	8	49.3	0.86	(47.5-51.8)	2.45		I I
V	19	47.3	4.19	(45.8-49.5)	1.93		I I
IV	14	46.7	0.57	(44.4-48.1)	2.28		I I
III	10	44.9	1.51	(42.5-48.3)	5.31		I I
II	2	41.8	2.90	(40.4-43.3)	4.90		I
Males							
VIII	10	51.8	1.13	(49.5-55.2)	3.44	32.64	I
VII	6	51.6	1.30	(49.0-53.4)	3.08	2.17	I
V	20	49.8	0.76	(47.3-53.7)	3.40		I
VI	9	49.7	1.52	(46.0-52.7)	4.60		I I
IV	13	46.8	0.95	(43.3-49.6)	3.66		I I
III	4	44.4	2.25	(42.3-47.4)	5.06		I
I	1	40.9	---	(40.9-40.9)	---		I I
II	5	39.2	2.19	(37.1-42.7)	6.26		I
Condylobasilar length							
Females							
VIII	15	48.4	0.75	(46.9-51.6)	2.98	36.40	I
VII	8	48.3	0.90	(46.4-50.9)	2.63	2.23	I
VI	10	47.3	0.67	(45.2-48.9)	2.25		I I
V	20	45.7	0.45	(44.0-48.2)	2.21		I I
IV	14	44.6	0.57	(42.7-46.3)	2.37		I
III	12	42.4	1.27	(39.9-45.6)	5.19		I
II	2	39.3	2.60	(38.0-40.6)	4.68		I

TABLE 1.—Continued.

Measurement, sex, and age class	*N*	Mean	± 2SE	Range	CV	F_s *F*	SS-STP				
Males											
VIII	12	50.6	1.07	(48.1-54.3)	3.66	36.44	I				
VII	7	49.6	1.63	(46.6-52.3)	4.32	2.17	I				
VI	9	48.3	1.47	(44.5-52.3)	4.57		I				
V	20	48.2	0.82	(45.3-52.8)	3.82		I				
IV	13	44.7	0.95	(41.1-46.8)	3.81			I			
III	4	42.0	2.94	(39.6-46.1)	6.99			I			
I	1	38.6	—	(38.6-38.6)	—			I	I		
II	5	36.7	2.09	(34.8-40.1)	6.38				I		
Zygomatic breadth											
Females											
VIII	14	27.4	0.52	(26.0-29.6)	3.54	34.92	I				
VII	6	26.8	0.54	(26.0-27.7)	2.46	2.23	I				
VI	14	26.3	0.41	(25.1-28.0)	2.88		I	I			
V	19	25.6	0.36	(24.5-27.1)	3.09			I	I		
IV	14	24.7	0.33	(23.6-25.9)	2.54				I	I	
III	13	23.7	0.54	(22.6-25.5)	4.15					I	I
II	2	22.5	0.60	(22.2-22.8)	1.89						I
Males											
VIII	11	28.2	0.51	(27.0-29.9)	2.99	49.56	I				
VII	7	27.3	0.72	(26.1-28.5)	3.47	2.17	I	I			
VI	8	26.7	0.54	(25.4-28.1)	2.85		I	I			
V	19	26.6	0.44	(25.3-28.7)	3.57			I			
IV	13	24.8	0.49	(23.4-26.4)	3.56				I		
III	6	24.3	1.13	(22.9-26.1)	5.69				I		
I	3	20.6	1.64	(19.0-21.7)	6.88					I	
II	5	20.5	1.30	(18.9-22.6)	7.07					I	
Least interorbital constriction											
Females											
VI	15	6.8	0.19	(6.1-7.5)	5.55	2.01	ns				
VII	9	6.7	0.17	(6.2-7.0)	3.78	2.21					
VIII	16	6.6	0.13	(6.2-7.1)	3.92						
V	20	6.6	0.12	(6.1-7.1)	4.07						
IV	14	6.6	0.12	(6.1-6.9)	3.49						
III	14	6.5	0.18	(6.0-7.3)	5.15						
II	2	6.2	0.10	(6.1-6.2)	1.15						
Males											
VII	10	7.0	0.23	(6.5-7.7)	5.19	5.97	I				
VIII	12	6.8	0.13	(6.5-7.1)	3.32	2.14	I	I			
VI	10	6.8	0.18	(6.4-7.1)	4.20		I	I	I		
V	20	6.7	0.11	(6.2-7.2)	3.60		I	I	I	I	
III	7	6.6	0.20	(6.3-6.9)	3.97		I	I	I	I	
IV	13	6.5	0.18	(6.1-7.1)	4.90			I	I	I	
II	6	6.4	0.31	(5.9-6.9)	5.87				I	I	
I	3	6.2	0.20	(6.1-6.4)	2.79					I	
Breadth at mastoids											
Females											
VIII	15	19.4	0.36	(18.3-21.0)	3.55	7.96	I				
VI	11	19.3	0.40	(18.1-20.2)	3.42	2.23	I	I			
VII	10	19.2	0.38	(18.1-20.0)	3.12		I	I	I		
V	19	18.7	0.20	(17.9-19.7)	2.32			I	I	I	
IV	13	18.7	0.20	(17.9-19.2)	1.91				I	I	
III	12	18.3	0.30	(17.7-19.5)	2.82					I	
II	2	17.9	0.60	(17.6-18.2)	2.37					I	

TABLE 1.—Continued.

Measurement, sex, and age class	*N*	Mean	± 2SE	Range	CV	F_s *F*	SS-STP				
Males											
VIII	11	20.5	0.51	(19.3-22.4)	4.15	16.91	I				
VII	10	19.6	0.33	(18.7-20.2)	2.66	2.15	I	I			
V	20	19.6	0.37	(18.3-20.8)	4.20		I	I	I		
VI	8	19.1	0.73	(17.4-20.3)	5.43			I	I		
IV	13	18.7	0.27	(17.6-19.6)	2.59			I	I		
III	5	18.6	0.36	(18.1-19.0)	2.17				I	I	
II	6	17.0	0.48	(16.3-17.7)	3.45					I	
I	1	16.9	---	(16.9-16.9)	---					I	
Length of rostrum											
Females											
VII	10	19.5	0.51	(18.2-21.0)	4.11	19.25	I				
VIII	15	19.4	0.29	(18.6-20.5)	2.92	2.21	I				
VI	16	19.0	0.44	(17.3-21.1)	4.62		I	I			
V	19	18.3	0.26	(17.5-19.8)	3.14			I			
IV	15	18.1	0.36	(16.7-19.4)	3.84			I	I		
III	12	17.2	0.61	(15.9-18.6)	6.11				I	I	
II	2	15.8	0.90	(15.3-16.2)	4.04					I	
Males											
VIII	11	20.5	0.64	(19.4-22.9)	5.19	37.51	I				
VII	8	20.4	0.44	(19.3-21.2)	3.08	2.14	I				
V	20	19.7	0.43	(18.0-21.7)	4.92		I				
VI	11	19.2	0.51	(18.0-20.9)	4.38		I	I			
IV	13	18.2	0.49	(16.4-19.6)	4.88			I			
III	6	17.5	0.95	(16.1-18.8)	6.66			I			
I	3	14.7	1.92	(12.8-15.9)	11.32				I		
II	6	14.4	0.94	(13.2-15.6)	7.99				I		
Breadth of rostrum											
Females											
VIII	16	8.5	0.17	(8.0-9.4)	4.10	8.62	I				
VII	9	8.5	0.21	(8.0-9.0)	3.64	2.21	I	I			
VI	15	8.2	0.12	(7.7-8.5)	2.84		I	I	I		
V	20	8.1	0.15	(7.3-8.5)	4.11			I	I	I	
IV	15	7.9	1.16	(7.4-8.4)	3.89				I	I	
III	13	7.8	0.23	(7.3-8.5)	5.20				I	I	
II	1	7.6	---	(7.6-7.6)	---					I	
Males											
VIII	12	8.9	0.14	(8.6-9.3)	2.64	17.51	I				
VII	9	8.6	0.24	(8.2-9.2)	4.10	2.14	I	I			
V	20	8.4	0.17	(7.8-9.4)	4.54		I	I	I		
VI	11	8.2	0.46	(6.1-8.8)	9.35			I	I		
IV	13	8.1	0.20	(7.5-9.0)	4.58			I	I	I	
III	7	7.7	0.23	(7.2-8.1)	3.90				I	I	I
II	6	7.0	0.44	(6.3-7.6)	7.79					I	I
I	3	7.0	0.46	(6.6-7.4)	5.71						I
Alveolar length of maxillary toothrow											
Females											
IV	15	9.9	0.17	(9.3-10.5)	3.31	2.32	I				
VII	10	9.8	0.17	(9.4-10.3)	2.75	2.21	I	I			
V	20	9.7	0.14	(9.1-10.3)	3.15		I	I			
VI	16	9.7	0.17	(9.3-10.5)	3.49		I	I			
III	13	9.7	0.13	(9.4-10.1)	2.41		I	I			
II	2	9.6	0.50	(9.3-9.8)	3.70		I	I			
VIII	16	9.5	0.18	(8.9-10.0)	3.82			I			

TABLE 1.—Concluded.

Measurement, sex, and age class	*N*	Mean	± 2SE	Range	CV	F_s *F*	SS-STP				
Males											
V	20	9.9	0.12	(9.2-10.4)	2.64	2.13	ns				
IV	13	9.9	0.19	(9.3-10.6)	3.43	2.14					
III	7	9.8	0.19	(9.6-10.3)	2.55						
VIII	12	9.7	0.26	(9.0-10.4)	4.68						
VII	10	9.7	0.26	(8.9-10.2)	4.22						
VI	11	9.6	0.23	(9.1-10.3)	4.05						
I	3	9.5	0.18	(9.3-9.6)	1.61						
II	6	9.4	0.28	(8.9-9.8)	3.66						
Length of palatal bridge											
Females											
VII	10	8.6	0.20	(8.0-9.1)	3.72	4.91	I				
VIII	16	8.5	0.25	(7.8-9.4)	5.96	2.21	I	I			
VI	16	8.2	0.17	(7.5-8.8)	4.13		I	I	I		
V	20	8.2	0.15	(7.4-8.7)	4.15			I	I		
IV	15	8.1	0.19	(7.3-8.6)	4.44			I	I		
III	13	8.1	0.16	(7.6-8.8)	3.67				I		
II	2	7.6	0.10	(7.6-7.7)	0.92				I		
Males											
VII	9	9.0	0.44	(7.9-9.8)	7.47	14.27	I				
VIII	12	9.0	0.21	(8.5-9.7)	4.05	2.14	I	I			
VI	11	8.5	0.25	(7.6-9.0)	4.81		I	I	I		
V	20	8.4	0.23	(7.4-9.5)	6.15			I	I	I	
III	6	8.1	0.33	(7.6-8.7)	4.96				I	I	
IV	13	7.9	0.18	(7.4-8.4)	4.07				I	I	I
I	2	7.4	0.60	(7.1-7.7)	5.73					I	I
II	6	7.1	0.41	(6.5-7.9)	7.02						I
Length of nasals											
Females											
VIII	15	19.4	0.30	(18.7-20.4)	3.03	20.54	I				
VII	10	19.3	0.36	(18.4-20.4)	2.96	2.21	I				
VI	16	18.9	0.44	(17.6-20.3)	4.70		I	I			
V	19	18.1	0.25	(17.2-19.3)	3.04			I	I		
IV	15	17.9	0.42	(16.2-19.2)	4.55				I	I	
III	12	16.8	0.61	(15.4-18.5)	6.26					I	I
II	2	16.0	2.00	(15.0-17.0)	8.84						I
Males											
VII	8	20.3	0.42	(19.1-21.0)	2.94	29.19	I				
VIII	11	20.2	0.83	(18.3-23.3)	6.77	2.14	I				
V	20	19.5	0.43	(18.3-21.5)	4.90		I	I			
VI	11	19.0	0.60	(17.7-20.5)	5.20		I	I	I		
IV	13	18.1	0.52	(16.0-19.5)	5.21			I	I		
III	6	17.0	1.12	(15.5-19.0)	8.06				I	I	
I	3	14.8	2.07	(12.8-16.2)	12.10					I	I
II	6	14.4	0.91	(13.3-15.7)	7.69						I

puted for measurements involving dimensions of the anterior portions of skulls. In studies of *Neotoma micropus*, Allen (1894a:240) noticed that relative growth of the preorbital region exceeded that of the postorbital area in postpartum development. Hall (1926:396) observed similar relative rates of growth for *Spermophilus beecheyi* and considered them a common feature of mammalian development. Therefore, it was expected that measurements such as length of rostrum and length of nasals would be most critical in terms of group-

ing animals of different ages for other analyses. Animals of age-group V usually were significantly different from animals of older groups, thus indicating that specimens of age-group V should not be included with older woodrats. Although this resulted in reduction of the sizes of available samples, comparisons of smaller, more homogeneous samples are more reliable than those involving heterogeneous samples.

Secondary Sexual Variation

Although no detailed analytical tests comparing woodrats of different sexes from the same geographic areas are available, males and females generally have been treated separately in studies of geographic variation (Hooper, 1938, 1940; Hoffmeister and de la Torre, 1960). However, Schwartz and Odum (1957) apparently treated both sexes of *N. floridana* in the same samples. Using only specimens of age groups VI, VII, and VIII, males and females were tested by single classification ANOVA to determine if secondary sexual variation was present in external and cranial dimensions of *N. f. baileyi*, *N. f. campestris*, *N. f. attwateri*, *N. m. micropus*, and *N. m. canescens* (Table 2).

In one sample, *N. f. campestris*, size variation attributable to sex was observed in most measurements. Samples of *campestris* generally included more individuals than other samples. Means for males were larger at the 0.01 level of significance ($P < 0.01$) in eight of the 14 measurements, and significantly larger ($P < 0.05$) in two of the remaining six. Only in length of ear did the mean for females exceed that for males. In *N. m. micropus*, the taxon represented by fewest individuals, no significant differences in means were detected, but means of measurements for males were larger than those for females in nine characters. This suggests that non-significant results were a function of the small samples rather than absence of real differences between sexes. Males of *baileyi* were found to be larger than females in only six measurements and the difference was significant only in one (least interorbital constriction). Size of females exceeded that of males in three characters, but the difference was significant in none. Means accurate to the nearest tenth of a millimeter were identical in five dimensions considered. Although larger samples might alter the results, it appears that *baileyi* has less secondary sexual variation than other taxa considered. Samples of *canescens* and *attwateri* were relatively large. Seven significant differences (one at the 0.01 level and six at the 0.05 level) apparently resulting from secondary sexual variation were observed for *attwateri*, whereas only four (one at the 0.01 level and three at the 0.05 level) were exhibited by *canescens*.

Significant secondary sexual variation was not demonstrated for length of tail vertebrae, length of ear, breadth of rostrum, and alveolar length of maxillary toothrow. Total length, condylobasilar length, and length of nasals varied significantly between the sexes in all of the taxa having samples of more than 10 individuals of each sex.

When all taxa and characters are considered, it is seen that sufficient secondary sexual variation exists to discourage treatment of males and females as a single sample. Therefore, the sexes were treated separately in geographic considerations of mensural data. Specimens of both sexes were treated as a single sample in only one set of analyses that included mensural data (discriminant function analysis). Because discriminant function analysis was used in comparisons of individuals and not in comparisons of sample means, the sex of each individual could be considered when interpreting results.

As discussed beyond (comparative reproduction), it was observed in the laboratory that males capable of physically dominating females in breeding cages were the more successful breeders and, conversely, females that were physically subordinate were more successful breeders than large dominant females. Thus secondary sexual variation in size

TABLE 2. Secondary sexual variation in 14 external and cranial measurements of selected samples of adult *Neotoma floridana* and *N. micropus*. F_s was calculated by single classification analysis of variance. Tabular F values are given at the level of significance or at $P<0.05$ if not significant. One asterisk and two asterices indicate significance at $P<0.05$ and $P<0.01$, respectively, whereas ns indicates no significant difference.

Measurements and sex	N	Mean	± 2SE	Range	CV	F_s F
			Sample 1 *(Neotoma floridana baileyi)*			
Total length						
Females	9	374.4	9.87	(350.0-393.0)	3.95	<1.00
Males	7	381.3	10.04	(361.0-398.0)	3.48	4.60 ns
Length of tail vertebrae						
Females	9	161.7	9.00	(136.0-180.0)	8.35	<1.00
Males	7	159.7	10.20	(138.0-176.0)	8.44	4.60 ns
Length of hind foot						
Females	11	39.1	0.51	(38.0-41.0)	2.14	3.00
Males	8	39.8	0.60	(38.0-41.0)	2.12	4.45 ns
Length of ear						
Females	5	26.6	1.20	(25.0-28.0)	5.04	<1.00
Males	2	27.5	3.00	(26.0-29.0)	7.71	6.61 ns
Greatest length of skull						
Females	11	48.8	0.44	(47.5-49.7)	1.51	<1.00
Males	7	48.4	1.11	(46.5-50.7)	3.03	4.49 ns
Condylobasilar length						
Females	11	47.4	0.55	(46.0-48.9)	1.92	<1.00
Males	7	47.4	1.17	(45.7-49.8)	3.27	4.49 ns
Zygomatic breadth						
Females	11	26.1	0.27	(25.4-26.6)	1.72	<1.00
Males	7	25.9	0.61	(24.8-27.1)	3.10	4.49 ns
Least interorbital constriction						
Females	11	6.7	0.15	(6.3-7.0)	3.63	6.34
Males	9	6.9	0.17	(6.6-7.4)	3.68	4.41*
Breadth at mastoids						
Females	11	19.0	0.13	(18.2-19.6)	2.35	<1.00
Males	8	19.0	0.51	(18.0-20.4)	3.79	4.45 ns
Length of rostrum						
Females	11	18.8	0.32	(17.5-19.4)	2.86	<1.00
Males	8	18.9	0.43	(17.8-19.6)	3.22	4.45 ns
Breadth of rostrum						
Females	11	7.9	0.13	(7.5-8.2)	2.76	<1.00
Males	9	7.9	0.17	(7.5-8.2)	3.26	4.41 ns
Alveolar length of maxillary toothrow						
Females	11	9.4	0.17	(8.8-9.9)	3.07	<1.00
Males	9	9.5	0.20	(9.2-10.0)	3.10	4.41 ns
Length of palatal bridge						
Females	11	8.7	0.34	(7.3-9.2)	6.42	<1.00
Males	9	8.7	0.33	(8.2-9.6)	5.66	4.41 ns
Length of nasals						
Females	11	18.7	0.33	(18.0-20.2)	2.96	<1.00
Males	8	18.7	0.43	(17.6-19.4)	3.22	4.45 ns

TABLE 2.—Continued.

Measurements and sex	N	Mean	± 2SE	Range	CV	F_s F
Samples 2, 3, and 4 *(Neotoma floridana campestris)*						
Total length						
Females	41	369.8	5.33	(340.0-409.0)	4.61	10.42
Males	27	384.2	7.47	(341.0-434.0)	5.05	7.04 **
Length of tail vertebrae						
Females	41	155.3	3.03	(136.0-175.0)	6.24	1.48
Males	27	158.7	5.12	(120.0-178.0)	8.37	3.99 ns
Length of hind foot						
Females	42	39.4	0.46	(36.0-42.0)	3.80	9.71
Males	33	40.6	0.72	(36.0-44.0)	5.07	7.01 **
Length of ear						
Females	25	27.8	0.71	(25.0-32.0)	6.35	3.02
Males	17	28.7	0.82	(26.0-33.0)	5.88	4.08 ns
Greatest length of skull						
Females	35	49.6	0.46	(47.0-53.3)	2.76	10.02
Males	25	51.0	0.84	(46.0-55.2)	4.12	7.12 **
Condylobasilar length						
Females	33	48.1	0.47	(45.2-51.6)	2.82	11.84
Males	28	49.6	0.83	(44.5-54.3)	4.43	7.12 **
Zygomatic breadth						
Females	34	26.8	0.32	(25.1-29.6)	3.53	6.53
Males	26	27.5	0.42	(25.4-29.9)	3.85	4.02 *
Least interorbital constriction						
Females	40	6.7	0.09	(6.1-7.5)	4.56	7.44
Males	32	6.9	0.10	(6.4-7.7)	4.29	7.01 **
Breadth at mastoids						
Females	36	19.3	0.22	(18.1-21.0)	3.35	5.96
Males	29	19.8	0.37	(17.4-22.4)	4.97	4.00 *
Length of rostrum						
Females	41	19.3	0.24	(17.3-21.1)	3.98	11.40
Males	30	20.0	0.38	(18.0-22.9)	5.26	7.04 **
Breadth of rostrum						
Females	40	8.4	0.10	(7.7-9.4)	3.97	3.35
Males	32	8.6	0.20	(6.1-9.3)	6.77	3.98 ns
Alveolar length of maxillary toothrow						
Females	42	9.6	0.11	(8.9-10.5)	3.60	<1.00
Males	33	9.7	0.14	(8.9-10.4)	4.21	3.98 ns
Length of palatal bridge						
Females	42	8.4	0.13	(7.5-9.4)	5.06	12.48
Males	32	8.8	0.18	(7.6-9.8)	5.83	7.01 **
Length of nasals						
Females	41	19.2	0.23	(17.6-20.4)	3.84	7.91
Males	30	19.8	0.44	(17.7-23.3)	6.03	7.04 **
Samples 5, 6, and 7 *(Neotoma floridana attwateri)*						
Total length						
Females	20	364.6	8.89	(329.0-397.0)	5.45	8.28
Males	18	386.9	13.02	(345.0-450.0)	7.14	7.39 **

TABLE 2.—Continued.

Measurements and sex	*N*	Mean	± 2SE	Range	CV	F_s F
Length of tail vertebrae						
Females	20	157.2	4.23	(142.0-170.0)	6.02	<1.00
Males	18	160.1	4.18	(139.0-175.0)	5.54	4.11 ns
Length of hind foot						
Females	21	38.1	0.96	(34.0-42.0)	5.75	4.51
Males	19	39.4	0.69	(36.0-42.0)	3.81	4.10 *
Length of ear						
Females	15	27.1	1.79	(23.0-38.0)	12.76	<1.00
Males	15	26.7	0.93	(25.0-30.0)	6.70	4.20 ns
Greatest length of skull						
Females	21	49.4	0.70	(47.0-52.2)	3.23	5.49
Males	18	50.7	0.80	(47.4-53.5)	3.36	4.11 *
Condylobasilar length						
Females	21	48.1	0.77	(45.6-51.7)	3.68	5.90
Males	18	49.6	0.87	(46.1-52.2)	3.74	4.11 *
Zygomatic breadth						
Females	22	26.9	0.39	(25.6-29.1)	3.42	5.61
Males	17	27.7	0.55	(25.7-29.2)	4.12	4.11 *
Least interorbital constriction						
Females	23	6.5	0.13	(6.1-7.2)	4.81	2.67
Males	20	6.7	0.18	(6.0-7.8)	6.01	4.08 ns
Breadth at mastoids						
Females	23	19.2	0.31	(17.8-20.4)	3.84	5.98
Males	18	19.9	0.49	(16.9-21.0)	5.23	4.10 *
Length of rostrum						
Females	21	19.2	0.32	(18.1-20.6)	3.77	3.17
Males	20	19.7	0.43	(17.9-21.5)	4.85	4.10 ns
Breadth of rostrum						
Females	21	8.1	0.11	(7.7-8.5)	3.24	3.31
Males	19	8.3	0.21	(7.5-9.1)	5.45	4.10 ns
Alveolar length of maxillary toothrow						
Females	23	9.4	1.54	(8.7-10.1)	3.95	2.63
Males	20	9.6	1.62	(9.0-10.2)	3.78	4.08 ns
Length of palatal bridge						
Females	23	8.5	1.60	(7.6-9.3)	4.50	2.27
Males	20	8.7	1.98	(7.9-9.6)	5.08	4.08 ns
Length of nasals						
Females	20	19.1	0.36	(17.8-21.3)	4.17	6.03
Males	19	19.8	0.37	(18.0-21.6)	4.12	4.11 *
Samples B and C (*Neotoma micropus canescens*)						
Total length						
Females	31	355.8	5.97	(310.0-382.0)	4.67	7.11
Males	23	370.0	9.46	(334.0-411.0)	6.13	4.03 *
Length of tail vertebrae						
Females	31	147.1	3.70	(130.0-165.0)	7.01	3.22
Males	23	152.6	5.10	(131.0-175.0)	8.01	4.03 ns
Length of hind foot						
Females	30	38.4	0.54	(36.0-41.0)	3.85	1.95
Males	25	39.2	1.01	(35.0-45.0)	6.46	4.03 ns

TABLE 2.—Continued.

Measurements and sex	N	Mean	± 2SE	Range	CV	F_s F
Length of ear						
Females	24	27.1	0.56	(25.0-30.0)	5.10	<1.00
Males	16	27.1	0.72	(25.0-29.0)	5.31	4.10 ns
Greatest length of skull						
Females	27	48.8	0.70	(44.2-51.8)	3.75	1.89
Males	25	49.5	0.63	(46.4-52.9)	3.17	4.03 ns
Condylobasilar length						
Females	29	47.0	0.58	(42.8-50.0)	3.34	8.72
Males	24	48.3	0.66	(44.6-50.9)	3.33	7.17 **
Zygomatic breadth						
Females	30	26.5	0.39	(24.7-29.1)	4.06	<1.00
Males	26	26.7	0.36	(25.1-28.8)	3.47	4.03 ns
Least interorbital constriction						
Females	32	6.3	0.10	(5.8-7.0)	4.72	<1.00
Males	27	6.3	0.11	(5.8-6.9)	4.39	4.02 ns
Breadth at mastoids						
Females	27	19.1	0.23	(17.9-20.3)	3.10	1.86
Males	24	19.3	0.28	(18.0-20.8)	3.58	4.04 ns
Length of rostrum						
Females	30	18.9	0.27	(17.2-20.2)	3.98	7.13
Males	26	19.4	0.28	(17.8-20.7)	3.67	4.03 *
Breadth of rostrum						
Females	32	8.3	0.14	(7.2-9.3)	4.92	<1.00
Males	27	8.3	0.14	(7.5-9.2)	4.41	4.02 ns
Alveolar length of maxillary toothrow						
Females	32	9.4	0.14	(8.5-10.1)	4.35	<1.00
Males	27	9.3	0.12	(8.7-10.1)	3.47	4.02 ns
Length of palatal bridge						
Females	31	7.9	0.19	(7.1-9.5)	6.56	<1.00
Males	26	8.1	0.18	(6.8-8.9)	5.72	4.02 ns
Length of nasals						
Females	30	19.2	0.35	(16.7-21.2)	5.04	6.03
Males	26	19.8	0.32	(18.0-21.1)	4.11	4.03 *
Sample P *(Neotoma micropus micropus)*						
Total length						
Females	4	354.5	24.84	(333.0-377.0)	7.01	<1.00
Males	3	364.3	24.04	(362.0-366.0)	5.71	6.61 ns
Length of tail vertebrae						
Females	4	173.5	19.77	(155.0-193.0)	11.40	<1.00
Males	3	169.7	4.06	(166.0-173.0)	2.07	6.61 ns
Length of hind foot						
Females	4	36.5	1.29	(35.0-38.0)	3.54	2.76
Males	3	38.0	1.15	(37.0-39.0)	2.63	6.61 ns
Length of ear						
Females	4	28.2	2.22	(25.0-30.0)	7.85	<1.00
Males	2	28.0	2.00	(27.0-29.0)	5.05	7.71 ns
Greatest length of skull						
Females	4	45.8	1.49	(43.9-47.1)	3.25	1.21
Males	3	46.6	0.42	(46.2-46.9)	0.77	6.61 ns

TABLE 2.—Concluded.

Measurements and sex	*N*	Mean	± 2SE	Range	CV	F_s F
Condylobasilar length						
Females	4	43.2	1.44	(41.7-44.5)	3.32	1.24
Males	3	44.2	0.75	(43.6-44.9)	1.47	6.61 ns
Zygomatic breadth						
Females	4	24.0	0.38	(23.5-24.4)	1.57	3.88
Males	3	25.0	1.17	(24.4-26.2)	4.04	6.61 ns
Least interorbital constriction						
Females	4	6.3	0.36	(6.0-6.8)	5.68	1.42
Males	3	6.0	0.29	(5.8-6.3)	4.17	6.61 ns
Breadth at mastoids						
Females	4	18.2	0.48	(17.6-18.6)	2.64	<1.00
Males	3	18.3	0.44	(18.0-18.7)	2.07	6.61 ns
Length of rostrum						
Females	4	17.6	0.91	(16.4-18.5)	5.19	<1.00
Males	3	17.4	0.47	(17.0-17.8)	3.33	6.61 ns
Breadth of rostrum						
Females	4	7.4	0.25	(7.2-7.8)	3.38	<1.00
Males	3	7.5	0.12	(7.4-7.6)	1.33	6.61 ns
Alveolar length of maxillary toothrow						
Females	4	8.9	0.34	(8.6-9.4)	3.82	<1.00
Males	3	9.1	0.41	(8.8-9.5)	3.84	6.61 ns
Length of palatal bridge						
Females	4	7.8	0.42	(7.5-8.4)	5.39	<1.00
Males	3	7.5	0.81	(6.8-8.2)	9.33	6.61 ns
Length of nasals						
Females	4	17.1	0.80	(16.3-18.2)	4.70	2.42
Males	3	17.9	0.35	(17.6-18.2)	1.68	6.61 ns

(with males being larger than females) might convey a selective advantage. However, the laboratory breeding cage was clearly an unnatural situation. In the natural environment, domination of females by males may not be important if females tolerate males only during estrus but are willing to accept any male at that time. Considering the habit of solitary occupancy of dens and competition for den sites during times of high population density (see Fitch and Rainey, 1956:517), females that are large enough to protect choice dens for maternity purposes may rear more young than less robust females. On the other hand, most adult male *N. micropus* collected in western Kansas in June, 1967, had what appeared to be fresh wounds in the region of the lower back, but no "battle scars" were noted for females at that time (see Fitch and Rainey, 1956:521, for similar comments pertaining to *N. floridana*). Perhaps in the natural environment, physical competition and fighting is most common between males, which would cause selection for large size to be more intense in males than females.

Brown (1968) and Brown and Lee (1969) studied various physiological and morphological responses of woodrats to differing thermal regimes. It was found that body size was related to temperature, and although no comparisons of sexes were reported, it is clear that selective responses to temperature and other environmental factors play a major role in determination of size of woodrats. Such factors probably act similarly on animals of both sexes, tending to reduce

secondary sexual variation. The magnitude of secondary sexual variation probably is controlled by several interacting forces, some of which favor secondary sexual differences while others operate to minimize such differences. The result is as seen in Table 2; perceptible differences exist, but these appear to be more pronounced in some taxa (*campestris*, for example) than in others (such as *baileyi*).

Individual Variation

Of more than 2000 woodrats examined during this investigation, only five had obviously atypical coloration that I assumed to be genetically based. Three of these, *Neotoma micropus canescens* that were previously reported by Baker (1956:286), are from near Sabinas, Coahuila; all were collected on the same day. One is a young adult female that was lactating and the other two are juveniles nearing completion of the postjuvenal molt. Most hairs of the venter are white to the base on all three, and white hairs extend onto the sides and lower rump. The female probably is the mother of the two juveniles. The status of the color pattern in the population from which these specimens originated would be of interest. The other two abnormally colored specimens are *Neotoma floridana attwateri*. One (OSU 4541) is a young adult female from northeastern Dewey County, Oklahoma; dorsal coloration is a uniform creamy tan and the ears are nearly white. The other (KU 18682), from Anderson County, Kansas, is an albino in fresh winter pelage. The ears, plantar surfaces of the feet, hair, and underlying skin are devoid of pigment; written on the data label are the words "eyes pink."

A specimen of *Neotoma micropus* obtained in western Kansas in June 1967 and another from Prowers County, Colorado captured in April 1968 were distinctly reddish dorsally, at the time of capture. Both were in old pelage and the one from Colorado was still in reddish pelage when sacrificed about six weeks after capture. The other was molting at the time of capture and eventually completed molt into a gray pelage lacking the reddish coloration. This reddish coloration is not considered to be genetically based, but probably was the result of chemical alterations of pigment in old pelage and likely caused by extrinsic factors such as high concentrations of ammonia in the nest.

Because coefficients of variation reflect the ratio of the standard deviation to the mean, the statistic is useful in comparing the degree of variation between populations of a single species or between populations of different taxa. The coefficient of variation can be used also to compare the relative reliability of different measurements of a single sample. Long (1968, 1969) recently summarized patterns of individual variation and comparative variation of measurements commonly used in taxonomic investigations.

Coefficients of variation for each sex of three samples of *floridana* and three samples of *micropus* are shown in figure 9. The coefficients are superimposed on Dice-grams illustrating the trends of variation among the measurements taken. Size of all samples except the two (one male, one female) for *canescens* from Coahuila (M) are given in table 2. Sample M consisted of 12 females and 13 males. Length of tail vertebrae and length of ear are the most variable dimensions considered, and also are two of the four recorded from specimen labels. Length of hind foot and total length were recorded from specimen labels. The former shows about average variability, whereas total length is more variable than all except one cranial measurement, but less variable than lengths of tail and ear.

Of the 10 cranial measurements, length of the palatal bridge is the most variable. This measurement varies in part with the shape of the posterior margin of the palate (see beyond under geographic variation of qualitative cranial characters), which is relatively vari-

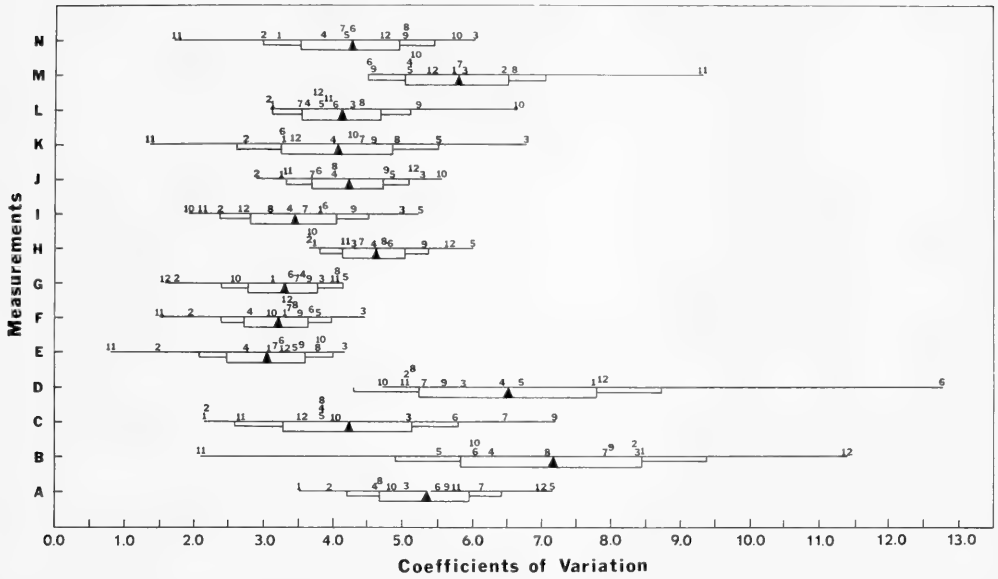

FIG. 9. Coefficients of variation for 14 external and cranial measurements showing variability of that statistic in each. Measurements are as follows: A—total length; B—length of tail vertebrae; C—length of hind foot; D—length of ear; E—greatest length of skull; F—condylobasilar length; G—zygomatic breadth; H—least interorbital constriction; I—breadth at mastoids; J—length of rostrum; K—breadth of rostrum; L— alveolar length of maxillary toothrow; M—length of palatal bridge; N—length of nasals. Numbers plotted on the horizontal lines are individual coefficients of variation for each sample of adult woodrats, as defined below; odd numbers are males, and even numbers are females (see figure 8 for geographic areas included within the coded localities indicated in parentheses): 1 and 2, *Neotoma floridana baileyi* (1); 3 and 4, *N. f. campestris* (2, 3, and 4); 5 and 6, *N. f. attwateri* (5, 6, and 7); 7 and 8, *N. micropus canescens* (B and C); 9 and 10, *N. m. canescens* (M); 11 and 12, *N. m. micropus* (P). The apex of the darkened triangle is the arithmetic mean of the coefficients of variation of the 12 samples, and the thick horizontal bar is plus and minus two standard errors of the mean; the thin horizontal bar is plus and minus one standard deviation of the mean, and the horizontal line is the range.

able even at the intra populational level. All cranial measurements were recorded only to the nearest tenth of a millimeter and length of palatal bridge is one of the smaller dimensions; thus, the precision of data recorded relative to size of the character measured would be only about one-fifth of that for, say, greatest length of skull. Least interorbital constriction was the next most variable cranial measurement and also is one of the smaller dimensions; however, other characters measured having means of less than 10 (alveolar length of maxillary toothrow and breadth of rostrum) demonstrate near average variability. Greatest length of skull, condylobasilar length, zygomatic breadth, and mastoid breadth are the least variable characters measured; all having average coefficients of variation less than 4.0.

To compare the relative variation of the 14 characters simultaneously between the 12 groups, three simple tallies were made. When only extreme coefficients were considered, one or the other of the two samples of *baileyi* is least variable in six of the 14 measurements and one or the other of the samples of *attwateri* is most variable in five instances. This tally also shows that a sample of males is most variable in 10 of the 14 characters considered. Each pair of samples from each locality next was compared for all measurements to determine if males were in fact more highly variable than females. Of the 84 comparisons (six localities times 14 measurements) made, males are

more variable than females in 49 instances and less variable in 35, a difference not significant at $P < 0.05$ as tested by Chi-square. Lastly, the coefficients of variation for each character were assigned values on a rank-order basis so that the lowest coefficient for a character accrued one unit and the highest accrued 12 units to the respective taxa. These scores then were totaled for each sample by summing the 14 rank-order scores; thus a low total implies less variation and a high total more variation. As determined by this crude technique, the sample of *baileyi* females is least variable (41.5) and the sample of *campestris* males is most variable (134.0). Males were shown to be more variable than their female counterparts at four localities (*N. m. micropus* from locality P, and *N. m. canescens* from combined localities B and C being the two exceptions); they have a rank-order total of 587 compared to 504 for females (different at $P < 0.05$, as tested by Chi square). When scores of the sexes were summed for each locality, the sample of *baileyi* is least variable (106.5) and that of *attwateri* is most variable (215.5). Coefficients of variation in the sample of *micropus* is intermediate (158.0) between *baileyi* and the four samples of widely distributed taxa (201.5-215.5); but in *micropus* the distribution of coefficients is erratic, probably reflecting the small sample size available.

The tendency for samples of males to be more variable than those of females is indicated by all three methods of analysis that I employed. Long (1969:298) found males of domestic mammals more variable than conspecific females, but indicated that no basis presently exists for attributing greater variation to males. The apparent presence of relatively less individual variation in the isolated subspecies, *baileyi*, as compared to widely distributed taxa is not surprising; small, isolated populations are prone to loss of variation by chance or "drift." Additionally, they lack one of the most important means of acquiring "new" genetic variation, i.e. immigration. Mayr (1963:177) suggested that a reasonable estimate of "new" genes normally acquired by a local population through immigration is at least 90 percent and possibly exceeds 99 percent.

It was expected *a priori* that individual variation in the samples of *campestris* would be more pronounced than in other taxa. In part the prediction was correct; the sample of *campestris* males is more variable than other samples, but only *baileyi* females and *micropus* males are less variable than *campestris* females. Possibly selection acting on populations that live in similar environments maintains the observed degree of homogeneity (Ehrlich and Raven, 1969), or perhaps there is more interpopulational gene flow in *campestris* than my observations have indicated.

Variation Resulting from Captivity

The most striking differences observed between a specimen that had been reared, or at least maintained, in the laboratory for an extended period of time and one that had been killed at the time of capture were in the teeth. The cheekteeth of woodrats fed on laboratory chow did not wear at a rate comparable to that in natural populations. The molars of cleaned skulls of laboratory rats often are as much as a third or a half longer than those of non-laboratory animals. Furthermore, the reentrant angles of laboratory-reared woodrats extend much nearer to the alveolus than do those of comparably aged non-laboratory rats. Although this may be the result of reduced tooth growth to compensate reduced wear, the stimulus that stops or slows growth is unknown. In some laboratory specimens, alveolar tissue near the base of the molars appeared reduced and slightly porous. If the alveolar tissue of laboratory rats grows abnormally slow or if it is resorbed, the molar may undergo normal growth but have higher crowns.

The incisors of woodrats living in the laboratory frequently are broken, resulting in abnormal occlusion and the ab-

sence of wear on the opposing incisor. The frequency of abnormal growth of incisors is relatively high in laboratory animals, whereas woodrats living in the natural environment and having malocclucding incisors probably are destined to early death.

Comparisons of size of woodrats reared in the laboratory with non-laboratory animals from the same geographic areas are shown in table 3. Only specimens at least 30 weeks of age that either were born in the laboratory or were captured before they had completed the postjuvenal molt were included in laboratory samples. After specimens meeting these criteria were separated by sex, only three samples, *Neotoma micropus canescens* (localities B and C) males and females, and *Neotoma floridana campestris* (localities 3 and 4) females, contained enough specimens (10 or more) for conducting the tests. Non-laboratory comparative samples included all available specimens of age groups VI, VII, and VIII from the grouped localities indicated above.

Differences in two measurements, total length and alveolar length of maxillary toothrow, are highly significant ($P < 0.01$) between the two samples of *N. f. campestris* females; no highly significant differences were observed for *N. m. canescens*. Significant differences ($P < 0.05$) were observed for two other characters (length of hind foot and length of nasals) in *floridana*, one measurement (total length) of *micropus* females, and five measurements (length of hind foot, length of ear, greatest length of skull, condylobasilar length, and breadth of rostrum) for *N. m. canescens* males. Total length of *micropus* females is the only dimension significantly larger in the non-laboratory or "wild" sample. On the average, laboratory samples are slightly larger in most measurements that are not significantly different.

Increased size of laboratory animals may be the result of a more nutritious diet or it may reflect differences in age. Many animals in the laboratory samples were near two years of age. It is doubtful that the average age of non-laboratory animals equals that of the laboratory sample.

GEOGRAPHIC VARIATION

In the discussion beyond, I will interpret patterns of both qualitative and quantitative variation of morphological characteristics primarily from an evolutionary point of view in an attempt to elucidate the relationships of woodrats. If it can be determined whether patterns of variation are concordant or discordant, and clinal or abrupt, one can surmise which patterns have resulted from primary intergradation, secondary intergradation, or from present restrictions to gene flow. Also, I will attempt to ascertain if natural hybridization is introgressive in *N. floridana* and *N. micropus*.

Pelage, Molt, and Color

Finley (1958:232) described the succession of molts and pelages of woodrats as juvenal pelage, postjuvenal molt, subadult pelage, second molt, first autumn pelage, third molt, first winter pelage, annual molt. My observations agree in a general way with this scheme. Animals born late in summer or early in autumn, however, do not undergo the complete sequence, but spend the first winter in either the subadult pelage or first autumn pelage.

Remarkably little published information pertaining to molt in adult *Neotoma* is available. Goldman (1910:12) summarized his understanding of molt on adults as follows: "The molting season is somewhat irregular, especially in the southern part of the range of the group. The northern species molt once a year, toward the end of summer or fall. The southern forms usually molt in early winter, but individuals in worn and in fresh pelage may often be seen together." Linsdale and Tevis (1951:450-458) described and discussed molt in *Neotoma fuscipes*, and Finley (1958) studied it in those species of woodrats that occur in

TABLE 3. Size comparisons of woodrats reared in the laboratory and those killed at the time of initial capture (wild). Statistics given are sample size, mean, two standard errors of the mean, range, coefficient of variation, F_s (F value calculated by single classification ANOVA), and F (tabular F value at level of significance or at $P<0.05$ if not significant). One asterisk and two asterices indicate significance at the 0.05 and 0.01 levels, respectively, whereas ns indicates no significant difference.

Measurement and treatment	N	Mean	± 2SE	Range	CV	F_s F
			Neotoma floridana campestris females (Samples 3 and 4)			
Total length						
Wild	33	370.8	6.23	(340.0-409.0)	4.83	9.86
Laboratory	10	394.2	17.94	(331.0-421.0)	7.20	7.31 **
Length of tail vertebrae						
Wild	33	154.9	3.59	(136.0-175.0)	6.66	3.70
Laboratory	10	162.7	8.93	(129.0-178.0)	8.68	4.07 ns
Length of hind foot						
Wild	34	39.3	0.55	(36.0-42.0)	4.09	5.94
Laboratory	10	40.7	0.45	(39.0-43.0)	3.48	4.07 *
Length of ear						
Wild	19	2.8	0.72	(25.0-32.0)	5.53	<1.00
Laboratory	10	2.9	0.13	(24.0-31.0)	7.01	4.21 ns
Greatest length of skull						
Wild	29	5.0	0.52	(47.0-53.3)	2.81	<1.00
Laboratory	12	5.0	1.17	(46.2-52.4)	4.05	4.10 ns
Condylobasilar length						
Wild	26	48.2	0.56	(45.2-51.6)	2.97	2.83
Laboratory	12	49.1	0.99	(45.2-51.2)	3.49	4.11 ns
Zygomatic breadth						
Wild	27	27.0	0.38	(25.1-29.6)	3.68	<1.00
Laboratory	12	27.2	0.63	(25.7-29.0)	4.03	4.11 ns
Least interorbital constriction						
Wild	32	6.7	0.11	(6.1-7.5)	4.72	<1.00
Laboratory	12	6.7	0.21	(6.2-7.5)	5.31	4.07 ns
Breadth at mastoids						
Wild	29	19.4	0.24	(18.1-21.0)	3.31	<1.00
Laboratory	12	19.6	0.35	(18.5-20.5)	3.13	4.10 ns
Length of rostrum						
Wild	33	19.4	0.25	(17.8-21.1)	3.70	1.85
Laboratory	12	19.8	0.72	(17.4-21.2)	6.35	4.07 ns
Breadth of rostrum						
Wild	32	8.5	0.12	(7.9-9.4)	3.85	1.34
Laboratory	11	8.6	0.25	(7.8-9.2)	4.81	4.08 ns
Alveolar length of maxillary toothrow						
Wild	34	9.7	0.09	(9.1-10.3)	2.84	11.27
Laboratory	12	10.0	0.09	(9.6-10.3)	1.61	7.24 **
Length of palatal bridge						
Wild	34	8.5	0.14	(7.8-9.4)	4.72	<1.00
Laboratory	12	8.6	0.25	(8.2-9.6)	5.09	4.06 ns
Length of nasals						
Wild	33	19.2	0.26	(17.6-20.4)	3.93	5.30
Laboratory	12	19.8	0.57	(18.0-21.1)	4.97	4.07 *

TABLE 3.—Continued.

Measurement and treatment	*N*	Mean	± 2SE	Range	CV	F_s F
Neotoma micropus canescens females (Samples B and C)						
Total length						
Wild	31	355.8	5.97	(310.0-382.0)	4.67	4.47
Laboratory	11	351.8	11.25	(326.0-382.0)	5.30	4.08 *
Length of tail vertebrae						
Wild	31	147.1	3.70	(130.0-165.0)	7.01	<1.00
Laboratory	11	146.2	8.32	(126.0-171.0)	9.43	4.08 ns
Length of hind foot						
Wild	30	38.4	0.54	(36.0-41.0)	3.85	2.90
Laboratory	13	39.2	0.69	(37.0-41.0)	3.15	4.08 ns
Length of ear						
Wild	24	27.1	0.56	(25.0-30.0)	5.10	4.00
Laboratory	13	28.1	0.86	(25.0-30.0)	5.53	4.13 ns
Greatest length of skull						
Wild	27	48.8	0.70	(44.2-51.8)	3.75	<1.00
Laboratory	14	48.9	0.86	(46.2-51.4)	3.31	4.10 ns
Condylobasilar length						
Wild	29	47.0	0.58	(42.8-50.0)	3.34	<1.00
Laboratory	15	47.4	0.71	(45.0-49.4)	2.92	4.07 ns
Zygomatic breadth						
Wild	30	26.5	0.39	(24.7-29.1)	4.06	<1.00
Laboratory	14	26.7	0.43	(25.2-30.0)	3.04	4.07 ns
Least interorbital constriction						
Wild	32	6.3	0.11	(5.8-7.0)	4.72	2.80
Laboratory	15	6.2	0.15	(5.7-6.6)	4.73	4.06 ns
Breadth at mastoids						
Wild	27	19.1	0.23	(17.9-20.3)	3.10	3.21
Laboratory	14	19.4	0.17	(18.9-19.9)	1.65	4.08 ns
Length of rostrum						
Wild	30	18.9	0.27	(17.2-20.2)	3.98	<1.00
Laboratory	14	18.8	0.39	(17.8-20.2)	3.93	4.07 ns
Breadth of rostrum						
Wild	32	8.3	0.14	(7.2-9.3)	4.92	<1.00
Laboratory	15	8.4	0.21	(7.9-9.3)	4.87	4.06 ns
Alveolar length of maxillary toothrow						
Wild	32	9.4	0.14	(8.5-10.1)	4.35	<1.00
Laboratory	15	9.3	0.19	(8.4-9.9)	3.92	4.06 ns
Length of palatal bridge						
Wild	31	8.0	0.19	(7.1-9.5)	6.56	<1.00
Laboratory	15	8.0	0.18	(7.4-8.5)	4.38	4.06 ns
Length of nasals						
Wild	30	19.2	0.35	(16.7-21.2)	5.04	<1.00
Laboratory	14	19.4	0.43	(18.0-20.9)	4.15	4.07 ns
Neotoma micropus canescens males (Samples B and C)						
Total length						
Wild	23	370.1	9.46	(334.0-411.0)	6.13	2.16
Laboratory	8	383.0	11.84	(354.0-398.0)	4.37	4.18 ns

TABLE 3.—Concluded.

Measurement and treatment	*N*	Mean	± 2SE	Range	CV	F_s *F*
Length of tail vertebrae						
Wild	23	152.6	5.10	(131.0-175.0)	8.01	<1.00
Laboratory	8	154.8	7.52	(142.0-172.0)	6.87	4.18 ns
Length of hind foot						
Wild	25	39.2	1.01	(35.0-45.0)	6.46	6.18
Laboratory	10	41.3	0.79	(39.0-43.0)	3.03	4.15 *
Length of ear						
Wild	16	27.1	0.72	(25.0-29.0)	5.31	7.39
Laboratory	11	28.7	1.05	(27.0-32.0)	6.05	4.24 *
Greatest length of skull						
Wild	25	49.5	0.63	(46.4-52.9)	3.17	4.79
Laboratory	10	50.6	0.43	(49.4-51.9)	1.35	4.15 *
Condylobasilar length						
Wild	24	48.3	0.66	(44.6-50.9)	3.33	5.24
Laboratory	10	49.5	0.44	(48.3-50.6)	1.39	4.15 *
Zygomatic breadth						
Wild	26	26.7	0.36	(25.1-28.8)	3.47	<1.00
Laboratory	11	26.9	0.39	(26.1-28.2)	2.42	4.13 ns
Least interorbital constriction						
Wild	27	6.3	0.11	(5.8-6.9)	4.39	<1.00
Laboratory	11	6.4	0.13	(6.1-6.9)	3.38	4.11 ns
Breadth at mastoids						
Wild	24	19.3	0.28	(18.0-20.8)	3.58	<1.00
Laboratory	11	19.4	0.10	(19.2-19.8)	0.87	4.15 ns
Length of rostrum						
Wild	26	19.4	0.28	(17.8-20.7)	3.67	<1.00
Laboratory	10	19.5	0.40	(18.3-20.4)	3.23	4.13 ns
Breadth of rostrum						
Wild	27	8.4	0.14	(7.5-9.2)	4.41	4.86
Laboratory	11	8.6	0.22	(8.0-9.2)	0.22	4.11 *
Alveolar length of maxillary toothrow						
Wild	27	9.3	0.12	(8.7-10.1)	3.47	2.19
Laboratory	11	9.5	0.22	(9.0-10.0)	3.81	4.11 ns
Length of palatal bridge						
Wild	26	8.1	0.18	(6.8-8.9)	5.73	3.37
Laboratory	10	8.4	0.13	(7.9-8.6)	2.54	4.13 ns
Length of nasals						
Wild	26	19.8	0.32	(18.0-21.1)	4.11	<1.00
Laboratory	10	19.9	0.35	(19.0-20.7)	2.79	4.13 ns

Colorado. In both studies it was concluded that only a single annual molt occurs in adult woodrats.

Seasonal occurrence of molt in selected samples of *N. floridana* and *N. micropus* is shown in table 4. Specimens of age-groups V-VIII were included in these tabulations. With one exception, animals were considered to be molting if new pelage appeared to have been replacing old pelage regardless of whether the replacement was symmetrical or involved a complete replacement of hair. Many woodrats have a varying number of tiny spots of actively growing hair. These probably are areas in which hair

lost while fighting or in other ways not directly associated with seasonal molt is replaced. Specimens with such "spots" that were not molting elsewhere were not considered to be molting.

As can be seen in table 4, some woodrats obtained in every month were molting. It was thought that possibly only animals of age-groups V and VI (which still might have been in some stage of maturational molt) were molting at times other than late summer and autumn as has been reported previously. However, when only specimens of age-groups VII and VIII were considered, the seasonal array of molting and nonmolting individuals remained approximately the same.

In northern populations of the two species studied, adults are almost invariably in a dense, luxuriant winter pelage by late November or early December. Beginning in late winter or early spring, the winter pelage of many individuals begins to deteriorate; it becomes thinner, less luxuriant, has many broken tips, and appears "scruffy." In other rats, the winter pelage seems to be well maintained into late May or early June. When the pelage begins to deteriorate, it generally is replaced erratically over the body, usually beginning in those areas where the winter pelage is thinnest or most worn. This "molt" has little or no symmetry of pattern. In occasional individuals, the winter pelage is nearly or completely replaced by a shorter, usually darker "summer" pelage. Some rats have only localized spots of this pelage and others show no sign of replacement until July or August. At this time they apparently begin the "annual molt" and molt the old winter pelage directly into a new winter pelage. Those individuals that replaced some or all of the pelage earlier also molt into a new winter pelage in late summer and autumn.

The molting sequence in southern populations of both species is less clear. Even the new winter pelage of southern woodrats is shorter than "summer pelage" of those from northern populations, and the "annual molt" (molt into winter pelage) is only weakly synchronized among animals of the same population. Usually this molt occurs anytime from June to October, and generally is complete by November.

Whether one wishes to consider the replacement of worn winter pelage prior to the attainment of new winter pelage as a "vernal molt" and the resultant pelage as a "summer pelage" is primarily a question of semantics. Almost certainly the only molt that is consistently complete and common to all adults is the

TABLE 4. Seasonal distribution of molt in selected samples of *Neotoma floridana* and *N. micropus*. See figure 8 for geographic areas included in coded localities.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Sample 1 (*Neotoma floridana baileyi*)												
Females												
Molting	—	—	—	—	0	—	1	2	—	—	—	—
Examined	—	—	—	—	1	—	1	3	—	—	—	—
Males												
Molting	—	—	—	—	1	—	—	2	—	2	—	—
Examined	—	—	—	—	1	—	—	2	—	2	—	—
Samples 2, 3, and 4 (*Neotoma floridana campestris*)												
Females												
Molting	—	—	—	3	0	2	—	2	5	—	1	0
Examined	—	—	—	3	1	3	—	3	5	—	2	9
Males												
Molting	—	—	—	1	—	5	—	1	3	—	0	1
Examined	—	—	—	1	—	5	—	1	3	—	2	11

TABLE 4.—Concluded.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Samples 5, 6, and 7 (*Neotoma floridana attwateri*)												
Females												
Molting	0	5	2	1	----	----	----	1	1	1	6	1
Examined	2	11	12	2	----	----	----	1	1	2	11	12
Males												
Molting	0	1	0	0	----	----	----	3	1	2	5	0
Examined	4	2	8	4	----	----	----	3	1	2	9	6
Samples 8, 9, 10 (*Neotoma floridana attwateri*)												
Females												
Molting	2	----	0	2	----	1	0	----	1	4	3	2
Examined	9	----	1	2	----	3	1	----	2	6	6	9
Males												
Molting	1	0	0	0	----	3	----	----	----	5	3	1
Examined	8	2	6	3	----	3	----	----	----	5	4	6
Samples 11 and 12 (*Neotoma floridana attwateri*)												
Females												
Molting	----	0	1	----	----	----	----	----	0	2	5	3
Examined	----	3	1	----	----	----	----	----	1	3	6	5
Males												
Molting	----	1	0	----	----	----	----	----	2	2	5	1
Examined	----	2	2	----	----	----	----	----	2	3	5	2
Samples A, B, C, and F (*Neotoma micropus canescens*)												
Females												
Molting	0	----	----	0	1	8	3	1	2	2	0	----
Examined	2	----	----	1	1	10	7	6	2	2	3	----
Males												
Molting	1	1	----	0	0	3	2	6	----	3	1	0
Examined	1	1	----	1	1	5	4	6	----	4	5	4
Samples D, G, H, and I (*Neotoma micropus canescens*)												
Females												
Molting	0	----	----	----	0	1	6	----	1	3	0	0
Examined	2	----	----	----	1	3	7	----	1	3	1	9
Males												
Molting	0	0	----	----	3	2	----	----	----	----	----	0
Examined	3	2	----	----	3	3	----	----	----	----	----	10
Samples J, K, L, and M (*Neotoma micropus canescens*)												
Females												
Molting	----	0	0	3	0	1	0	1	1	----	4	0
Examined	----	1	2	4	1	2	1	2	1	----	12	1
Males												
Molting	0	----	1	4	0	1	1	----	1	----	10	----
Examined	1	----	1	6	1	1	3	----	1	----	16	----
Samples N and P (*Neotoma micropus micropus*)												
Females												
Molting	----	----	----	----	0	2	1	1	2	----	2	0
Examined	----	----	----	----	4	4	1	1	2	----	10	1
Males												
Molting	----	----	0	----	3	2	2	4	----	----	3	0
Examined	----	----	1	----	4	2	4	5	----	----	9	2

autumn molt or in Finley's (1958) terminology, the annual molt. The "vernal molt" apparently is primarily a mechanism to maintain the pelage and may be complete, abbreviated, or absent. For many years it was thought that members of the genus *Peromyscus* molted only once a year (see Layne, 1968:141, for review), but recent studies have shown that at least in some species molting also occurs at other times of the year (Brown, 1963; Lawlor, 1965). Possibly the seasonal molting regimes of members of the two genera are similar, but characterized by much more individual and geographic variation than previously has been thought.

An attempt was made to correlate reproductive data from specimen labels with molt in females. Pregnant or lactating females that were collected in spring or early summer usually were in the old winter pelage; however, pregnant and lactating females collected in late summer often were actively molting. An adult female *N. f. campestris* (KU 120844) was captured in December in a relatively new winter pelage. She was maintained in the laboratory until late March without having been placed with a male. At that time she was undergoing what probably would have been a nearly complete molt from her typical winter pelage, which was in remarkably good repair, to a new shorter darker "summer pelage." On 20 March she was placed with a male and on 26 April she gave birth to a litter. Insofar as I could determine, the molt had progressed very little between those dates and remained without change until she was killed on 10 June. The specimen shows no line of "current" activity between the two pelages, which are markedly different in length, color, and general texture. Apparently molt of woodrats is influenced by the hormones of reproduction and shortly after this female became pregnant the molt was arrested.

Other factors that probably influence the timing and degree of completeness of the "vernal molt" include age, condition of health, and condition of the existing pelage. Although exchange of pelages clearly is necessary, especially in northern woodrats preparing for winter, molt may be one of the body processes that is under a relatively loose genetic control and easily altered when it is physiologically advantageous for an individual to divert energy or reserves elsewhere.

The variation in molts and pelages of woodrats in spring and summer resulted in some difficulty selecting specimens for color measurements. Ideally, only adults in fresh winter pelage would be considered in analyses of geographic variation in color. However, sufficient samples from the various aggregate localities were not available when samples were thus limited. It was necessary to include all specimens whose pelage was in relatively good repair, regardless of season.

The effect of including animals collected at different times of the year was tested for each of the three reflectance readings and for the total (value obtained by summing the three individual reflectance readings for each individual) by pooling readings of animals from localities 5 through 11 (all *Neotoma floridana attwateri*) and separating the individuals into four seasonal samples. Each sample included animals killed during a three-month period so that four samples corresponding roughly to winter (December-February), spring (March-May), summer (June-August), and autumn (September-November) were available. Seasonal variation is not significantly different in reflectance of blue or green, but is significantly different ($0.05 > P > 0.01$) for reflectance of red and for total reflectance. These data were separated by sex to test males against females. Males were significantly paler ($0.05 > P > 0.01$) as indicated by reflectance of red, but F_s values were less than unity for blue and green, and less than F for total reflectance.

Explanation of the slight seasonal variation is commensurate with the above

discussion of molt and pelages. Most woodrats are darkest in fresh winter pelage and palest in old pelage just before undergoing molt into winter pelage, which is the only more or less synchronous molt of adults. This molt usually occurs in September, October, or early November; thus most animals in the autumn sample recently had molted or were molting. The high coefficients of variation for this sample are attributable to the fact that all specimens were not in the same pelage. The three seasonal samples involving mostly animals in winter pelage were not significantly different in color, and even the sample composed mostly of summer specimens was not significantly different from the spring or winter samples.

Specimens of both sexes and from all seasons were pooled for each locality for studies of geographic variation. Results of univariate analyses of intraspecific color variation in *Neotoma floridana* are shown in table 5. Highly significant ($P < 0.01$) differences exist in comparisons of group-means for all reflectance readings. In no case, however, are animals from localities 5-13 (all samples of *N. f. attwateri* and the single sample of *N. f. rubida*) significantly different from each other with respect to color. Specimens from localities 12 (southern Texas), 6 (northeastern Kansas), and 11 (northern Texas) tend to be slightly paler in color than other specimens. Samples 5 (north-central Kansas), 10 (southeastern Oklahoma), and 13 (*N. f. rubida*) generally are darkest. Within the subspecies *N. f. campestris*, a rather clear trend exists from paler animals in the west (localities 2 and 3) to darker ones in the east (locality 4) where the range of *campestris* meets that of *attwateri*. In no case is the difference between animals from localities 2 and 3 significant, but those from locality 4 are significantly darker than those from 2 in all reflectance readings. Specimens in sample 4 also are significantly paler in all readings from those of *attwateri* from adjacent locality 5. Only in reflectance of blue are differences between samples 3 and 4 shown to be significantly different. The darker color of specimens from locality 4 as compared to those in samples 2 and 3 probably has resulted from intergradation with the darker *attwateri* population to the east. With respect to color, the zone of intergradation would appear to have been assigned largely to *campestris*, although in size (see beyond) animals from locality 5 are more like those from locality 4 than from locality 6.

Neotoma floridana baileyi (locality 1) is paler than all samples of *attwateri*, and significantly darker than *campestris* (with the exception of the sample of *campestris* from the narrow zone where *campestris* intergrades with *attwateri* at locality 4). The pale coloration of *baileyi* is less tannish than that of *campestris*, and although most specimens of *baileyi* are distinctly paler than specimens of *attwateri*, their coloration more closely resembles that of *attwateri*, than that of *campestris*. The habitat in which *baileyi* occurs resembles that where *attwateri* is found, but most adjacent habitat types in northern Nebraska, which thus far have not been found to support woodrats, are mostly shortgrass pasture (more like the habitat of *campestris*). The pale color seen in *baileyi* and *campestris* probably signifies convergence, which has resulted from adaptation to an arid environment, from a darker common ancestor.

Table 6 contains results of univariate analyses of intraspecific color variation for *Neotoma micropus*. As opposed to the pattern of color variation in *floridana*, that in *micropus* is clearly clinal and lacks noticeable steps. Specimens from locality E (New Mexico) are paler on the average than those from White Sands National Monument (locality O, previously *N. m. leucophea*). Therefore, there seems to be no sound reason for recognizing the name *leucophea*. (If larger samples separable by season had been available, the White Sands population might have averaged paler, but cer-

tainly the differences are slight.) When all samples of *micropus* are considered, specimens from localities in New Mexico (E and O) and western Texas (F and J) generally are palest in color as evinced by higher reflectance readings.

Those from localities D, G, H, K, L, N, and P generally are darker than those from A, B, C, I, and M, which tend to be intermediate. Darkest populations generally occur at localities in the eastern parts of the range of the species, and palest populations are from the more arid western localities. As shown by the

TABLE 5. Geographic variation in color of selected samples of *Neotoma floridana*. F_s was calculated by single classification analysis of variance. Tabular F values are at the $P<0.05$ level of significance; ns indicates no significant difference within a group of means. Nonsignificant subsets (as calculated by the Sums of Squares Simultaneous Testing Procedure) of significantly different groups of means are shown in the last column. See figure 8 for geographic areas included within each coded locality.

Color reflectance measured, and coded localities	N	Mean	± 2SE	Range	CV	F_s F	SS-STP			
Red										
2	2	19.2	0.50	(19.0-19.5)	1.84	12.78	I			
3	19	17.0	1.06	(13.0-20.5)	13.66	1.83	I			
1	23	15.6	0.88	(12.0-20.0)	13.56		I	I		
4	16	15.5	0.97	(12.0-19.5)	12.52		I	I	I	
12	16	14.1	0.92	(11.5-17.0)	12.96			I	I	I
9	7	13.1	1.18	(12.0-16.5)	11.98			I	I	I
6	12	13.0	0.85	(10.0-14.5)	11.33				I	I
11	7	12.7	0.69	(11.5-14.0)	7.13				I	I
7	28	12.7	0.53	(10.0-17.0)	11.07					I
13	5	12.6	1.66	(10.5-15.0)	14.69					I
8	4	12.5	0.82	(11.5-13.5)	6.53					I
10	5	12.2	0.93	(10.5-13.0)	8.50					I
5	6	11.2	1.09	(10.0-13.5)	11.90					I
Blue										
2	2	10.5	2.00	(9.5-11.5)	13.47	41.62	I			
3	19	9.6	0.45	(7.5-11.5)	10.20	1.83	I			
4	16	8.3	0.42	(7.0-10.5)	9.96			I		
1	23	8.0	0.32	(6.5-9.5)	9.61			I		
12	16	6.6	0.28	(5.5-7.5)	8.49				I	
5	6	6.5	0.52	(6.0-7.5)	9.73				I	
11	7	6.5	0.65	(5.5-8.0)	13.32				I	
8	4	6.5	0.00	(6.5-6.5)	0.00				I	
6	12	6.4	0.45	(5.0-7.5)	12.12				I	
9	7	6.3	0.37	(5.5-7.0)	7.76				I	
7	28	6.0	0.19	(5.5-7.0)	8.41				I	
13	5	5.6	0.37	(5.0-6.0)	7.47				I	
10	5	5.3	0.75	(4.0-6.0)	15.79				I	
Green										
2	2	12.0	2.00	(11.0-13.0)	11.79	39.62	I			
3	19	10.5	0.52	(8.5-12.5)	10.85	1.83	I	I		
4	16	9.4	0.49	(8.0-11.5)	10.40			I	I	
1	23	8.3	0.28	(7.5-9.5)	8.10				I	I
6	12	7.3	0.40	(6.5-8.5)	9.35					I I
8	4	7.2	0.65	(6.5-8.0)	8.90					I I
5	6	7.2	0.43	(6.5-8.0)	7.23					I I
12	16	7.2	0.36	(6.0-9.0)	10.11					I
11	7	7.2	0.61	(6.5-9.0)	11.22					I
7	28	6.9	0.20	(5.5-8.0)	7.65					I
9	7	6.9	0.29	(6.5-7.5)	5.51					I
13	5	6.5	0.32	(6.0-7.0)	5.44					I
10	5	6.2	0.68	(5.0-7.0)	12.23					I

TABLE 5.—Concluded.

Color reflectance measured, and coded localities	N	Mean	± 2SE	Range	CV	F_s F	SS-STP
Total							
2	2	41.8	4.50	(39.5-44.0)	7.62	29.51	I
3	19	37.1	1.90	(29.0-44.5)	11.19	1.83	I I
4	16	33.2	1.66	(28.0-41.5)	9.96		I I
1	23	31.7	1.21	(26.0-35.5)	9.14		I I
12	16	28.0	1.40	(23.0-33.5)	10.00		I I
6	12	26.8	1.44	(22.5-30.5)	9.31		I
11	7	26.4	1.77	(23.5-31.0)	8.84		I
8	4	26.2	0.87	(25.5-27.5)	3.30		I
9	7	26.2	1.41	(24.0-30.0)	7.12		I
7	28	25.7	0.79	(22.0-31.5)	8.18		I
5	6	24.9	1.85	(22.5-29.0)	9.10		I
13	5	24.7	2.14	(22.0-28.0)	9.67		I
10	5	23.7	2.20	(19.5-25.5)	10.40		I

sequence of means and arrangement of maximal non-significant subsets in table 6, however, the trends in color variation in *N. micropus* take the form of gradual clines.

Qualitative Cranial Characters

Finley (1958:248-252) discussed several cranial features of woodrats that vary among taxa. Three cranial characters can be employed to distinguish skulls of *Neotoma angustipalata, N. floridana,* and *N. micropus,* although none is diagnostic. A fourth varies greatly with sex and age but is useful in skull identification. The three most useful characters, the anterior palatal spine, the posterior margin of the bony palate, and the sphenopalatine vacuities (Fig. 10), are discussed individually below and analyzed geographically. The fourth, shape of the interorbital region, was assessed in the measurement of least interorbital constriction. In *micropus,* the supraorbital region tends to be narrower and more ridged than in *floridana.* Especially in mature *micropus* males (less frequently in females), ridging is so pronounced that a structure resembling a postorbital shelf is formed. In *floridana* such a "shelf" is never present and the interorbital region usually is nearly level. Ridging between the orbits and presence of the "shelf" generally are distinctive to *micropus,* but because of variation with sex and age, absence of these characters is not distinctive to *floridana.* The number of adult *N. angustipalata* available for analysis of normal variation in the interorbital region is small; however, specimens examined tend to be more like *micropus* than *floridana* in this character.

Berry and Searle (1963) discussed occurrence and frequency in several rodent species of characters similar to the three considered below. Hedges (1969) studied such characters interspecifically and geographically in two species of *Apodemus.* These authors, and others, referred to such characters as "epigenetic characters." Berry and Searle (1963:607) stated that "many genes are concerned in the determination of each character, while environmental factors are also very important, so that the effects of individual genes cannot be isolated." I am not presently prepared to comment on the relative genetic versus environmental control of the germane characters, but planned study of these through several generations of laboratory-bred woodrats should be elucidating. Although the term "epigenetic" may well apply to characters such as these, I prefer to avoid use of the term until more is known about their developmental control and functional importance. However, "qualitative characters" is also

TABLE 6. Geographic variation in color of selected samples of *Neotoma micropus*. F_s was calculated by single classification analysis of variance. Tabular F values are at the $P<0.05$ level of significance; ns indicates no significant difference within a group of means. Non-significant subsets (as calculated by the Sums of Squares Simultaneous Testing Procedure) of significantly different groups of means are shown in the last column. See figure 8 for geographic areas included within each coded locality.

Color reflectance measured, and coded localities	N	Mean	± 2SE	Range	CV	F_s F	SS-STP
Red							
E	5	17.1	0.97	(16.5-19.0)	6.34	5.44	I
O	2	16.8	0.50	(16.5-17.0)	2.11	1.76	I I
J	2	16.8	2.50	(15.5-18.0)	10.55		I I
F	2	16.8	0.50	(16.5-17.0)	2.11		I I I
B	18	16.2	0.98	(13.0-19.5)	12.87		I I I
C	17	15.6	0.88	(13.5-19.5)	11.56		I I I
M	32	15.1	0.78	(10.5-20.5)	14.69		I I I I
A	5	14.9	0.73	(14.0-16.0)	5.51		I I I I
I	3	14.5	0.58	(14.0-15.0)	3.45		I I I I
G	2	14.2	2.50	(13.0-15.5)	12.41		I I I I
H	18	13.9	0.72	(11.5-17.0)	10.94		I I I
L	3	13.7	2.40	(12.0-16.0)	15.18		I I I
P	10	13.4	1.09	(11.5-17.0)	12.81		I I
N	23	13.1	0.66	(11.0-16.5)	12.11		I
D	12	13.1	0.81	(10.0-14.5)	10.79		I
K	13	13.0	1.08	(8.5-15.5)	14.97		I
Blue							
F	2	12.2	3.50	(10.5-14.0)	20.20	11.62	I
E	5	10.5	1.18	(9.0-12.5)	12.60	1.76	I I
O	2	10.2	1.50	(9.5-11.0)	10.35		I I
J	2	10.0	2.00	(9.0-11.0)	14.14		I I
B	18	10.0	0.56	(8.0-12.5)	11.88		I I
C	17	9.4	0.42	(8.0-11.0)	9.21		I I I
A	5	9.1	0.66	(8.0-10.0)	8.15		I I I
M	32	8.9	0.52	(7.0-13.0)	16.69		I I I
I	3	8.8	0.67	(8.5-9.5)	6.54		I I I I
G	2	8.2	1.50	(7.5-9.0)	12.86		I I I I
H	18	8.2	0.42	(7.0-10.0)	10.88		I I I
D	12	7.9	0.46	(7.0-9.5)	10.02		I I I
L	3	7.5	1.00	(7.0-8.5)	11.55		I I I
K	13	7.3	0.56	(5.0-9.0)	13.84		I I
N	23	7.3	0.34	(6.0-9.5)	11.26		I
P	10	6.8	0.44	(5.5-7.5)	10.35		I
Green							
F	2	15.0	1.00	(14.5-15.5)	4.71	11.44	I
J	2	12.8	7.50	(9.0-16.5)	41.59	1.76	I I
E	5	10.7	1.21	(9.5-13.0)	12.63		I I I
B	18	10.4	0.68	(8.5-13.5)	13.83		I I I
O	2	10.0	1.00	(9.5-10.5)	7.07		I I I I
C	17	9.6	0.44	(8.0-11.0)	9.41		I I I I I
A	5	9.5	0.63	(8.5-10.5)	7.44		I I I I I
M	32	9.2	0.57	(6.5-13.5)	17.45		I I I I I
H	18	8.7	0.47	(7.0-11.0)	11.53		I I I I I I
G	2	8.5	1.00	(8.0-9.0)	8.32		I I I I I
I	3	8.5	1.00	(8.0-9.5)	10.19		I I I I I
L	3	8.3	1.20	(7.5-9.5)	12.49		I I I I
D	12	8.2	0.57	(7.0-10.5)	12.06		I I I
K	13	7.7	0.60	(5.5-9.5)	14.18		I I
N	23	7.6	0.35	(6.0-9.5)	10.86		I
P	10	7.2	0.58	(6.0-8.5)	12.76		I

TABLE 6—Concluded.

Color reflectance measured, and coded localities	N	Mean	± 2SE	Range	CV	F_s F	SS-STP
Total							
F	2	44.0	2.00	(43.0-45.0)	3.21	8.93	I
J	2	39.5	12.00	(33.5-45.5)	21.48	1.76	I I
E	5	38.3	3.20	(35.5-44.5)	9.35		I I
O	2	37.0	3.00	(35.5-38.5)	5.73		I I I
B	18	36.0	2.21	(27.5-43.5)	13.03		I I I
C	17	34.6	1.53	(29.5-40.5)	9.11		I I I I
A	5	33.5	1.70	(30.5-35.5)	5.68		I I I I
M	32	33.1	1.77	(24.5-46.5)	15.13		I I I I
I	3	31.8	1.33	(30.5-32.5)	3.63		I I I I I
G	2	31.0	5.00	(28.5-33.5)	11.40		I I I I I
H	18	30.8	1.47	(26.5-36.5)	10.10		I I I I
L	3	29.5	1.53	(28.0-30.5)	4.48		I I I I
D	12	29.2	1.67	(25.0-34.5)	9.92		I I I
N	23	28.0	1.22	(24.0-34.0)	10.41		I I
K	13	28.0	2.16	(19.0-33.5)	13.90		I
P	10	27.5	1.74	(23.5-33.0)	10.00		I

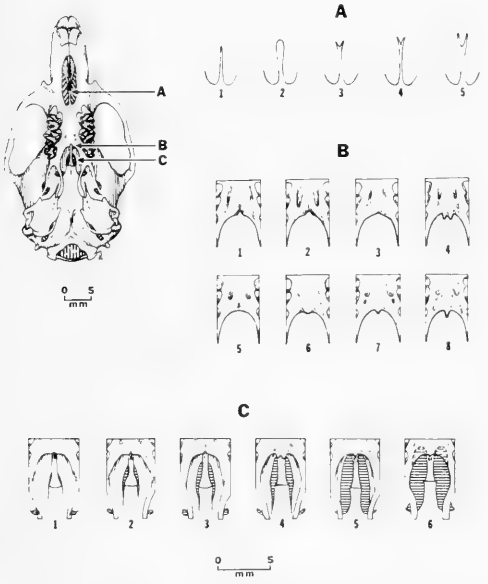

FIG. 10. Semidiagrammatic drawing of a skull of *Neotoma floridana* showing: A—anterior palatal spine; B—posterior margin of the bony palate; and C—sphenopalatine vacuities. Enlargements of A-C (scale at bottom applies to all) to the right illustrate the range of variation seen in these characters in *N. floridana* and *N. micropus*. Numbers represent sequential scoring values assigned to each character. KU numbers of skulls from which enlargements were drawn are: A—(1) 53908, (2) 3094, (3) 117335, (4) 117325, (5) 119707; B—(1) 119615, (2) 117786, (3) 117783, (4) 117324, (5) 119797, (6) 119796, (7) 119804, (8) 53906; C—(1) 16111, (2) 117774, (3) 117786, (4) 117324, (5) 119804, (6) 38922.

somewhat of a misnomer because the variation is nearly continuous and, as noted by Berry and Searle *(loc. cit.)*, must be treated by statistics rather than Mendelian methods.

Another important characteristic of woodrat skulls involves the relative development of the vomer within the narial passage and the resultant absence or presence and relative size of a maxillovomerine notch (Finley, 1958:249). In four species of *Neotoma,* the three discussed herein and *N. palatina* (Hall and Genoways, 1970), the vomerine septum is solid anterior to the palate (see also Anderson, 1969:47, Fig. 7). None of the specimens of *N. angustipalata, N. floridana,* or *N. micropus* from the Central Plains examined by me exhibit a maxillovomerine notch, but all specimens of *N. f. magister* in the Museum of Natural History of The University of Kansas have a deep notch and also lack a fork on the anterior palatal spine discussed below (but see Schwartz and Odum, 1957).

Anterior Palatal Spine.—Geographic variation in the morphology of the anterior palatal spine is shown graphically in figure 11 and in percent frequency of occurrence of the five categories (Fig. 10) in table 7. Calculations for making the pie diagrams (Fig. 11) were as follow: 1) the percent frequency of each

category was multiplied by the score shown (Table 7) for that category; 2) these values were summed for each grouped locality; 3) the lowest total was subtracted from each total; and 4) this value then was divided by the largest remaining value and converted to per cent development of the fork relative to the sample having the largest fork. This percentage value is represented by the darkened areas in the symbols of figure 11. Thus, circles that are most darkened represent samples having a greater frequency of occurrence and larger size of the fork on the palatal spine than samples from localities with more open circles.

Morphology of the anterior palatal spine varies geographically in both *N. floridana* and *N. micropus*. In *N. f. baileyi*, the bifurcate condition is observed in more than 91 percent of the specimens examined and in more than 40 percent of these the spine is classified as "large." As a result, *baileyi* represents 100 percent development for this character and the percent development for all other samples is relative to this situation in *baileyi*. Of the two specimens of *N. m. canescens* from White Sands National Monument, New Mexico (locality O, previously *N. m. leucophea*), examined for this character, neither has a fork; thus, that sample represents zero percent relative to the condition seen in *baileyi*.

TABLE 7. Percent frequency of occurrence of five morphological categories of the anterior palatal spine in 31 grouped samples of *Neotoma floridana, N. micropus,* and *N. angustipalata.* See figure 10 for illustrations of morphological categories and figure 8 for geographic areas included within each coded locality.

Locality code	*N*	Pointed (1)	Spatulate (2)	Small fork (3)	Medium fork (4)	Large fork (5)
1	49	8.16	—	8.16	40.82	42.86
2	43	9.30	—	55.82	25.58	9.30
3	79	10.13	5.06	48.10	26.58	10.13
4	69	8.70	11.60	33.33	31.88	14.49
5	12	—	—	58.33	33.34	8.33
6	67	13.43	4.48	55.23	19.40	7.46
7	63	11.11	11.11	34.92	31.75	11.11
8	73	24.66	4.11	41.09	17.81	12.33
9	93	6.45	—	13.98	47.31	32.26
10	63	17.46	—	28.57	33.33	20.64
11	27	14.82	14.82	33.33	33.33	3.70
12	50	38.00	6.00	46.00	8.00	2.00
13	17	41.18	5.88	47.06	—	5.88
A	37	97.30	—	2.70	—	—
B	98	76.53	7.14	16.33	—	—
C	117	94.02	1.71	3.42	0.85	—
D	69	92.75	1.45	4.35	—	1.45
E	23	82.61	4.35	13.04	—	—
F	55	89.09	1.82	9.09	—	—
G	37	89.19	—	10.81	—	—
H	43	86.05	—	13.95	—	—
I	108	89.81	1.85	5.56	2.78	—
J	45	95.56	—	4.44	—	—
K	35	94.28	—	2.86	2.86	—
L	50	94.00	2.00	4.00	—	—
M	71	73.24	8.45	18.31	—	—
N	44	86.36	—	13.64	—	—
O	2	100.00	—	—	—	—
P	16	87.50	6.25	—	6.25	—
Q	1	—	—	100.00	—	—
R	9	22.22	22.22	44.45	11.11	—
S	55	60.00	3.64	23.64	5.45	7.27

Only one sample of *N. micropus* (*N. m. planiceps*, locality Q) demonstrates a higher percentage than some samples of *N. floridana*. Because *planiceps* is known only by the holotype, which has a small fork on the spine, this sample is not necessarily indicative of the condition in the population. With the exception of *planiceps*, however, percent morphological development of the fork in *micropus* is consistently below 15, and populations geographically adjacent to *floridana* show no apparent increase either in the frequency of occurrence of a fork or in size of the fork as compared to those not geographically adjacent to *floridana*. A fork classified "large" is seen only in one specimen of *micropus* (KU 69604), but five other specimens from the same locality (Comanche County, Kansas) do not have forked spines. Medium-sized forks are uncommon in *micropus*, but all samples represented by more than 16 specimens have at least one individual with a bifurcated palatal spine. Grouping of samples was not conducive to demonstrating local populational variation; only one series of specimens from a single locality deviates noticeably in frequency of the palatal spine as compared to that of other specimens from the aggregate locality. Six of seven *micropus* (MHP 3377-81, 4634-35) collected on the same date from 3 mi S and 14 mi W Johnson, Stanton Co., Kansas, have small terminal forks on the anterior palatal spine. Two of five animals from other localities in Stanton County also have small forks. Therefore, although less than 10 percent of the other specimens from locality B have forked spines, 66.7 percent of those from Stanton County demonstrate the character.

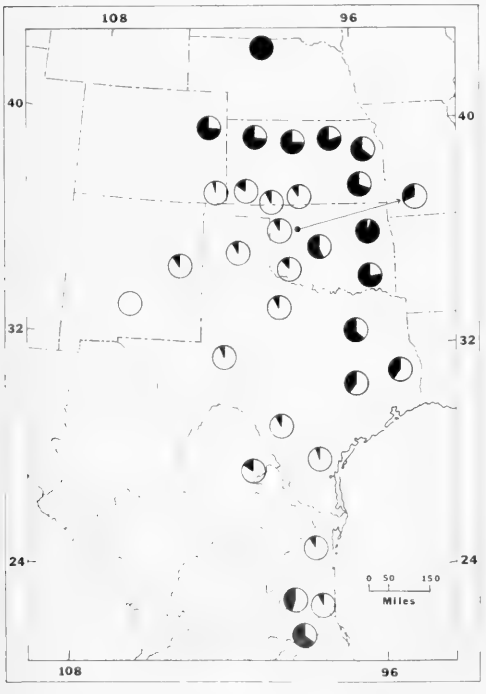

FIG. 11. Geographic variation in morphology of anterior palatal spine in three species of *Neotoma*. See figure 8 for geographic areas represented by each symbol and text for discussion of variation and calculations.

Considering intraspecific variation in *Neotoma floridana*, samples of both *campestris* and *attwateri* from Colorado and Kansas are similar, ranging from near 65 percent to 80 percent development. Of the three samples from Oklahoma, specimens from locality 10 (southeastern part of the state) have an average similar to that of samples of *floridana* from Kansas. Frequency of the fork is noticeably lower in specimens from locality 8, and even when present the forks tend to be relatively smaller. Many of the specimens in this sample originated from Blaine, Dewey, and Major counties, Oklahoma, all of which are near the known area of sympatry and natural hybridization of *floridana* with *micropus*. It should be reiterated that specimens from the locality of sympatry were not pooled with those from adjacent localities, but were treated separately as a single sample (S). The intermediacy of this sample is evident in figure 11.

Intermediacy of sample S was expected. If considered alone, the tendency toward intermediacy in sample 8 might lead to the conclusion that hybridization of the two species in central Oklahoma is introgressive. This observation must not be disregarded in evalua-

tion of the specific integrity of *floridana* and *micropus*. The importance of the reduced frequency and size of forks on the anterior palatal spine of specimens from sample 8 may be even more significant when considered in view of the high frequency of the fork on specimens from adjacent sample 9. When only specimens from Oklahoman localities 8 and 9 and the two adjacent localities for *micropus* (G and H) are considered, those from locality 8 appear almost perfectly intermediate. If these findings are interpreted as being the result of introgression, the flow of genetic materials then would appear to be eastward and not westward. However, Key (1968:19) has shown that in some instances hybrid suture zones are in a manner analogous to semipermeable membranes. If so, they probably allow flow of some genes in only one direction, others in the opposite direction, and still others to move in both directions. Lewontin and Birch (1966) have hypothesized, with supporting evidence, that a species may actually become better fit to expand its distribution as a result of having introgressed certain desirable genes from a closely related species. In neither case discussed did the original hybridizing taxa merge to form a single species.

Samples of *floridana* from Texas demonstrate the lowest percent scores of samples of that species. The sample of *N. f. rubida* (locality 13) shows least development of the spine and is not geographically adjacent to a population of *micropus*. Localities 11 and 12, however, are geographically adjacent to the range of *micropus* and the reduction in frequency and development of the fork in these populations could be interpreted as discussed above for specimens from locality 8. On the other hand, sample 8 and the Texas samples may represent no more than a geographic cline toward reduction and loss of the fork. Further interpretation must await additional material from Oklahoma and Texas as well as study of this character in eastern populations of *floridana*.

Morphology of the anterior palatal spine in *N. angustipalata* is highly variable (see Hooper, 1953:9-10, for notes on apparent excessive variation within this species), but is more similar to *floridana* than *micropus*. The presence of a small fork and the deep reentrant angle of M1 on the holotype of *N. m. planiceps* (both characters unlike typical *micropus* and resembling *angustipalata*) support my earlier suggestion that rats of these two nominal taxa may actually represent a single taxon. Additional specimens of *angustipalata* from localities in northern San Luis Potosí and more *planiceps* from near Río Verde should elucidate this question.

Because the anterior palatal spines of other species of *Neotoma* are not forked (Finley, 1958:252, reported the presence of a fork on one specimen of *N. albigula*), it seems logical to assume that the forked condition is derived, and that a pointed spine represents the original or "primitive" grade. A solid vomer is also the exception rather than the rule for *Neotoma*. Both characters apparently evolved together in the precursor of the *angustipalata-floridana-micropus* complex. Subsequently, evolution either has favored the solid vomer equally in all three species or the character was already "fixed" before speciation within the complex occurred. In the case of the forked spine, it appears that at least some members of the precursory species must have possessed the character but selection has favored it more strongly in *floridana* and *angustipalata* than in *micropus*. Alternatively, the frequency of occurrence may have been disproportionately in favor of the direct ancestors of *angustipalata* and *floridana* at the time of isolation.

Posterior Margin of Bony Palate.—Calculations of percent development of the posterior margin of the palate were conducted in a manner similar to those described for the palatal spine. Determination of sequence for scoring variation in the posterior margin of the palate was more difficult. On the palate, the

plain or rounded condition of the palatal margin probably is intermediate (primitive?) with the deep notch being one extreme (advanced?) and the large convexity being the other (also advanced?). The decision concerning which extreme to designate one and which to designate eight was arbitrary and does not imply evolutionary direction. Less arbitrary and more troublesome was the decision of scoring condition four (Fig. 10), in which two convexities form a median notch. Variation in morphology of the margin results from the manner in which the right and left halves of the developing hard palate adjoin. When a single projection is present, approximately half of the bone involved was contributed by each side of the palate. Conversely, when an indentation is present, it is because the two halves of the palate fuse anterior to the posterior margin. When two projections are present, each consists only of bone originating from a single half of the palate; the resultant "notch" between the projections clearly is homologous with the notch present in the absence of projections. Thus, two projections are homologous to the single projection characteristic of other animals. Because most (if not all) other species of woodrats tend to have either a rounded palatal margin or one with a convexity, is is most parsimonious to conclude that the notch is derived and that the double projection is an evolutionary grade in *N. f. baileyi*. It may be a condition derived from the single notch seen frequently in *N. floridana*. If the latter is the case, this condition probably should have been scored as one and placed at the left of the series. In any event, it apparently is more closely allied to the indentation than to the single convexity, and therefore, was scored as intermediate between the rounded margin and the smallest indentation.

On the average, the sample of *Neotoma micropus canescens* (locality E) from New Maxico exhibited greatest development of the posterior palatal convexity. Nearly 75 percent of specimens in that sample have convexities classified as medium or large. Therefore, this sample was established as 100 percent development of the palatal convexity. The palatal margins of specimens of *N. f. rubida* (locality 13) show the least tendency toward a convexity, with 11 of 12 specimens having an indentation and none having a convexity. Thus, sample 13 is considered zero percent relative to sample E for this character (see Table 8, and Fig. 12).

Geographic variation in the morphology of the posterior margin of the bony palate in *micropus* is slight, ranging from the established 100 percent in sample E to 75.9 percent for sample G. Intraspecific variation in *floridana* is greater than for *micropus*, ranging from the established zero percent at locality 13 to 53.7 percent at locality 5. In most samples of *floridana*, percent development of a convexity is between 10 and 30, but in three samples (1, 5, and 11) it exceeds 40 percent. In sample 1 *(baileyi)*, the high frequency (49 percent) of the double convex palatal margin discussed above accounts for the high index of development, but in samples 5 and 11, the frequency of this morph is not especially high. Both of these populations are characterized by a relatively high incidence of animals with rounded palatal margins. Rounded margins are common in laboratory hybrids having a *floridana* parent with an indentation and a *micropus* parent with a convexity. Locality 5, although adjacent in the broad sense to localities C and D, is situated geographically so that woodrats from there are not currently in contact with any population of *micropus*. If the two species occurred together in the vicinity of the Arkansas River at some date in the past (prior to settlement of the area by European man), it seems plausible that the intermediacy of population 5 could be the result of previous hybridization between the two species. However, specimens from locality 5 demonstrate no morphological or other proclivities toward *micropus* in other characters, and

TABLE 8. Percent frequency of occurrence of eight morphological categories of the posterior margin of the bony palate in 31 grouped samples of *Neotoma floridana, N. micropus,* and *N. angustipalata.* See figure 10 for illustrations of morphological categories and figure 8 for geographic areas included within each coded locality.

Locality code	*N*	Deep indentation (1)	Medium indentation (2)	Small indentation (3)	Indentation in convexity (4)	Rounded (5)	Small convexity (6)	Medium convexity (7)	Large convexity (8)
1	51	----	1.96	7.84	49.02	29.41	11.77	----	----
2	38	----	5.26	52.63	10.54	28.94	2.63	----	----
3	71	----	8.45	59.15	1.41	30.99	----	----	----
4	46	----	10.87	43.48	----	43.48	2.17	----	----
5	13	----	----	7.69	7.69	69.23	15.39	----	----
6	66	----	10.61	37.88	7.58	43.93	----	----	----
7	65	----	10.77	52.31	12.31	21.53	3.08	----	----
8	39	----	15.38	46.15	10.26	23.08	5.13	----	----
9	27	3.70	11.11	70.37	----	14.82	----	----	----
10	19	----	15.79	57.89	5.26	10.53	10.53	----	----
11	19	----	15.26	36.84	10.53	42.11	5.26	----	----
12	43	----	9.30	58.14	----	30.23	2.33	----	----
13	12	16.67	16.67	58.33	----	8.33	----	----	----
A	36	----	2.78	2.78	----	25.00	36.11	19.44	13.89
B	102	----	----	0.98	----	21.57	52.94	21.57	2.94
C	126	----	----	----	----	22.22	39.68	33.34	4.76
D	70	----	----	----	1.43	22.86	52.85	12.86	10.00
E	23	----	----	----	----	13.04	13.04	47.83	26.09
F	55	----	----	----	----	12.72	43.65	30.91	12.72
G	35	----	----	----	----	42.86	28.57	28.57	----
H	42	----	----	----	2.38	21.44	33.33	33.33	9.52
I	110	----	----	----	----	28.18	46.36	19.09	6.36
J	45	----	----	----	----	22.22	31.11	37.78	8.89
K	35	----	----	----	----	14.29	54.28	28.57	2.86
L	51	----	----	----	----	15.69	54.90	25.49	3.92
M	74	----	----	----	----	4.05	58.11	31.08	6.76
N	46	----	----	----	----	17.39	58.69	19.57	4.35
O	3	----	----	----	----	----	66.67	----	33.33
P	18	----	----	----	----	33.33	38.89	22.22	5.56
Q	1	----	----	----	----	----	100.00	----	----
R	8	----	----	----	----	25.00	62.50	12.50	----
S	53	----	13.21	18.87	5.66	43.39	11.32	5.66	1.89

the sample is relatively small (13 individuals). Probably it is best not to attribute the deviation seen in this population to past or present hybridization, but rather to interpret it either as a local population phenomenon or an artifact of the small sample.

Interpretation of palatal morphology in sample 11 is more difficult and may represent one result of hybridization of *floridana* and *micropus* in north-central Texas. Specimens of this sample also tend toward *micropus* with respect to the anterior palatal spine discussed above. As mentioned elsewhere, a sample of *floridana* from southwest of Dallas, Texas, was nearly intermediate in color between the two species (see beyond under discussion of results of discriminant function analysis). Specimens from locality 8, which show a marked tendency toward *micropus* in morphology of the anterior palatal spine, do not differ noticeably in morphology of the posterior palatal margin from specimens from localities remote from the range of *micropus*. Specimens from the locality of sympatry (sample S) are approximately intermediate between the adjacent populations of the two species in average morphology, but demonstrate a range of variation from medium indentations to large convexities. Increased variation in a hybrid population is, of course, to be expected. With respect to this character, specimens of the species *angustipalata* are more like *micropus* than *floridana*.

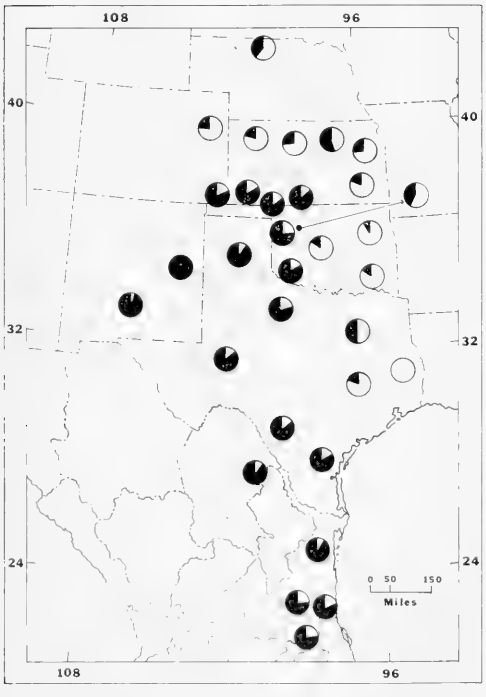

FIG. 12. Geographic variation in morphology of the posterior margin of the bony palate in three species of *Neotoma*. See figure 8 for geographic areas represented by each symbol and text for discussion of variation and calculations.

Sphenopalatine Vacuities.—Variation in form and size of the sphenopalatine vacuities was scored and treated in a manner similar to that explained previously. The range of observed variation and values assigned to each category are shown in figure 10; percent frequency of each category for each sample is shown in table 9, and the relative size of the vacuities for each population is shown geographically in figure 13. On the average, vacuities in specimens from locality G are largest. That sample was set as the standard of 100 percent development. Vacuities of specimens from locality 4 are smallest on the average, and were set at zero percent relative to the vacuities of animals from sample G.

The average size of the sphenopalatine vacuities is markedly different in samples of *micropus* as compared to that of *floridana;* samples of the former range from 60.3 percent *(N. m. planiceps)* to 100 percent (sample G), whereas those of *floridana* range from zero percent (locality 4) to 50.6 percent for sample 1 *(N. f. baileyi). Neotoma angustipalata* is highly variable with respect to morphology of the vacuities; it is clearly *floridana*-like when averages are considered. Specimens from the locality of sympatry (sample S) are intermediate (58.6 percent), but on the average nearer *micropus* than *floridana*.

Size of the sphenopalatine vacuities in specimens of *baileyi* is appreciably larger on the average than those of other

TABLE 9. Percent frequency of occurrence of six morphological categories of the sphenopalatine vacuities in 31 grouped samples of *Neotoma floridana*, *N. micropus*, and *N. angustipalata*. See figure 10 for illustrations of morphological categories and figure 8 for geographic areas included within each coded locality.

Locality code	*N*	Closed (1)	Minute (2)	Small (3)	Medium (4)	Large (5)	Very large (6)
1	47	----	----	44.68	38.30	17.02	----
2	38	----	23.68	44.74	23.68	7.90	----
3	63	----	23.81	55.56	15.87	4.76	----
4	44	----	72.73	27.27	----	----	----
5	12	----	25.00	66.67	8.33	----	----
6	59	1.70	22.03	67.80	8.47	----	----
7	56	1.79	41.07	51.78	5.36	----	----
8	27	----	18.52	59.26	22.22	----	----
9	13	----	15.38	84.62	----	----	----
10	12	----	8.33	75.00	16.67	----	----
11	16	----	25.00	75.00	----	----	----
12	41	----	36.58	53.66	9.76	----	----
13	12	8.33	33.33	41.67	16.67	----	----
A	34	----	----	5.88	44.12	41.18	8.82
B	87	----	----	2.30	29.88	66.67	1.15
C	78	----	----	1.28	12.82	79.49	6.41
D	43	----	----	2.33	41.86	43.48	2.33
E	14	----	----	14.29	50.00	28.57	7.14
F	16	----	----	12.50	56.25	31.25	----
G	14	----	----	----	21.43	42.86	35.71
H	30	----	----	10.00	23.33	63.34	3.33
I	2	----	----	----	50.00	50.00	----
J	18	----	----	5.56	50.00	38.88	5.56
K	19	----	----	----	36.84	42.11	21.05
L	10	----	----	20.00	60.00	10.00	10.00
M	55	----	----	----	21.82	76.36	1.82
N	37	----	----	16.22	56.75	27.03	----
O	3	----	----	----	66.67	33.33	----
P	15	----	----	20.00	26.67	33.33	20.00
Q	1	----	----	----	100.00	----	----
R	8	12.50	25.00	25.00	25.00	12.50	----
S	40	----	5.00	20.00	50.00	25.00	----

members of the species. The presence of relatively large vacuities, two marginal convexities on the palate, and a large palatal fork is more or less characteristic of members of the subspecies, and generally will suffice to distinguish the skull of a specimen of *baileyi* from skulls of *campestris* or *attwateri*. The relative distinctiveness of *baileyi* undoubtedly has resulted from the present state of isolation. It is possible that these cranial characters of *baileyi* are indicative of the more primitive condition of the species at the time *baileyi* became established in north-central Nebraska. However, it is equally plausible that the subspecies has differentiated during isolation and that the present state of these characters represents a derived condition. The well-developed fork on the anterior palatal spine would appear to be the latter situation, but the unique (possibly intermediate) palatal margin and intermediate-sized vacuities likely are the former.

Other samples of *N. floridana* do not differ appreciably from each other. Both samples 8 and 11, which deviate noticeably in one and both, respectively, of the characters discussed above, are below 20 percent in total development and show no noticeable tendency toward the adjacent populations of *N. micropus*.

Intraspecific variation in the size of the sphenopalatine vacuities in *micropus*

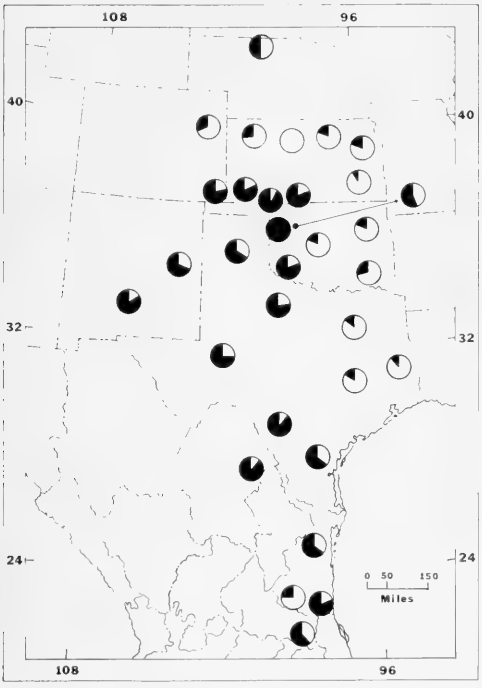

FIG. 13. Geographic variation in morphology of the sphenopalatine vacuities in three species of *Neotoma*. See figure 8 for geographic areas represented by each symbol and text for discussion of variation and calculations.

also is minor. When the sample of one individual for *N. m. planiceps* is disregarded, the sample most like *floridana* is sample L (63.8 percent). This sample is from an area geographically adjacent to part of the range of *floridana*. However, percent values of other samples, such as N (64.1 percent) and F (66.9 percent), are not appreciably higher than that of specimens from locality L. Therefore, I do not think that the 63.8 percent value calculated for sample L can be interpreted as evidence of hybridization or introgression. It also is noteworthy that sample G, set at 100 percent, is geographically adjacent to the hybrid zone in Oklahoma and to locality 8, which is somewhat *micropus*-like in other characters, and yet by definition is the sample least *floridana*-like for this character.

In summation for all characters labeled as qualitative cranial characters, it is noted that some samples from localities geographically adjacent to those of the other species deviate sufficiently toward the other species morphologically in one or at most two characters to warrant consideration of introgressive hybridization. However, these deviate samples can be interpreted without invoking introgression. Thus it probably is best to interpret these data otherwise until additional evidence clearly indicates that hybridization between *floridana* and *micropus* is or has been introgressive. In no case did all three characters vary in a manner that would indicate random gene flow, but the possibility of limited or directional gene flow was considered and left open. All three characters serve well to distinguish the skulls of the three species, but none is diagnostic. The three characters considered together usually suffice to distinguish *N. f. baileyi* from other subspecies of *N. floridana*.

Baculum

Burt and Barkalow (1942:290-295) first described the bacula of *N. floridana* and *N. micropus*, and compared the bacula of these two species with that of *N. albigula*. On the basis of their conclusion that the baculum of *micropus* is intermediate between the bacula of the other two species, these authors removed *micropus* from the *floridana* species-group and established a *micropus* species-group.

Burt (1960:60) later indicated that the bacula of *micropus* and *floridana* are similar and not distinguishable with certainty. Hooper (1960:4-6) described and compared the phalli and bacula of *floridana*, *micropus*, and *albigula* and found them similar, but reported "fewer distinctions between *floridana* and *micropus*." He further considered *floridana* to be intermediate in this character between the other two species. Alvarez (1963: 452) found that although the baculum of *N. angustipalata* is narrower and longer on the average, it resembles that of *N. micropus*.

The baculum of *albigula* is not considered here, but those of *angustipalata*,

floridana, and *micropus* were compared. Although the bacula of all three differ little, that of *floridana* usually can be distinguished from those of the other two species by its rectangular base as compared to a triangular base in both *angustipalata* and *micropus.* Individual variation of size and morphology overlaps among individuals of the three species. When measurements for several individuals (two to five in all samples except that of *angustipalata,* which was represented by the bone of a single individual) were averaged and the width of the base plotted against the length of the base, a separation obtains among the species (Fig. 14). The baculum of *N. m. micropus* from southern Tamaulipas (locality P, formerly *N. m. littoralis*) tends more toward that of *floridana* than do the bacula of specimens of *micropus* from any other locality. In all dimensions, the two bacula available from sample P are the largest studied. Besides the minor differences in color, the differences in size and to a lesser extent shape of the bacula were the only ways in which animals from locality P (previously *N. m. littoralis*) were found to differ from those from locality N.

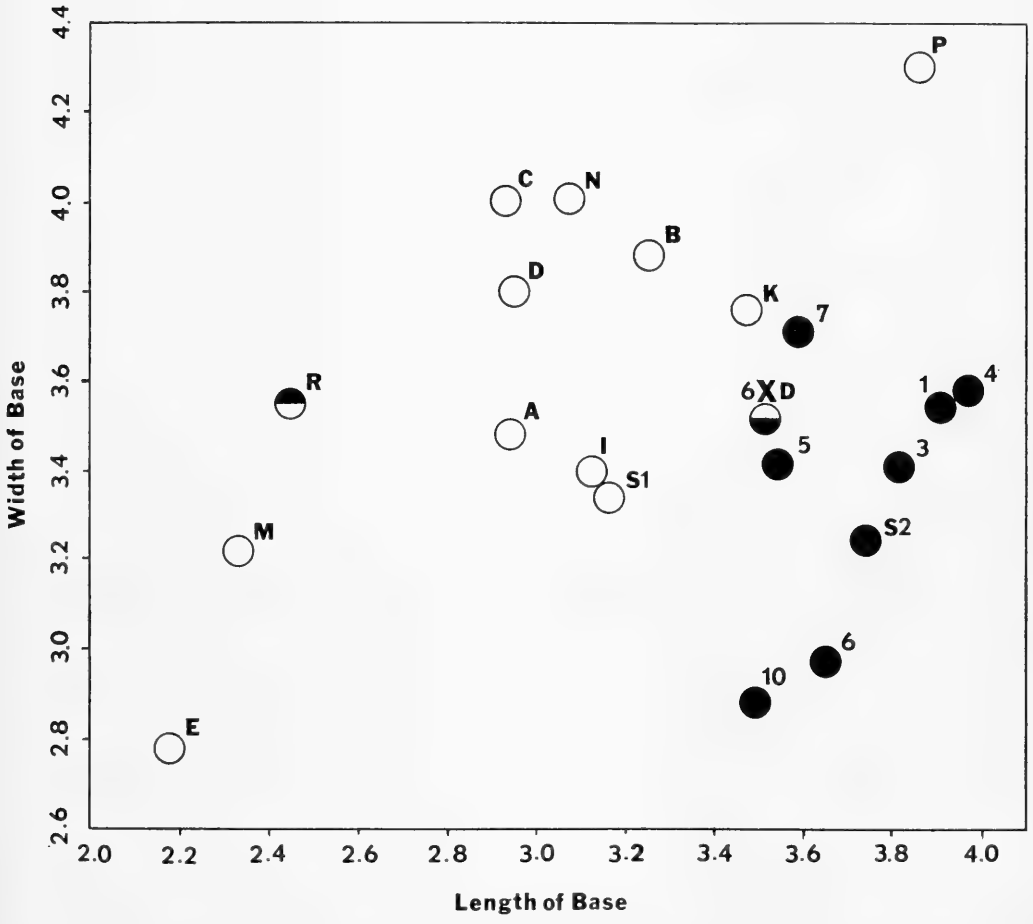

FIG. 14. Scatter diagram comparing bacular measurements of selected samples of *Neotoma angustipalata, N. floridana,* and *N. micropus.* See figure 8 for areas included within coded localities. "S1" and "S2" represent samples of *micropus*-like and *floridana*-like woodrats, respectively, from the same locality; "6 X D" is a sample of laboratory bred F_1 hybrids whose parents were from localities 6 and D.

The bacula of four adult F_1 hybrids between *micropus* from locality D and *floridana* from locality 6 also were measured, averaged, and plotted in the diagram. This sample was plotted in a position nearly intermediate between the parental populations, but more like *floridana* if all localities are considered. The intermediacy in the bacula of hybrids demonstrates the assumed genetic basis for determination of the shape of the bone.

Because woodrats from the locality of sympatry, 3 mi S Chester, Major Co., Oklahoma, were identified by characters of the skin and skull, but not the baculum, the three specimens most like *floridana* (S1) were averaged independently from the five most like *micropus* (S2). When plotted as above, the S1 sample appears to be typical of *floridana* and gives no indication of effects of hybridization. Sample S2 plots in a position marginal to other samples of *micropus,* but clearly more like *micropus* than *floridana.* Bacular measurements of woodrats from other localities do not indicate any obvious intraspecific or geographic trends nor do they seem to be noticeably correlated to any of the other measurements and characters studied. In most instances the baculum of *floridana* can be distinguished from that of *micropus* or *angustipalata,* but no completely diagnostic differences exist in the morphology or size of the bone.

Univariate Analyses of Mensural Characters

The four external and ten cranial measurements described previously were analyzed by Powers' UNIVAR Program in univariate assessment of geographic variation. This was done separately for each sex and each species, then separately for each sex with samples of both species treated simultaneously. These results are discussed below, in a consideration of general trends of geographic variation. A more detailed evaluation that includes discussion of each measurement and subset relationships of group-means as determined by SS-STP (as included exemplarily below for total length) may be found elsewhere (Birney, 1970).

Neotoma floridana.—Standard statistics computed on measurements of specimens from the 13 pooled localities of *Neotoma floridana* are shown in table 10. Interlocality variation in the measurements of total length is significantly ($P < 0.01$) different for both sexes. For males, localities are separated into two broadly overlapping, non-significant subsets (hereafter called subsets) indicating that animals from southeastern Texas (*N. f. rubida,* locality 13) and from southeastern Kansas (locality 7) are significantly larger than those from localities 6 (northeastern Kansas) and 9 (northeastern Oklahoma). Males from locality 12 (southern Texas), adjacent on the west to locality 13, also are large. Males from sample 7 are significantly larger than those from both adjacent localities (6 and 9), but not significantly larger than those from non-adjacent localities. In females, variation in total length is similar to that for males, but group-means separated into five subjects with females from locality 5 being significantly larger than those from localities 8, 6, 10, and 9 (hereafter written as locality $5 > 8, 6, 10, 9$), locality $13 > 6, 10, 9$ and locality $12 > 9$. The only adjacent localities showing significant differences are 5 and 6, the two samples from north-central and northeastern Kansas.

Hind foot length in both sexes is greatest in *N. f. campestris* and the sample of *N. f. attwateri* (5) that is geographically contiguous with *campestris.* Ear length is not significantly different for group-means in either sex. Coefficients of variation for external measurements are high compared to those for cranial measurements. Although analyses of these characters are indicative of total size relationships, they probably are less reliable than analyses of cranial dimensions. Differences that may actually exist in external size are difficult to document statistically because unre-

TABLE 10. Geographic variation in 14 external and cranial measurements of *Neotoma floridana* from Nebraska, Colorado, Kansas, Oklahoma, and Texas. See figure 8 for geographic areas included within each coded locality.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
				Total length				
1	7	381.3	10.04	(361.0-398.0)	9	374.4	9.88	(350.0-393.0)
2	9	379.6	11.04	(350.0-398.0)	8	365.8	9.40	(344.0-382.0)
3	12	385.1	10.25	(341.0-408.0)	19	376.4	6.57	(349.0-409.0)
4	9	379.4	18.10	(345.0-434.0)	14	363.2	10.65	(340.0-402.0)
5	2	386.5	21.00	(376.0-397.0)	2	397.0	26.00	(384.0-410.0)
6	5	357.4	11.60	(342.0-370.0)	8	354.0	14.83	(329.0-395.0)
7	14	394.3	14.22	(349.0-450.0)	12	371.8	9.41	(340.0-397.0)
8	15	380.0	11.99	(350.0-425.0)	9	357.1	10.87	(334.0-379.0)
9	20	359.5	7.70	(323.0-397.0)	17	349.3	12.05	(308.0-392.0)
10	12	377.0	11.29	(334.0-400.0)	13	352.1	9.82	(320.0-374.0)
11	8	369.4	20.56	(328.0-420.0)	8	374.1	19.55	(322.0-340.0)
12	7	388.0	25.61	(317.0-414.0)	8	384.6	11.96	(356.0-412.0)
13	4	407.0	18.20	(387.0-430.0)	5	396.0	27.33	(368.0-442.0)
				Length of tail vertebrae				
1	7	159.7	10.20	(138.0-176.0)	9	161.7	9.00	(136.0-180.0)
2	9	155.0	8.76	(130.0-167.0)	8	157.2	4.81	(146.0-168.0)
3	12	161.3	8.94	(120.0-178.0)	19	158.5	4.06	(144.0-175.0)
4	9	156.1	6.34	(139.0-174.0)	14	149.9	5.54	(136.0-172.0)
5	2	159.5	29.00	(145.0-174.0)	2	164.5	17.00	(156.0-173.0)
6	5	148.6	6.65	(139.0-156.0)	8	150.8	6.16	(142.0-169.0)
7	14	162.9	3.74	(153.0-175.0)	12	161.5	4.32	(148.0-170.0)
8	15	160.7	6.79	(149.0-185.0)	9	154.4	6.07	(137.0-165.0)
9	20	155.8	5.39	(132.0-176.0)	16	150.3	5.52	(136.0-170.0)
10	12	162.2	5.30	(143.0-172.0)	13	151.0	4.59	(138.0-163.0)
11	9	153.7	13.65	(130.0-195.0)	8	162.9	9.01	(138.0-174.0)
12	7	168.4	9.08	(147.0-181.0)	8	173.2	6.48	(156.0-185.0)
13	3	174.0	21.63	(159.0-195.0)	5	188.2	11.30	(175.0-207.0)
				Length of hind foot				
1	8	39.8	0.60	(38.0-41.0)	11	39.1	0.51	(38.0-41.0)
2	10	41.8	1.26	(39.0-44.0)	8	39.5	0.65	(38.0-41.0)
3	15	39.9	1.12	(36.0-43.0)	19	39.8	0.77	(36.0-42.0)
4	11	40.1	1.06	(36.0-42.0)	15	38.7	0.67	(36.0-40.0)
5	3	41.0	1.15	(40.0-42.0)	2	42.0	0.00	(42.0-42.0)
6	6	39.3	1.91	(36.0-42.0)	10	36.8	1.36	(34.0-40.0)
7	15	39.3	0.64	(37.0-42.0)	11	39.3	0.90	(37.0-42.0)
8	14	39.5	1.75	(36.0-49.0)	10	37.5	1.31	(35.0-42.0)
9	20	38.2	0.74	(35.0-41.0)	13	37.2	0.82	(35.0-40.0)
10	10	38.6	1.53	(35.0-43.0)	13	38.2	1.14	(35.0-42.0)
11	9	38.0	1.37	(34.0-41.0)	8	38.5	1.65	(35.0-42.0)
12	7	39.1	1.41	(37.0-42.0)	11	39.3	1.01	(36.0-42.0)
13	4	38.8	1.50	(38.0-41.0)	4	38.0	2.58	(35.0-41.0)
				Length of ear				
1	2	27.5	3.00	(26.0-29.0)	5	26.6	1.20	(25.0-28.0)
2	4	27.8	1.71	(26.0-30.0)	6	26.0	0.89	(25.0-28.0)
3	6	28.8	1.89	(26.0-33.0)	9	28.7	1.05	(27.0-32.0)
4	10	28.0	1.26	(25.0-31.0)	10	28.0	0.99	(25.0-30.0)
5	3	26.3	2.40	(24.0-28.0)	2	29.0	0.00	(29.0-29.0)
6	6	26.7	1.33	(25.0-29.0)	7	25.9	1.54	(23.0-28.0)
7	11	27.0	1.14	(25.0-30.0)	8	28.2	2.95	(25.0-38.0)
8	11	27.7	0.66	(26.0-30.0)	4	26.2	2.06	(24.0-29.0)
9	16	27.9	0.97	(25.0-32.0)	11	27.4	1.91	(25.0-36.0)
10	10	27.2	1.07	(25.0-30.0)	12	26.8	0.96	(25.0-29.0)
11	8	28.5	1.00	(27.0-30.0)	5	27.0	3.03	(21.0-29.0)

TABLE 10.—Continued.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
12	3	27.7	5.33	(25.0-33.0)	3	26.7	3.33	(25.0-30.0)
13	3	31.7	2.91	(29.0-34.0)	3	30.3	2.91	(28.0-33.0)
				Greatest length of skull				
1	7	48.4	1.11	(46.5-50.7)	11	48.8	0.44	(47.5-49.7)
2	7	49.6	2.06	(46.0-53.8)	6	48.9	0.87	(47.5-50.6)
3	12	51.1	0.81	(48.9-53.4)	18	49.7	0.72	(47.0-53.3)
4	9	51.4	1.41	(48.4-55.2)	11	49.7	0.74	(48.3-52.1)
5	3	51.3	2.66	(49.1-53.7)	2	51.2	1.20	(50.6-51.8)
6	5	50.1	1.58	(48.0-51.7)	10	48.6	0.94	(47.0-52.2)
7	15	50.8	0.91	(47.4-53.5)	11	50.2	0.79	(48.6-52.1)
8	15	50.5	1.13	(47.1-54.0)	8	48.6	1.00	(46.8-50.7)
9	16	50.2	0.82	(47.1-52.9)	14	48.2	0.84	(45.3-51.4)
10	13	50.2	0.69	(48.2-52.4)	13	48.3	1.01	(45.0-50.8)
11	9	49.6	1.75	(44.4-53.0)	8	50.7	0.70	(49.5-51.9)
12	9	51.6	1.09	(49.8-54.0)	8	50.4	1.27	(47.9-53.2)
13	5	53.0	1.39	(50.7-54.5)	4	52.3	1.31	(51.0-54.1)
				Condylobasilar length				
1	7	47.4	1.17	(45.7-49.8)	11	47.4	0.55	(46.0-48.9)
2	9	48.6	1.71	(44.5-52.9)	7	47.6	0.77	(46.4-48.9)
3	13	49.5	0.89	(47.3-52.3)	14	47.8	0.73	(45.2-50.9)
4	9	50.6	1.47	(47.6-54.3)	12	48.6	0.81	(47.4-51.6)
5	3	49.3	3.27	(47.7-52.6)	2	50.1	1.20	(49.5-50.7)
6	5	49.3	1.61	(47.1-51.1)	10	47.2	0.99	(45.6-51.2)
7	15	49.5	0.99	(46.1-52.2)	11	49.0	0.93	(47.3-51.7)
8	16	49.2	1.15	(45.2-53.2)	8	47.2	0.93	(44.9-48.8)
9	19	48.8	0.81	(45.5-52.4)	13	46.9	0.87	(50.0-54.0)
10	13	48.9	0.74	(47.1-51.0)	11	46.7	1.26	(42.9-49.3)
11	10	48.0	1.50	(43.2-50.9)	8	49.0	0.72	(47.6-50.5)
12	9	50.1	1.29	(48.1-52.4)	10	48.4	1.04	(46.3-51.2)
13	5	50.6	1.63	(47.4-52.0)	5	49.4	1.98	(46.4-52.6)
				Zygomatic breadth				
1	7	25.9	0.61	(24.8-27.1)	11	26.1	0.27	(25.4-26.6)
2	8	26.9	0.72	(25.4-28.6)	7	26.4	0.49	(25.2-27.0)
3	12	27.4	2.14	(26.2-28.3)	15	26.8	0.44	(25.1-28.0)
4	10	27.8	1.02	(25.5-29.9)	12	27.1	0.67	(25.9-29.6)
5	2	27.4	2.00	(26.4-28.4)	2	27.4	0.70	(27.1-27.8)
6	6	27.0	1.03	(25.7-28.9)	10	26.5	0.51	(25.6-28.3)
7	13	27.9	0.53	(25.9-29.2)	12	27.3	0.49	(26.2-29.1)
8	16	26.9	0.68	(24.4-29.0)	6	26.6	0.91	(25.4-28.1)
9	18	26.9	0.51	(24.4-28.9)	15	26.1	0.58	(24.0-27.9)
10	13	27.1	0.55	(25.2-28.5)	14	26.1	0.51	(23.3-27.1)
11	9	27.1	1.20	(22.8-29.3)	8	27.6	0.54	(26.1-28.3)
12	8	27.0	0.86	(25.5-28.7)	10	26.9	0.63	(25.5-29.2)
13	4	27.7	0.80	(26.6-28.5)	5	26.8	1.15	(25.5-28.4)
				Least interorbital constriction				
1	9	6.9	1.70	(6.6-7.4)	11	6.6	0.15	(6.3-7.0)
2	10	6.9	0.24	(6.4-7.7)	8	6.6	0.17	(6.2-6.9)
3	14	7.0	0.15	(6.4-7.5)	19	6.8	0.16	(6.1-7.5)
4	12	6.7	0.13	(6.4-7.0)	13	6.6	0.13	(6.2-6.9)
5	3	6.8	0.07	(6.8-6.9)	2	6.6	0.10	(6.5-6.6)
6	6	6.6	0.16	(6.4-7.0)	11	6.5	0.15	(6.2-6.9)
7	16	6.7	0.22	(6.0-7.8)	12	6.6	0.21	(6.1-7.2)
8	18	6.8	0.18	(6.2-7.6)	10	6.7	0.24	(6.1-7.2)
9	22	6.7	0.14	(5.8-7.2)	17	6.5	0.15	(6.1-7.3)
10	15	6.9	0.16	(6.5-7.5)	13	6.6	0.14	(6.2-7.2)

TABLE 10.—Continued.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
11	10	6.7	0.26	(6.0-7.2)	9	6.9	0.16	(6.5-7.2)
12	9	6.8	0.23	(5.2-7.5)	11	7.0	0.24	(6.4-7.7)
13	5	7.0	0.19	(6.8-7.3)	5	6.9	0.24	(6.7-7.3)
				Breadth at mastoids				
1	8	19.0	0.51	(18.0-20.4)	11	19.0	0.27	(18.2-19.6)
2	8	19.2	0.83	(17.4-20.7)	7	18.9	0.37	(18.1-19.3)
3	13	19.7	0.30	(18.7-20.5)	15	19.2	0.30	(18.1-20.2)
4	11	20.3	0.63	(18.5-22.4)	14	19.7	0.34	(18.7-21.0)
5	2	19.8	0.70	(19.5-20.2)	2	20.0	0.50	(19.7-20.2)
6	5	19.5	0.76	(18.5-20.6)	11	19.0	0.44	(17.8-20.1)
7	15	20.0	0.55	(16.9-21.0)	12	19.4	0.42	(18.2-20.4)
8	18	19.6	0.31	(18.2-20.7)	8	19.2	0.41	(18.5-20.2)
9	18	19.3	0.22	(18.7-20.2)	14	18.8	0.39	(16.5-19.6)
10	15	19.8	0.31	(19.0-20.9)	13	19.0	0.28	(18.1-19.6)
11	8	19.6	0.72	(17.4-20.6)	8	19.8	0.18	(19.4-20.1)
12	8	20.0	0.49	(19.0-21.0)	10	19.8	0.51	(18.8-21.6)
13	5	20.5	0.68	(19.5-21.6)	5	19.4	0.55	(18.5-20.0)
				Length of rostrum				
1	8	18.9	0.43	(17.8-19.6)	11	18.8	0.32	(17.5-19.4)
2	8	19.5	0.91	(18.0-21.9)	8	18.9	0.65	(17.3-20.0)
3	14	19.9	0.41	(18.7-21.2)	19	19.3	0.39	(17.8-21.1)
4	12	20.3	0.69	(17.9-22.9)	14	19.4	0.28	(18.7-20.5)
5	3	20.1	1.10	(19.2-21.1)	2	20.6	0.30	(20.4-20.7)
6	6	19.2	0.99	(17.7-20.5)	10	18.8	0.40	(18.1-20.0)
7	16	19.8	0.46	(18.1-21.5)	11	19.5	0.39	(18.6-20.6)
8	17	20.0	0.49	(18.4-21.6)	9	19.1	0.51	(18.2-20.4)
9	19	19.6	0.42	(18.2-21.1)	17	18.7	0.35	(17.3-19.9)
10	15	19.5	0.36	(18.2-20.4)	13	18.6	0.50	(16.4-19.5)
11	9	19.3	0.81	(17.0-21.0)	9	19.9	0.43	(19.0-20.6)
12	9	20.3	0.58	(19.1-21.7)	8	19.7	0.50	(18.9-20.7)
13	5	21.2	0.61	(20.1-21.9)	4	20.4	0.34	(19.9-20.7)
				Breadth of rostrum				
1	9	7.9	0.17	(7.5-8.2)	18	7.9	0.13	(7.5-8.2)
2	9	8.2	0.58	(6.1-9.0)	8	8.1	0.16	(7.7-8.4)
3	15	8.7	0.15	(8.3-9.2)	17	8.4	0.18	(7.9-9.4)
4	12	8.5	0.36	(7.6-9.3)	15	8.5	0.14	(7.9-9.0)
5	3	8.3	0.35	(8.0-8.6)	2	8.5	0.00	(8.5-8.5)
6	6	8.1	0.36	(7.6-8.7)	10	8.0	0.15	(7.7-8.3)
7	15	8.4	0.22	(7.5-9.1)	11	8.2	0.14	(7.8-8.5)
8	18	8.2	0.21	(7.6-9.0)	10	8.0	0.20	(7.5-8.5)
9	22	8.0	0.15	(7.4-8.7)	17	7.8	0.14	(7.3-8.2)
10	15	7.9	0.17	(7.3-8.5)	13	7.8	0.17	(7.4-8.3)
11	10	8.0	0.24	(7.1-8.4)	9	8.2	0.21	(7.7-8.7)
12	8	8.2	0.31	(7.5-8.7)	10	8.4	0.33	(7.5-9.2)
13	5	8.2	0.34	(7.8-8.6)	5	8.3	0.27	(7.9-8.7)
				Length of maxillary toothrow				
1	9	9.5	0.20	(9.2-10.0)	11	9.4	0.17	(8.8-9.9)
2	10	9.3	0.23	(8.9-10.0)	8	9.4	0.38	(8.9-10.5)
3	15	9.9	0.18	(9.4-10.4)	19	9.7	0.12	(9.2-10.0)
4	12	9.6	0.19	(9.1-10.0)	15	9.7	0.16	(9.1-10.3)
5	3	9.6	0.64	(9.0-10.0)	2	9.8	0.40	(9.6-10.0)
6	6	9.7	0.28	(9.3-10.0)	11	9.3	0.21	(8.8-9.9)
7	16	9.5	0.18	(9.0-10.2)	12	9.4	0.23	(8.7-10.1)
8	19	9.6	0.15	(8.7-10.2)	10	9.4	0.26	(8.9-10.1)
9	22	9.3	0.15	(8.8-9.9)	17	9.2	0.14	(8.7-9.6)

TABLE 10.—Concluded.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
10	15	9.2	0.20	(8.5-9.8)	14	9.4	0.14	(9.0-9.9)
11	8	9.4	0.26	(8.8-9.9)	9	9.4	0.24	(8.9-10.0)
12	9	9.0	0.28	(8.3-9.4)	11	9.1	0.22	(8.4-9.7)
13	5	9.6	0.19	(9.4-9.9)	5	9.4	0.43	(8.8-9.9)
				Length of palatal bridge				
1	9	8.7	0.33	(8.2-9.6)	11	8.7	0.34	(7.3-9.2)
2	9	8.5	0.30	(7.6-9.0)	8	8.1	0.28	(7.5-8.7)
3	15	8.8	0.23	(7.9-9.6)	19	8.4	0.15	(7.8-9.0)
4	12	8.9	0.37	(7.9-9.8)	15	8.6	0.24	(8.0-9.4)
5	3	8.7	0.74	(8.2-9.4)	2	8.8	0.40	(8.6-9.0)
6	6	8.5	0.35	(7.9-9.0)	11	8.4	0.27	(7.6-9.0)
7	16	8.8	0.20	(8.1-9.6)	12	8.7	0.16	(8.3-9.3)
8	18	8.6	0.32	(7.2-9.6)	10	8.3	0.18	(7.8-8.7)
9	22	8.5	0.23	(7.6-9.7)	16	8.2	0.21	(7.5-9.0)
10	15	8.3	0.12	(7.9-8.8)	14	8.5	0.21	(7.6-9.0)
11	10	8.7	0.39	(7.8-9.5)	9	8.7	0.32	(8.1-9.5)
12	9	8.5	0.36	(7.7-9.4)	10	8.4	0.45	(7.3-9.8)
13	5	8.7	0.15	(8.6-9.0)	5	8.7	0.61	(7.9-9.7)
				Length of nasals				
1	8	18.7	0.43	(17.6-19.4)	11	18.7	0.33	(18.0-20.2)
2	8	19.3	0.89	(17.7-20.9)	8	19.0	0.48	(18.0-20.3)
3	14	19.5	0.45	(18.3-20.9)	19	19.0	0.37	(17.6-20.3)
4	12	20.3	0.71	(18.5-23.3)	14	19.4	0.34	(18.5-20.4)
5	3	20.5	1.33	(19.3-21.6)	2	20.6	0.50	(20.3-20.8)
6	6	19.4	0.70	(18.5-20.7)	9	18.7	0.40	(17.8-19.5)
7	15	19.9	0.42	(18.0-21.6)	11	19.5	0.47	(18.6-21.3)
8	17	20.0	0.51	(17.7-21.5)	9	19.3	0.41	(18.3-20.5)
9	19	19.8	0.49	(17.8-21.6)	17	18.7	0.42	(16.7-20.2)
10	15	19.7	0.47	(18.2-20.9)	14	18.8	0.55	(16.5-19.8)
11	9	19.4	0.99	(17.3-21.9)	9	20.1	0.49	(18.9-21.1)
12	9	20.5	0.68	(19.2-22.1)	8	19.9	0.47	(18.8-20.7)
13	5	21.7	0.94	(20.4-23.3)	4	21.1	0.73	(20.2-22.0)

lated factors contribute to within-group variation. Thus, trends in external characters are not shown graphically, although some of the observed trends were not evinced by studies of cranial dimensions.

Standard statistics and geographic variation in greatest length of skull are illustrated as a graphic example of variation in a longitudinal cranial measurement (Fig. 15, males; Fig. 16, females). Results of SS-STP tests for this measurement for both sexes are shown in table 11. Table 12 illustrates observed results of samples of *floridana* and *micropus* tested together. Also included are comparisons of subset relationships involving additional variance between groups, and results of SS-STP testing for greatest length of skull for both species treated simultaneously.

Comparisons of males show that specimens from locality 11 are the smallest end of a gradual north to south cline in greatest length of skull. Females from locality 11 are noticeably larger than those from localities immediately to the north and more nearly equivalent in size to samples 12 and 13 from farther south and east in Texas. Otherwise, males and females are more or less similar with expected minor shifts in sequence of means.

Condylobasilar length was expected to differ little from greatest length of skull because both are measurements of the long axis of the skull. However, a remarkable amount of shifting in sequence of means is evident between the

TABLE 11. Results of SS-STP tests comparing means of greatest length of skull for males and females separately from 13 localities of *Neotoma floridana* and 14 localities for *N. micropus*. See figure 8 for geographic areas included within each coded locality.

Males								Females							
Locality code	Mean	Maximal non-significant subsets						Locality code	Mean	Maximal non-significant subsets					
Neotoma floridana															
13	53.0	I						13	52.3	I					
12	51.6	I	I					5	51.2	I	I				
4	51.4	I	I					11	50.7	I	I				
5	51.3	I	I					12	50.4	I	I	I			
3	51.1	I	I					7	50.2	I	I	I	I		
7	50.8	I	I					4	49.7	I	I	I	I	I	
8	50.5	I	I					3	49.7	I	I	I	I	I	
9	50.2	I	I					2	48.9	I	I	I	I	I	
10	50.2	I	I					1	48.8		I	I	I	I	
6	50.1	I	I					8	48.6		I	I	I	I	
2	49.6	I	I					6	48.6			I	I	I	
11	49.6	I	I					10	48.3				I	I	
1	48.4		I					9	48.2					I	
Neotoma micropus															
L	51.0	I						D	49.7	I					
H	50.6	I	I					C	48.8	I	I				
D	50.5	I	I	I				B	48.8	I	I				
C	49.7	I	I	I	I			L	48.6	I	I	I			
G	49.6	I	I	I	I	I		I	48.5	I	I	I			
A	49.4	I	I	I	I	I		G	48.3	I	I	I	I		
B	49.2	I	I	I	I	I	I	F	47.7	I	I	I	I		
K	48.7	I	I	I	I	I	I	H	47.6	I	I	I	I		
I	48.3		I	I	I	I	I	K	47.1	I	I	I	I		
F	48.1		I	I	I	I	I	M	46.7		I	I	I		
J	47.9			I	I	I	I	A	46.5			I	I		
N	46.8				I	I	I	J	46.2				I		
P	46.6					I	I	P	45.8				I		
M	46.6						I	N	45.7				I		

two characters. Also, no significant differences were detected in group-means of males for condylobasilar length.

No significant differences exist among group-means for zygomatic breadth of males. Although specimens of *rubida* (13) are larger, on the average, than individuals from more northerly samples of the species in the measurements of longitudinal axis of the skull, they are narrower in zygomatic breadth than males from localities 7 and 4 (Fig. 17). However, the differences are not significant. Highly significant ($P < 0.01$) differences were detected in zygomatic breadth of females (Fig. 18).

Least interorbital constriction is one of the least variable measurements considered for *N. floridana*. Group-means are not significantly different for males, and sequence of means for this character (Fig. 19, males; Fig. 20, females) does not follow that seen in other measurements for either sex. The pattern of geographic variation in mastoidal breadth closely approximates that seen for zygomatic breadth.

Woodrats from localities 3, 4, and 5 (the two samples of *campestris* from northwestern Kansas and the sample of *attwateri* from adjacent north-central Kansas) are generally larger in breadth of rostrum than are woodrats from southern Texas (12 and 13). In measurements of length, specimens from locality 13 are consistently larger than specimens from northern Kansas. It is visually perceptible that the skulls of specimens of

campestris tend to be broader, more heavily structured and robust than those of *rubida*. To a lesser extent the same differences prevail between *campestris* and *attwateri* with the exception of specimens from locality 5. The latter are like other samples of *attwateri* in color, but in several aspects of overall size and general shape of the skull, they more closely resemble *campestris*.

Patterns of variation for alveolar length of the maxillary toothrow are similar to those of rostral breadth, but unique in certain aspects. Notably, specimens from locality 12 are smallest both for males and females, whereas those from localities 1 *(baileyi)* and 6 (northeastern Kansas), which are among the smallest in most dimensions, are relatively much larger. Results of computations for this measurement also are somewhat unique in that more total variation exists between means of males than between those of females.

Of the dimensions analyzed, palatal bridge length demonstrates the least amount of geographic variation. Group-means are not significantly different for males and are significant only at the 0.05 level for females. Coefficients of variation for measurements of this character are noticeably larger than for other cranial dimensions. The reduction in significant geographic variation in length of palatal bridge may be a result of high within-group variation.

Geographic variation in nasal length exceeds that for other cranial dimensions. Geographic trends for this demension are similar to those for length of rostrum. These two measurements include the same region of the skull, but

TABLE 12. Results of SS-STP tests comparing means of greatest length of skull for males and females treated separately and localities of *Neotoma floridana* and *N. micropus* tested simultaneously. See figure 8 for geographic areas included within each coded locality.

Males			Females		
Locality code	Mean	Maximal non-significant subsets	Locality code	Mean	Maximal non-significant subsets
13	53.0	I	13	52.3	I
12	51.6	I I	5	51.2	I I
4	51.4	I I	11	50.7	I I I
5	51.3	I I	12	50.4	I I I I
3	51.1	I I	7	50.2	I I I I I
L	51.0	I I I	4	49.7	I I I I I I
7	50.8	I I I I	D	49.7	I I I I I I
H	50.6	I I I I I	3	49.7	I I I I I I I
D	50.5	I I I I I	2	48.9	I I I I I I I I
8	50.5	I I I I I	C	48.8	I I I I I I I I
9	50.2	I I I I I I	B	48.8	I I I I I I I I
10	50.2	I I I I I I I	1	48.8	I I I I I I I I
6	50.1	I I I I I I I	8	48.6	I I I I I I I I I
C	49.7	I I I I I I I	L	48.6	I I I I I I I I
G	49.6	I I I I I I I I	6	48.6	I I I I I I I I
2	49.6	I I I I I I I I	I	48.5	I I I I I I I I I
11	49.6	I I I I I I I I	G	48.3	I I I I I I I I I
A	49.4	I I I I I I I I	10	48.3	I I I I I I I I
B	49.2	I I I I I I I I	9	48.2	I I I I I I I I
K	48.7	I I I I I I I	F	47.7	I I I I I I I
1	48.4	I I I I I I I	H	47.6	I I I I I I I
I	48.3	I I I I I I	K	47.1	I I I I I I
F	48.1	I I I I I	M	46.7	I I I I I
J	47.9	I I I I	A	46.5	I I I I
N	46.8	I I I	J	46.2	I I I
P	46.6	I I	P	45.8	I I
M	46.6	I	N	45.7	I

differ in that rostral length is in part dependent on shape of the anterior end of the zygomatic arch.

When all measurements are considered, there is general agreement between the patterns of variation as indicated by separate analyses of males and females except for specimens from locality 11 (northern Texas). Males from that locality are smaller (as determined by rank-order scoring of means for the 14 characters) than samples of males from all localities except northeastern Oklahoma (9). Rank-order scores of males from localities 9, 11, 6, and 1 were so close as to be indistinguishable by this method of analysis. In comparisons of females, however, specimens from locality 11 were surpassed in total size only by those from samples 5 and 13.

When the rank-order scores for males and females are summed, a general trend of geographic variation for *floridana* in the Central Great Plains can be seen. *Neotoma floridana rubida* is slightly larger than any of the samples of *attwateri* or *campestris,* and appreciably larger than *baileyi.* Specimens of *campestris* from localities in Kansas are larger than those from Colorado and larger than specimens of *attwateri* from all except adjacent localities in north-central Kansas. Within the subspecies *attwateri,* there is appreciable variation in size, but this variation does not follow expected trends. Specimens from north-central Kansas (5) are largest, followed in sequence by those from southern Texas (12), southeastern Kansas (7), and western Oklahoma (8). Specimens from eastern Oklahoma (9 and 10) and northeastern Kansas (6) are the smallest examples of the subspecies. *Neotoma floridana baileyi* is slightly larger than the smaller representatives of *attwateri,* but smaller than the larger representatives of that subspecies. The only contiguous localities from which samples of specimens frequently are significantly different in size are those in north-central Kansas (5) and northeastern Kansas (6). However, on the basis of color, specimens from these localities are similar and individuals in both samples are significantly darker than specimens of *campestris.*

Neotoma micropus and *N. angustipalata.*—In univariate analysis of geographic variation in *Neotoma micropus* and *N. angustipalata,* specimens from localities O (White Sands National Monument, New Mexico) and Q (Río Verde, San Luis Potosí) were not included in UNIVAR computations because only single specimens were available. Sample R *(N. angustipalata)* was not included because only one adult specimen of each sex was available at the time UNIVAR analyses were conducted. Subsequently, two additional adult females were examined and included with calculations of standard statistics shown in table 13. Sample E (*N. m. canescens* from New Mexico) also was omitted from UNIVAR analyses because New Mexico was not included in the study area at the time computations were conducted. Standard statistics of this sample are shown in table 13. In all four instances, sequence of means were considered for rank-order analysis of trends in size variation, but significance levels are not known for these four samples.

Considering the remaining 14 samples of *N. micropus,* differences in group-means of total length are not significant for males, but they are significant ($P < 0.05$) for females. Specimens from localities N and P (coastal Tamaulipas) are relatively large in this character, whereas those from adjacent Coahuila and Nuevo León are small. Specimens of both sexes from localities P and N *(N. m. micropus)* have the longest tails of any samples of the species. This is in marked disagreement with trends in cranial measurements, wherein specimens of *N. m. micropus* are among the smallest. Furthermore, they exhibit a marked tendency toward being unicolored, especially in southern parts of Tamaulipas.

Although somewhat variable and less reliable than cranial measurements, external dimensions demonstrate certain overall trends. The two samples com-

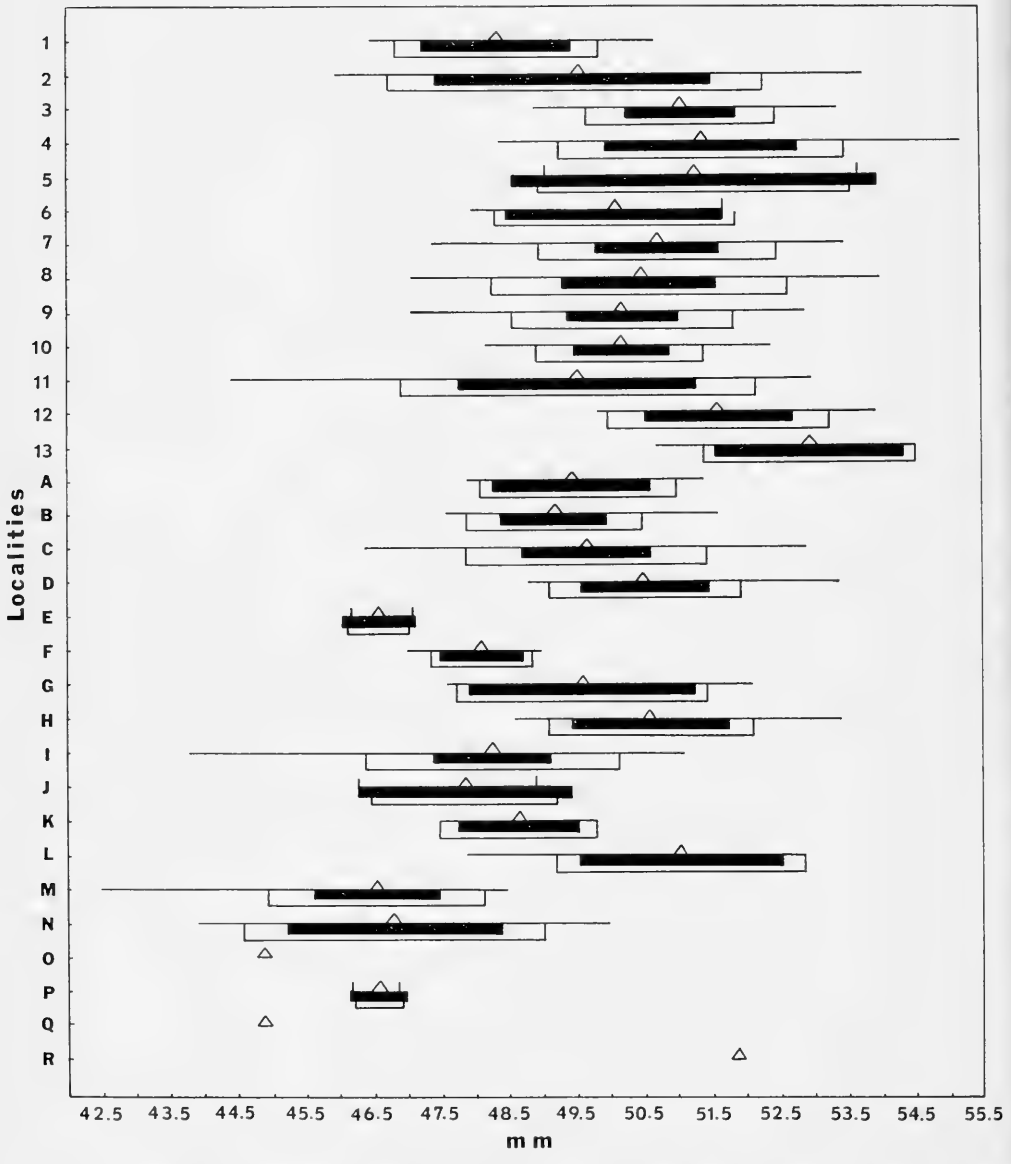

FIG. 15. Dice-grams illustrating geographic variation in greatest length of skull of male *Neotoma angustipalata, N. floridana,* and *N. micropus.* The upper point of the triangle is the arithmetic mean; the darkened bar is plus and minus two standard errors of the mean; the open bar is plus and minus one standard deviation of the mean, and the horizontal or vertical lines indicate the range. See figure 8 for geographic areas included within the coded localities indicated on the ordinate.

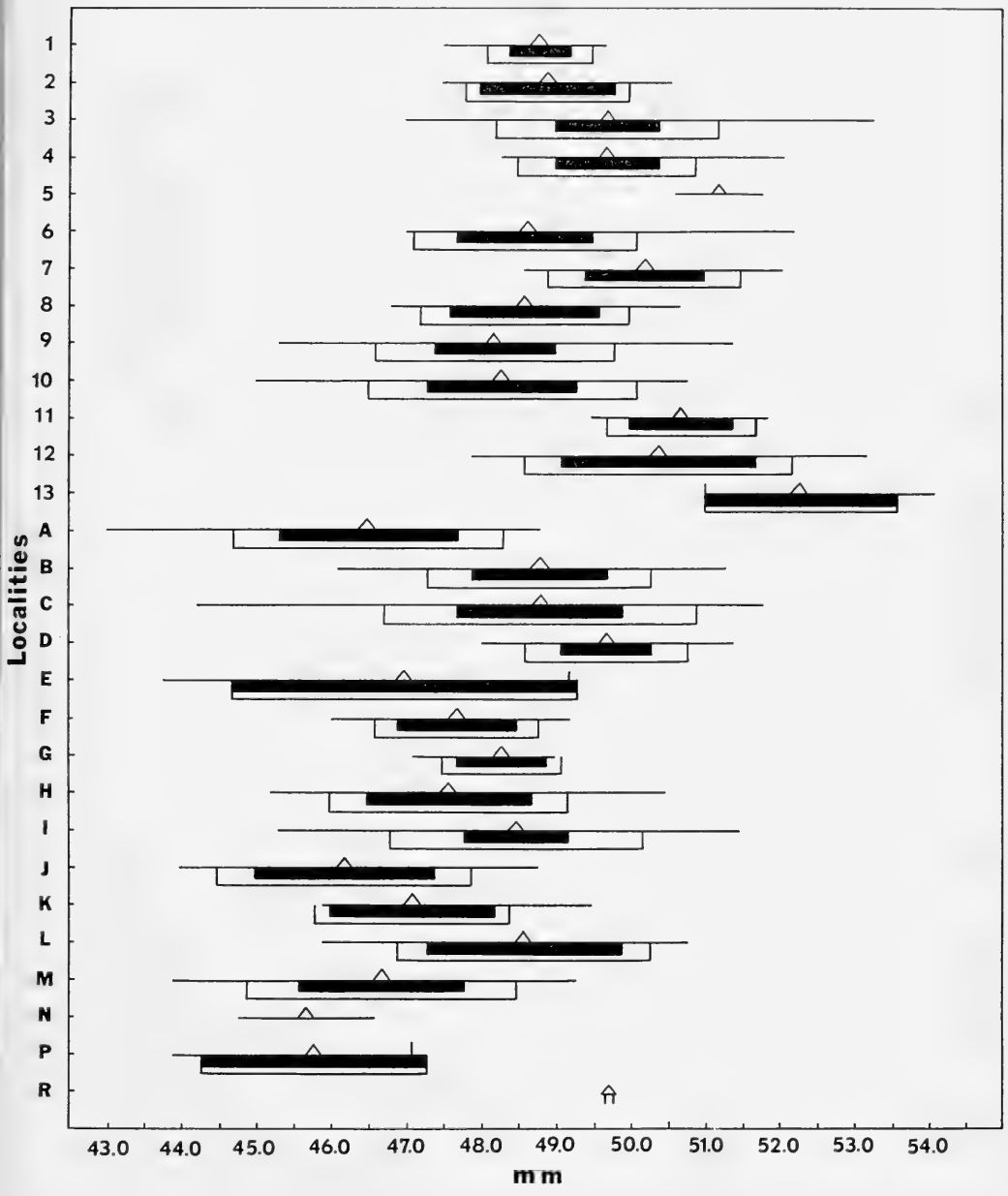

FIG. 16. Dice-grams illustrating geographic variation in greatest length of skull of female *Neotoma angustipalata, N. floridana,* and *N. micropus.* See figure 15 for explanation of symbols and figure 8 for geographic areas included within the coded localities indicated on the ordinate.

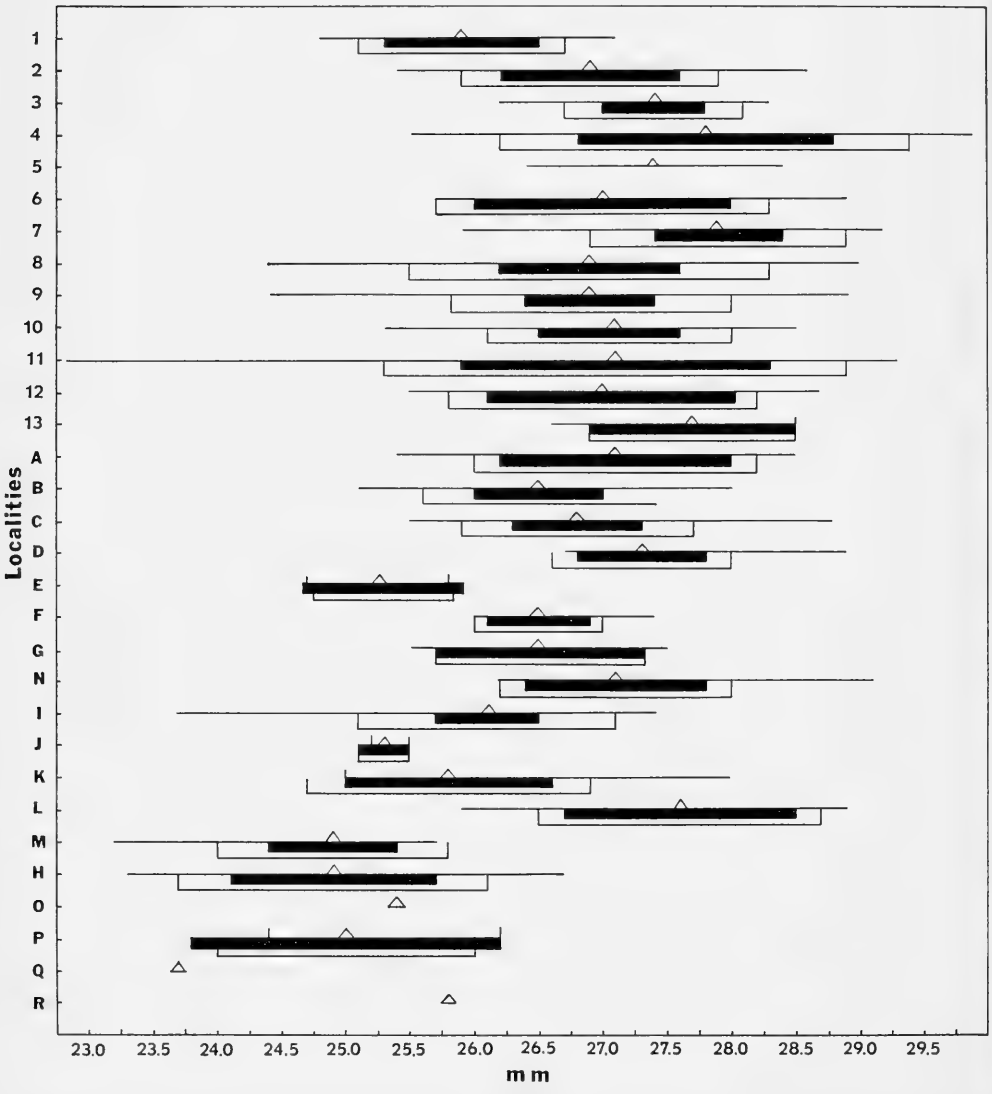

FIG. 17. Dice-grams illustrating geographic variation in zygomatic breadth of male *Neotoma angustipalata, N. floridana,* and *N. micropus.* See figure 15 for explanations of symbols and figure 8 for geographic areas included within the coded localities indicated on the ordinate.

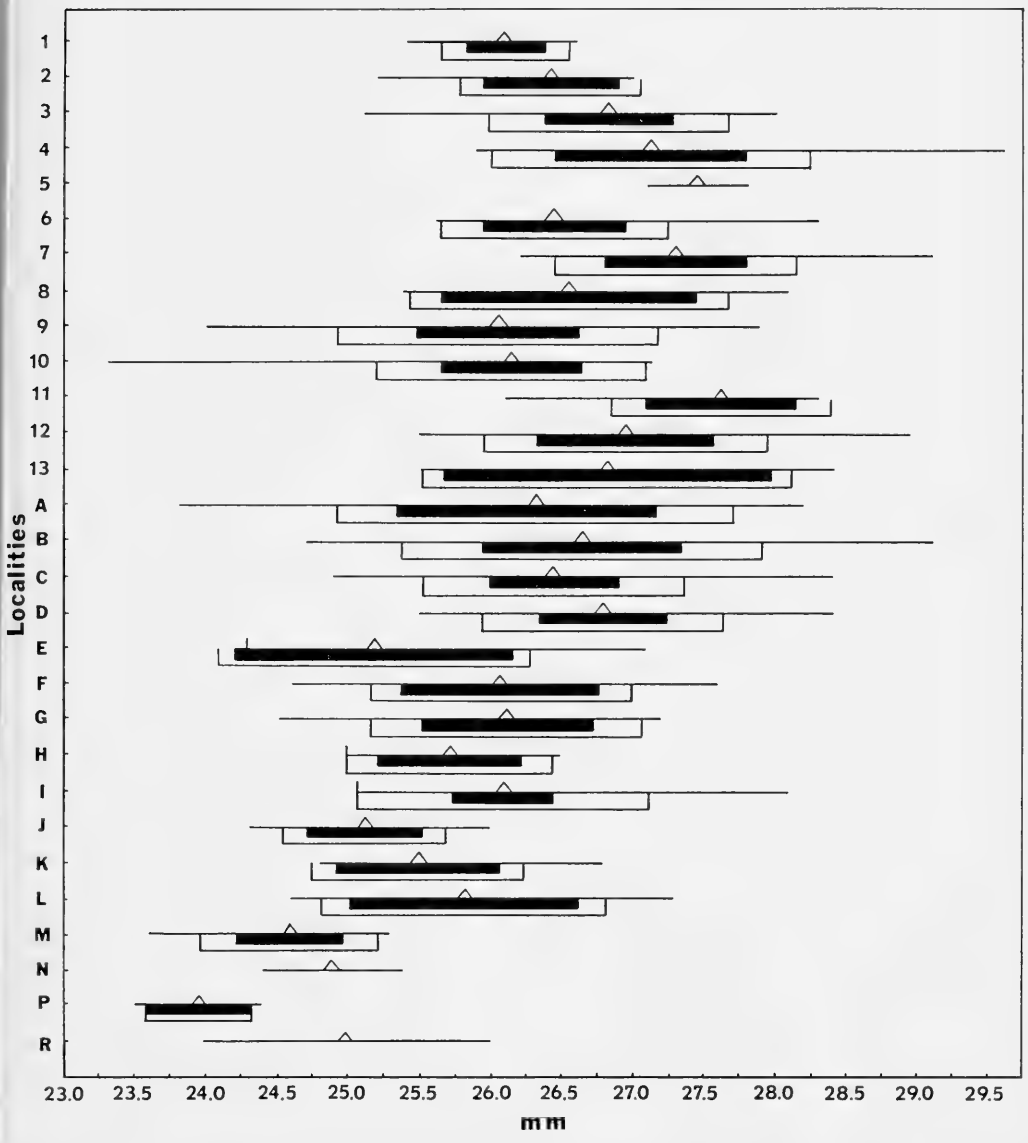

FIG. 18. Dice-grams illustrating geographic variation in zygomatic breadth of female *Neotoma angustipalata*, *N. floridana*, and *N. micropus*. See figure 15 for explanation of symbols and figure 8 for geographic areas included within the coded localities indicated on the ordinate.

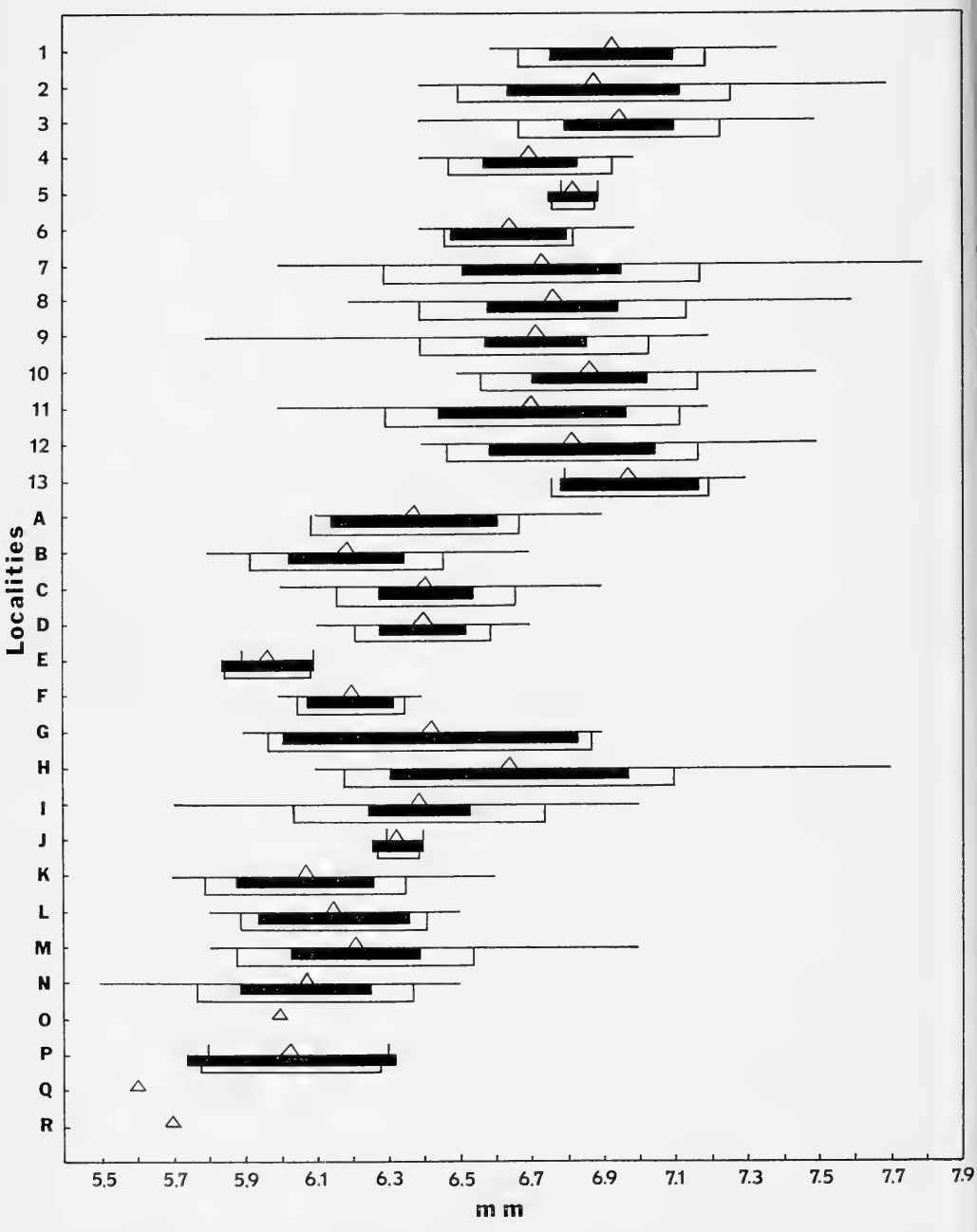

FIG. 19. Dice-grams illustrating geographic variation in least interorbital constriction of male *Neotoma angustipalata*, *N. floridana*, and *N. micropus*. See figure 15 for explanation of symbols and figure 8 for geographic areas included within the coded localities indicated on the ordinate.

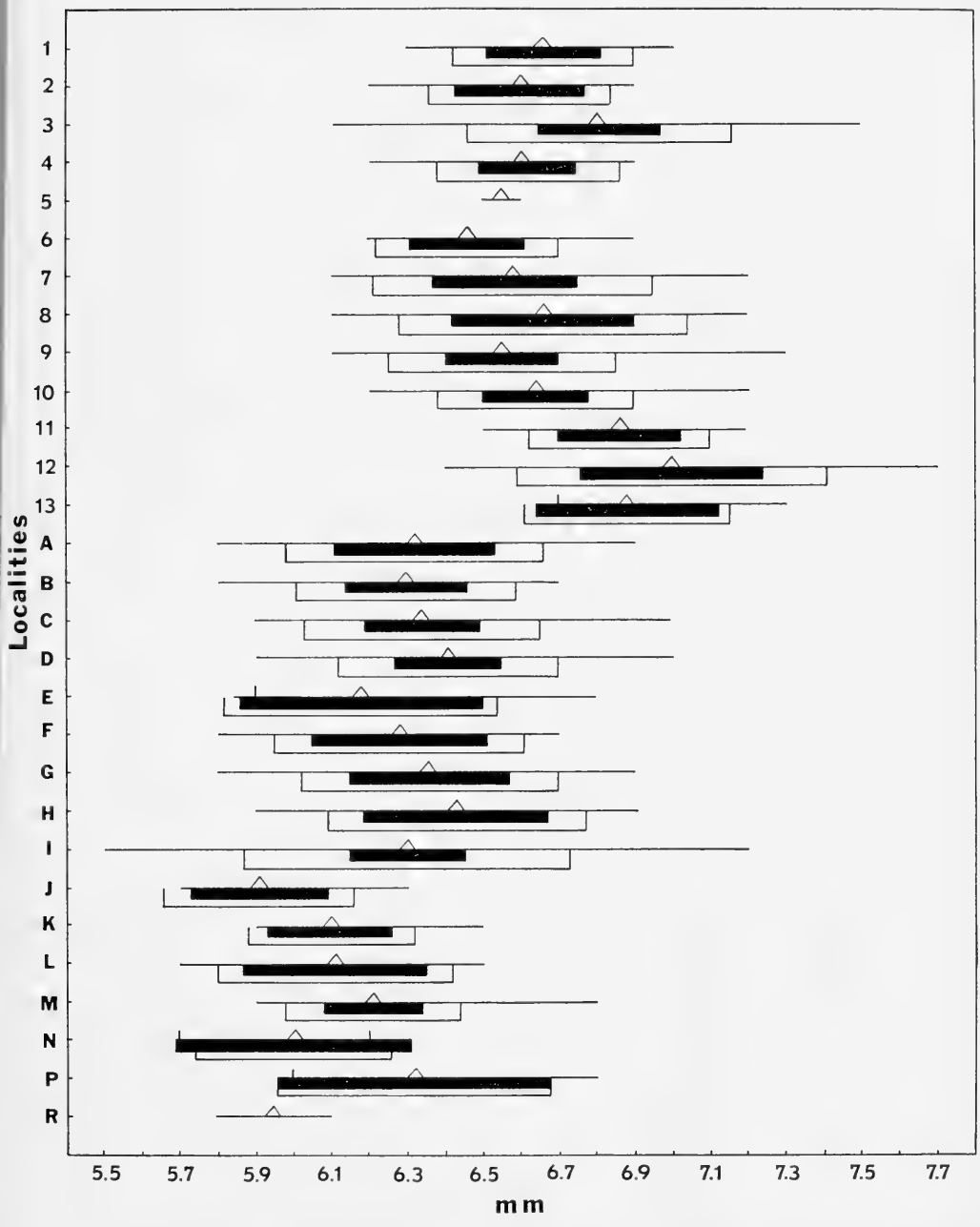

FIG. 20. Dice-grams illustrating geographic variation in least interorbital constriction of female *Neotoma angustipalata*, *N. floridana*, and *N. micropus*. See figure 15 for explanation of symbols and figure 8 for geographic areas included within the coded localities indicated on the ordinate.

posed of largest individuals (exclusive of the tail) tend to be L and D. Locality L is composed of specimens from along the Gulf Coast of Texas and D represents specimens from south-central Kansas. Specimens from localities N and P (*N. m. micropus*) have noticeably longer tails than even the samples of *N. m. canescens* characterized by large size. Specimens from southwestern Texas, in the general region of the Big Bend area (J), appear smallest in external characters.

Geographic variation in greatest length of skull is shown graphically for *Neotoma micropus* in figures 15 (males) and 16 (females). Results of SS-STP tests illustrating maximally connected non-significant subsets for this dimension are given in table 11 for tests conducted only on the specimens of *N. micropus* from grouped localities, and in table 12 for tests made when specimens from grouped localities of *N. floridana* and *N. micropus* were tested simultaneously. Means of samples of the two species overlap broadly, but samples shown to be significantly different by the two methods are generally the same.

The pattern of geographic variation seen in this measurement is typical of most cranial measurements. The samples of largest woodrats are from localities L (southern coastal Texas), C, D, and G (south-central Kansas and adjacent western Oklahoma inclusive of the panhandle). The smallest are *N. m. micropus* (N and P) from Tamaulipas and *N. m. canescens* from samples J (southwest Texas) and M (Coahuila and Nuevo León). Specimens from other localities tend to form gradual clines with the large and small samples listed above. The single exception is the marked change in size between specimens from coastal Texas (*N. m. canescens*, locality L) and northern Tamaulipas (*N. m. micropus*, locality N).

Specimens of both sexes from localities in Colorado, Kansas, northern Texas, and Oklahoma generally are larger in condylobasilar length than those from southern localities, including sample I (northeastern part of the range in Texas just south of the Red River). The only breaks in this trend result from the large size of specimens from the Gulf Coast of Texas and the relatively small size of females (A) from Colorado. Geographic trends in zygomatic breadth are shown in figures 17 (males) and 18 (females). Except the females from Colorado (A) appear larger and more nearly the size of females from other northern localities, these are comparable to those discussed for condylobasilar length.

Trends in geographic variation of the least interorbital constriction are shown in figures 19 (males) and 20 (females). This dimension differs from other cranial characters of *micropus* in three respects. First, variation in group-means is not significant for females. Second, means of both sexes from locality L are relatively low, placing this population more nearly with others in the southern part of the distribution rather than with the larger northern populations. Thirdly, specimens from locality H, which generally are intermediate in size (especially females), have the broadest average interorbital constriction. Interorbital constriction is consistently broader in *floridana* than *micropus*, and the possibility exists that the wide constriction in specimens of *micropus* from these localities has resulted from introgression of *floridana* genes.

The pattern of variation for breadth at the mastoids is typical of most cranial measurements save for the unusually large size of specimens from localities A and B. Analysis of rostral length, especially for males, exemplifies the north to south and east to west clines in diminishing size. The pattern of geographic variation in rostral breadth deviates from this general trend of variation in the large size of males from locality J (southwestern Texas). In other characters, woodrats from locality J tend to be more like the smaller woodrats from western and southern parts of the range of the species.

Variation in alveolar length of maxil-

TABLE 13. Geographic variation in 14 external and cranial measurements of *Neotoma micropus* and *N. angustipalata*. See figure 8 for geographic areas included within each coded locality.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
Locality								
A	3	360.1	10.73	(353.0-371.0)	10	348.5	12.74	(318.0-372.0)
B	8	364.4	17.76	(340.0-410.0)	13	357.3	8.08	(323.0-381.0)
C	15	373.1	11.13	(334.0-411.0)	18	354.8	8.62	(310.0-382.0)
D	8	374.8	12.45	(351.0-404.0)	14	362.3	10.52	(337.0-398.0)
E	3	321.0	16.04	(305.0-330.0)	5	329.0	18.25	(310.0-354.0)
F	7	362.7	10.58	(340.0-380.0)	8	358.5	12.46	(333.0-378.0)
G	4	363.5	8.89	(355.0-376.0)	10	353.9	8.21	(328.0-373.0)
H	5	363.2	12.42	(348.0-385.0)	7	341.7	11.14	(311.0-355.0)
I	23	358.4	10.21	(317.0-398.0)	30	345.3	9.32	(303.0-400.0)
J	4	358.2	10.72	(350.0-374.0)	8	330.1	12.16	(310.0-352.0)
K	7	350.3	23.44	(302.0-380.0)	7	351.3	22.63	(304.0-390.0)
L	6	378.0	22.72	(348.0-422.0)	8	365.9	18.16	(319.0-388.0)
M	12	345.4	1.12	(302.0-368.0)	12	339.2	9.40	(313.0-366.0)
N	9	370.3	9.78	(349.0-390.0)	2	361.5	23.00	(350.0-373.0)
0	1	318.0	---	(--- ---)	0	---	---	(--- ---)
P	3	364.3	2.40	(362.0-366.0)	4	354.5	24.84	(333.0-377.0)
Q	1	351.0	---	(--- ---)	0	---	---	(--- ---)
R	1	402.0	---	(--- ---)	3	390.3	25.36	(365.0-404.0)
				Length of tail vertebrae				
A	3	139.7	4.81	(135.0-143.0)	10	139.6	4.29	(130.0-150.0)
B	8	145.2	7.28	(131.0-160.0)	13	144.8	4.36	(130.0-157.0)
C	15	156.6	5.99	(135.0-175.0)	18	148.8	5.51	(130.0-165.0)
D	8	147.0	9.19	(120.0-164.0)	14	148.7	5.77	(126.0-168.0)
E	3	127.7	7.51	(121.0-134.0)	5	133.8	7.60	(126.0-144.0)
F	7	146.3	6.34	(133.0-156.0)	8	152.9	7.68	(138.0-170.0)
G	4	149.0	3.74	(145.0-154.0)	10	150.2	4.99	(136.0-162.0)
H	5	147.4	10.97	(136.0-165.0)	7	149.6	5.40	(138.0-159.0)
I	22	146.0	4.98	(129.0-166.0)	30	144.8	5.39	(120.0-195.0)
J	4	148.5	8.19	(140.0-156.0)	8	137.4	10.65	(110.0-153.0)
K	7	149.7	10.62	(126.0-169.0)	7	149.9	7.65	(133.0-161.0)
L	6	156.3	9.53	(150.0-180.0)	8	157.5	6.29	(147.0-173.0)
M	13	141.2	6.33	(113.0-154.0)	12	140.4	4.88	(121.0-153.0)
N	9	164.9	7.00	(147.0-177.0)	2	164.5	15.00	(157.0-172.0)
O	1	120.0	---	(--- ---)	0	---	---	(--- ---)
P	3	169.7	4.06	(166.0-173.0)	4	173.5	19.77	(155.0-193.0)
Q	1	167.0	---	(--- ---)	0	---	---	(--- ---)
R	1	200.0	---	(--- ---)	3	190.7	11.79	(179.0-198.0)
				Length of hind foot				
A	6	38.0	1.37	(35.0-40.0)	10	37.3	1.08	(34.0-39.0)
B	9	38.7	1.76	(36.0-45.0)	13	38.5	0.89	(36.0-41.0)
C	16	39.5	1.25	(35.0-43.0)	17	38.4	0.68	(36.0-41.0)
D	9	40.2	0.93	(38.0-42.0)	15	39.1	0.73	(37.0-41.0)
E	3	36.3	0.67	(36.0-37.0)	5	36.6	1.85	(35.0-40.0)
F	6	37.5	2.35	(33.0-41.0)	8	35.9	0.80	(34.0-37.0)
G	5	38.2	1.33	(36.0-40.0)	9	38.2	1.14	(36.0-41.0)
H	7	36.6	1.37	(35.0-39.0)	8	37.0	1.20	(35.0-40.0)
I	21	37.3	1.54	(28.0-43.0)	31	36.7	0.79	(32.0-40.0)
J	4	36.0	0.82	(35.0-37.0)	8	34.6	1.25	(33.0-38.0)
K	9	39.1	0.62	(38.0-40.0)	7	36.6	2.64	(30.5-40.0)
L	6	40.3	1.91	(37.0-43.0)	7	39.9	1.45	(37.0-43.0)
M	13	37.2	1.49	(32.0-41.0)	12	37.9	0.87	(36.0-41.0)
N	10	37.5	1.00	(35.0-40.0)	3	37.3	1.33	(36.0-38.0)
O	1	36.0	---	(--- ---)	0	---	---	(--- ---)
P	3	38.0	1.15	(37.0-39.0)	4	36.5	1.29	(35.0-38.0)

TABLE 13.—Continued.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
Q	1	38.0	----	(---- ----)	0	----	----	(---- ----)
R	1	42.0	----	(---- ----)	3	38.7	2.91	(36.0-41.0)
				Length of ear				
A	6	28.3	0.42	(28.0-29.0)	9	27.0	0.94	(25.0-29.0)
B	9	27.1	1.02	(25.0-29.0)	12	27.3	0.62	(25.0-29.0)
C	7	27.0	1.07	(25.0-29.0)	12	26.8	0.95	(25.0-30.0)
D	6	28.2	0.61	(27.0-29.0)	11	28.1	1.31	(25.0-32.0)
E	3	26.3	1.76	(25.0-28.0)	5	28.4	1.85	(27.0-32.0)
F	4	25.2	3.77	(20.0-28.0)	6	28.2	0.61	(27.0-29.0)
G	5	27.0	1.10	(25.0-28.0)	7	26.1	0.81	(25.0-28.0)
H	6	26.3	0.42	(26.0-27.0)	6	26.7	0.99	(25.0-28.0)
I	21	25.9	1.15	(20.0-30.0)	24	25.9	0.79	(22.0-30.0)
J	4	26.2	3.40	(22.0-29.0)	8	26.1	1.33	(23.0-28.0)
K	6	28.8	2.39	(25.0-34.0)	2	23.5	7.00	(20.0-27.0)
L	6	28.2	1.50	(25.0-30.0)	6	29.1	1.42	(27.0-32.0)
M	12	28.7	0.92	(26.0-31.0)	10	28.4	0.84	(26.0-30.0)
N	10	29.4	0.90	(27.0-32.0)	3	29.0	1.15	(28.0-30.0)
O	0	----	----	(---- ----)	0	----	----	(---- ----)
P	2	28.0	2.00	(27.0-29.0)	4	28.2	2.22	(25.0-30.0)
Q	0	----	----	(---- ----)	0	----	----	(---- ----)
R	1	36.0	----	(---- ----)	3	28.7	3.33	(27.0-32.0)
				Greatest length of skull				
A	6	49.4	1.17	(47.9-51.4)	9	46.5	1.20	(43.0-48.8)
B	11	49.2	0.78	(47.6-51.6)	12	48.8	0.86	(46.1-51.3)
C	14	49.7	0.95	(46.4-52.9)	15	48.8	1.09	(44.2-51.8)
D	9	50.5	0.95	(48.8-53.4)	15	49.7	0.56	(48.0-51.4)
E	3	46.6	0.53	(46.2-47.1)	4	47.0	2.33	(43.8-49.2)
F	6	48.1	0.61	(47.0-49.0)	8	47.7	0.81	(46.0-49.2)
G	5	49.6	1.65	(47.6-52.1)	8	48.3	0.55	(47.1-49.0)
H	7	50.6	1.15	(48.6-53.4)	8	47.6	1.15	(45.2-50.5)
I	19	48.3	0.86	(43.8-51.1)	28	48.5	0.65	(45.3-51.5)
J	3	47.9	1.58	(46.3-48.8)	8	46.2	1.17	(44.0-48.8)
K	7	48.7	0.86	(47.5-50.5)	6	47.1	1.08	(45.9-49.5)
L	6	51.0	1.50	(47.9-53.0)	7	48.6	1.27	(45.9-50.8)
M	12	46.6	0.92	(42.5-48.5)	11	46.7	1.07	(43.9-49.3)
N	8	46.8	1.58	(43.9-50.0)	2	45.7	1.80	(44.8-46.6)
O	1	44.9	----	(---- ----)	0	----	----	(---- ----)
P	3	46.6	0.42	(46.2-46.9)	4	45.8	1.49	(43.9-47.1)
Q	1	44.9	----	(---- ----)	0	----	----	(---- ----)
R	1	51.0	----	(---- ----)	2	49.8	0.10	(49.7-49.8)
				Condylobasilar length				
A	6	48.8	0.95	(47.7-50.3)	9	45.1	1.38	(41.1-47.5)
B	11	48.2	0.75	(46.1-49.9)	13	47.0	0.68	(44.8-48.8)
C	13	48.3	1.06	(44.6-50.9)	16	47.1	0.92	(42.8-50.0)
D	9	49.1	0.74	(47.2-51.3)	15	47.8	0.51	(45.7-49.2)
E	3	44.8	1.05	(43.8-45.6)	5	45.1	1.60	(42.3-47.0)
F	7	46.9	0.77	(45.4-48.3)	8	46.1	0.66	(44.7-47.1)
G	5	47.7	0.92	(46.6-49.2)	8	46.3	0.78	(45.0-47.8)
H	8	48.4	0.76	(46.7-49.7)	8	45.9	1.08	(43.7-48.4)
I	22	46.9	0.79	(42.6-49.6)	30	46.4	0.58	(43.7-49.9)
J	3	46.5	1.14	(45.4-47.2)	8	44.7	1.36	(41.7-47.5)
K	7	46.7	0.91	(45.0-48.8)	7	45.6	1.10	(43.8-48.1)
L	6	49.4	1.48	(46.1-51.1)	7	46.8	1.21	(44.2-48.9)
M	11	44.7	0.93	(41.3-46.2)	11	44.5	0.84	(41.9-46.7)
N	8	45.2	1.40	(42.7-48.5)	2	44.4	0.80	(44.0-44.8)
O	1	43.9	----	(---- ----)	0	----	----	(---- ----)

TABLE 13.—Continued.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
P	3	44.2	0.75	(43.6-44.9)	4	43.2	1.44	(41.7-44.5)
Q	1	44.0	—	(— —)	0	—	—	(— —)
R	1	49.6	—	(— —)	2	47.4	0.30	(47.3-47.6)
				Zygomatic breadth				
A	6	27.1	0.90	(25.4-28.5)	8	26.3	0.99	(23.8-28.2)
B	11	26.5	0.55	(25.1-28.0)	13	26.7	0.70	(24.7-29.1)
C	15	26.8	0.48	(25.5-28.8)	17	26.5	0.45	(24.9-28.4)
D	9	27.3	0.45	(26.7-28.9)	15	26.8	0.44	(25.5-28.4)
E	3	25.3	0.64	(24.7-25.8)	5	25.2	0.99	(24.3-27.1)
F	7	26.5	0.39	(26.0-27.4)	7	26.1	0.70	(24.6-27.6)
G	5	26.5	0.75	(25.5-27.5)	10	26.1	0.60	(24.5-27.2)
H	8	27.1	0.67	(26.2-29.1)	8	25.8	0.51	(25.0-26.5)
I	23	26.1	0.41	(23.7-27.4)	32	26.1	0.36	(23.0-28.1)
J	3	25.3	0.20	(25.2-25.5)	8	25.1	0.40	(24.3-26.0)
K	7	25.8	0.81	(25.0-28.0)	7	25.5	0.58	(24.8-26.8)
L	6	27.6	0.88	(25.9-28.9)	7	25.8	0.80	(24.6-27.3)
M	13	24.8	0.50	(23.2-25.7)	11	24.6	0.39	(23.6-25.3)
N	8	24.9	0.82	(23.3-26.7)	2	24.9	1.00	(24.4-25.4)
O	1	25.4	—	(— —)	0	—	—	(— —)
P	3	25.0	1.17	(24.4-26.2)	4	24.0	0.38	(23.5-24.4)
Q	1	23.7	—	(— —)	0	—	—	(— —)
R	1	25.8	—	(— —)	2	25.0	2.00	(24.0-26.0)
				Least interorbital constriction				
A	6	6.4	0.23	(6.1-6.9)	10	6.3	0.21	(5.8-6.8)
B	11	6.2	0.16	(5.8-6.7)	14	6.3	0.16	(5.8-6.7)
C	16	6.4	0.13	(6.0-6.9)	18	6.3	0.15	(5.9-7.0)
D	9	6.4	0.12	(6.1-6.7)	16	6.4	0.14	(5.9-7.0)
E	3	6.0	0.13	(5.9-6.1)	5	6.2	0.32	(5.9-6.8)
F	7	6.2	0.12	(6.0-6.4)	8	6.3	0.23	(5.8-6.7)
G	5	6.4	0.41	(5.9-6.9)	10	6.4	0.21	(5.8-6.9)
H	8	6.6	0.33	(6.1-7.7)	8	6.4	0.24	(5.9-6.9)
I	24	6.4	0.14	(5.7-7.0)	33	6.3	0.15	(5.5-7.2)
J	3	6.3	0.07	(6.3-6.4)	8	5.9	0.18	(5.7-6.3)
K	9	6.1	0.19	(5.7-6.6)	7	6.1	0.16	(5.9-6.5)
L	6	6.2	0.21	(5.8-6.5)	7	6.1	0.24	(5.7-6.5)
M	13	6.2	0.18	(5.8-7.0)	12	6.2	0.13	(5.9-6.8)
N	11	6.1	0.18	(5.5-6.5)	3	6.0	0.31	(5.7-6.2)
O	1	6.0	—	(— —)	0	—	—	(— —)
P	3	6.0	0.29	(5.8-6.3)	4	6.3	0.36	(6.0-6.8)
Q	1	5.6	—	(— —)	0	—	—	(— —)
R	1	5.7	—	(— —)	2	6.0	0.30	(5.8-6.1)
				Breadth at mastoids				
A	6	19.9	0.57	(18.9-20.9)	8	18.9	0.50	(18.0-19.9)
B	11	19.1	0.40	(18.0-20.1)	11	19.3	0.35	(18.3-20.3)
C	13	19.5	0.38	(18.1-20.8)	16	18.9	0.27	(17.9-19.8)
D	8	19.6	0.25	(19.1-20.1)	14	19.0	0.23	(18.2-19.5)
E	3	18.4	0.76	(17.7-19.0)	5	18.3	0.53	(17.5-19.0)
F	7	18.9	0.59	(17.6-20.0)	8	18.8	0.29	(18.2-19.3)
G	5	19.2	0.49	(18.7-20.1)	8	18.9	0.42	(17.7-19.6)
H	8	19.6	0.23	(19.0-20.0)	7	19.0	0.58	(18.2-20.1)
I	18	18.9	0.26	(18.0-20.0)	25	19.0	0.27	(17.6-20.7)
J	4	18.8	0.46	(18.2-19.3)	8	18.5	0.32	(17.8-19.2)
K	8	19.0	0.40	(18.5-20.1)	7	18.8	0.38	(18.0-19.7)
L	6	19.7	0.42	(18.9-20.5)	8	19.4	0.50	(18.4-20.6)
M	12	19.0	0.47	(17.5-19.9)	10	18.6	0.23	(17.8-19.1)
N	9	18.8	0.71	(17.5-20.4)	2	17.7	0.20	(17.6-17.8)

TABLE 13.—Continued.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
O	1	18.1	—	(— —)	0	—	—	(— —)
P	3	18.3	0.44	(18.0-18.7)	4	18.2	0.48	(17.6-18.6)
Q	1	18.0	—	(— —)	0	—	—	(— —)
R	1	19.5	—	(— —)	2	18.9	0.20	(18.8-19.0)
				Length of rostrum				
A	6	19.5	0.69	(18.5-20.7)	9	17.7	0.63	(18.8-19.0)
B	11	19.2	0.40	(18.2-20.2)	13	18.8	0.44	(17.7-20.2)
C	15	19.5	0.37	(17.8-20.7)	17	18.9	0.36	(17.2-20.1)
D	9	19.9	0.67	(18.6-21.6)	16	19.9	0.34	(18.6-20.8)
E	3	17.9	0.77	(17.5-18.7)	4	18.2	1.13	(16.7-18.6)
F	7	18.7	0.20	(18.5-19.2)	8	18.5	0.35	(17.7-19.2)
G	5	19.0	0.59	(18.2-20.0)	10	18.8	0.47	(17.6-20.1)
H	7	19.8	0.49	(18.7-20.7)	8	18.6	0.52	(17.6-19.7)
I	21	18.9	0.41	(16.6-20.2)	30	18.8	0.31	(17.3-20.7)
J	4	18.5	0.89	(17.2-19.2)	8	17.7	0.69	(16.6-19.4)
K	9	18.9	0.46	(17.9-20.0)	7	18.2	0.51	(17.0-19.2)
L	6	19.8	0.94	(17.7-20.9)	8	18.6	0.74	(17.0-20.5)
M	13	17.7	0.47	(15.7-18.6)	12	17.5	0.56	(16.0-18.9)
N	11	17.6	0.63	(16.0-19.7)	3	17.2	0.98	(16.2-17.8)
O	1	17.4	—	(— —)	0	—	—	(— —)
P	3	17.4	0.47	(17.0-17.8)	4	17.6	0.91	(16.4-18.5)
Q	1	17.1	—	(— —)	0	—	—	(— —)
R	1	20.7	—	(— —)	3	19.1	0.50	(18.8-19.6)
				Breadth of rostrum				
A	6	8.6	0.47	(8.1-9.3)	9	7.9	0.30	(7.0-8.5)
B	11	8.3	0.26	(7.5-9.2)	14	8.2	0.23	(7.2-8.9)
C	16	8.4	0.16	(7.8-9.0)	18	8.3	0.18	(7.7-9.3)
D	9	8.5	0.23	(8.1-9.1)	16	8.3	0.17	(7.7-9.1)
E	3	7.9	0.12	(7.8-8.0)	5	8.1	0.36	(8.2-8.4)
F	7	8.2	0.18	(7.8-8.5)	8	7.9	0.11	(7.7-8.2)
G	5	8.3	0.20	(8.0-8.6)	10	8.1	0.23	(7.6-8.6)
H	8	8.2	0.23	(7.7-8.7)	8	7.9	0.24	(7.5-8.5)
I	24	8.0	0.17	(7.4-8.9)	32	8.0	0.11	(7.4-8.8)
J	3	8.4	0.18	(8.2-8.5)	8	7.8	0.25	(7.2-8.4)
K	9	7.8	0.19	(7.5-8.4)	7	7.9	0.31	(7.4-8.5)
L	6	8.3	0.41	(7.8-8.9)	7	8.0	0.39	(7.6-9.1)
M	13	7.7	0.20	(7.1-8.0)	12	7.8	0.19	(7.3-8.5)
N	11	7.9	0.26	(7.0-8.7)	3	7.4	0.35	(7.1-7.7)
O	1	8.0	—	(— —)	0	—	—	(— —)
P	3	7.5	0.12	(7.4-7.6)	14	7.4	0.25	(7.2-7.8)
Q	1	7.6	—	(— —)	0	—	—	(— —)
R	1	8.1	—	(— —)	3	8.1	0.18	(7.9-8.2)
				Alveolar length of maxillary toothrow				
A	6	9.0	0.37	(8.5-9.6)	10	8.7	0.27	(8.2-9.4)
B	11	9.3	0.19	(8.7-9.8)	14	9.5	0.21	(8.8-10.0)
C	16	9.4	0.17	(8.7-10.1)	18	9.3	0.20	(8.5-10.1)
D	9	9.4	0.24	(8.6-9.8)	16	9.3	0.22	(8.6-10.1)
E	3	9.0	0.58	(8.5-9.5)	5	8.6	0.36	(8.2-9.1)
F	7	9.0	0.25	(8.5-9.4)	8	8.9	0.26	(8.1-9.2)
G	5	9.1	0.45	(8.6-9.9)	10	9.2	0.26	(8.7-9.9)
H	8	9.1	0.20	(8.7-9.6)	8	9.1	0.31	(8.4-9.7)
I	22	9.4	0.20	(8.6-10.3)	9	9.1	0.17	(8.0-10.1)
J	4	9.1	0.19	(9.0-9.4)	8	8.9	0.22	(8.4-9.4)
K	8	9.3	0.27	(8.8-9.8)	7	9.1	0.28	(8.6-9.5)
L	6	9.7	0.34	(9.0-10.1)	8	9.4	0.34	(8.6-9.9)
M	13	8.5	0.25	(8.0-9.5)	12	8.7	0.33	(7.9-10.0)

TABLE 13.—Concluded.

Locality Code	Males N	Mean	± 2SE	Range	Females N	Mean	± 2SE	Range
N	10	8.7	0.27	(8.1-9.4)	3	8.5	0.75	(7.8-9.1)
O	1	9.2	—	(— —)	0	—	—	(— —)
P	3	9.1	0.41	(8.8-9.5)	4	9.0	0.34	(8.6-9.4)
Q	1	9.4	—	(— —)	0	—	—	(— —)
R	1	9.9	—	(— —)	3	9.8	0.58	(9.3-10.3)
				Length of palatal bridge				
A	6	8.6	0.25	(8.3-9.1)	10	7.9	0.24	(7.1-8.4)
B	11	8.2	0.33	(6.8-8.9)	13	7.9	0.23	(7.1-8.3)
C	15	8.0	0.19	(7.3-8.5)	18	8.0	0.28	(7.1-9.5)
D	9	8.3	0.35	(7.7-9.0)	16	8.0	0.18	(7.4-8.5)
E	3	7.9	0.23	(7.7-8.1)	5	7.7	0.20	(7.6-8.1)
F	7	7.8	0.43	(6.9-8.4)	8	8.0	0.20	(7.5-8.4)
G	5	8.2	0.60	(7.0-8.7)	10	8.0	0.34	(7.1-8.9)
H	7	7.9	0.19	(7.7-8.4)	8	7.9	0.32	(7.4-8.4)
I	24	8.1	0.17	(7.4-9.0)	33	8.0	0.14	(7.1-8.9)
J	3	7.9	0.70	(7.2-8.3)	8	7.4	0.60	(7.0-7.9)
K	8	7.8	0.23	(7.2-8.2)	7	7.8	0.35	(7.3-8.5)
L	6	8.4	0.51	(7.3-9.0)	7	8.2	0.32	(7.8-9.1)
M	13	7.6	0.19	(7.0-8.1)	13	7.5	0.22	(6.9-8.1)
N	11	8.1	0.26	(7.2-8.9)	3	7.6	0.76	(7.0-8.3)
O	1	8.6	—	(— —)	0	—	—	(— —)
P	3	7.5	0.81	(6.8-8.2)	4	7.8	0.42	(7.5-8.4)
Q	1	8.6	—	(— —)	0	—	—	(— —)
R	1	9.3	—	(— —)	3	8.7	0.31	(8.5-9.0)
				Length of nasals				
A	6	19.9	0.64	(18.8-20.8)	9	18.4	0.61	(16.9-19.4)
B	11	19.7	0.46	(18.0-20.7)	13	19.2	0.55	(17.9-20.7)
C	15	19.9	0.45	(18.5-21.1)	17	19.3	0.48	(16.7-21.2)
D	9	20.1	0.55	(18.9-21.4)	16	20.3	0.30	(19.3-21.6)
E	3	18.3	1.21	(17.6-19.5)	4	18.7	1.51	(16.9-20.4)
F	7	19.6	0.43	(18.5-20.2)	8	18.8	0.41	(18.0-19.7)
G	5	19.7	0.77	(18.8-21.1)	10	19.2	0.54	(17.5-20.8)
H	7	20.5	0.68	(19.5-22.0)	8	19.1	0.65	(17.6-20.6)
I	21	19.3	0.46	(16.6-20.8)	30	19.2	0.35	(17.8-21.0)
J	4	19.0	1.15	(17.4-20.0)	8	18.0	0.80	(16.4-19.8)
K	9	19.0	0.44	(17.8-19.7)	7	18.4	0.55	(17.6-19.4)
L	6	20.5	1.00	(18.6-22.0)	8	19.0	0.54	(17.8-19.9)
M	13	18.1	0.51	(16.3-19.2)	12	17.9	0.60	(16.2-19.3)
N	11	18.0	0.76	(16.1-20.3)	3	17.2	0.19	(15.4-18.7)
O	1	17.9	—	(— —)	0	—	—	(— —)
P	3	17.9	0.35	(17.6-18.2)	4	17.1	0.81	(16.3-18.2)
Q	1	17.9	—	(— —)	0	—	—	(— —)
R	1	19.6	—	(— —)	3	19.0	1.39	(17.9-20.3)

lary toothrow deviates noticeably from the anticipated trends. For example, samples such as L and D, are large and M and N are smaller. Specimens from other localities, such as P and K, have proportionately longer toothrows, whereas those from locality A are atypically short. The patterns of variation in palatal bridge length shown by sequence of means are similar to those of toothrow length except that specimens from locality P are among the smallest. The pattern of variation in nasal length is similar to that of rostral length.

The rank-order system of scoring means described above was employed to search for trends in size variation in *N. micropus*. Specimens from localities D (south-central Kansas) and L (coastal Texas) were thus calculated to be larger

than other specimens in the range of the species. Moving away from locality D, size decreases gradually but consistently in specimens to the south (localities G, H, and I) and west (localities C, B, and A). Specimens from localities southwest (localities F, E, O, and J) of the above-listed seven localities decrease in size clinally. The large area in central Texas from which specimens of *N. micropus* are absent (see Fig. 6 and discussion of distribution for *N. m. canescens*) lies between locality I and the two in southern Texas (K and L). It is possible that the only route for gene flow between locality L and I is through western Texas; or in other words, animals from locality L may be effectively isolated from the northern populations of woodrats that they resemble in size. Specimens from locality K are considerably smaller than those from L, slightly smaller than those from I and slightly larger than those from J. Specimens from Coahuila (locality M) are probably smallest of *N. m. canescens*, but if so, they are only slightly smaller than those from New Mexico and the Big Bend area (J) of Texas. Specimens of *N. m. micropus* from coastal Tamaulipas have proportionately longer tails, and thus have high means for total length and tail length. Cranially they are as small or possibly smaller than those from adjacent locality M. The single break in the gradual cline in size is across the lower Rio Grande River. Locality L, having among the largest specimens of the species, is contiguous with locality N, which supports small woodrats having relatively long and often unicolored tails *(N. m. micropus)*. The steepness of this "step" in the cline decreases to the northwest along the Rio Grande. For example, specimens from locality K are considerably smaller than those from L, but considerably larger than those from M. Farther west, specimens from Chihuahua are indistinguishable from those in southwest Texas.

Size relationships between specimens of *N. m. micropus* from northern Tamaulipas and southern Tamaulipas (previously *N. m. littoralis*) demonstrate that rats from the two localities are similar, especially with respect to external and cranial dimensions and, to a lesser extent, color. I detect no real basis for continuing to recognize *littoralis* as a subspecies.

Because the only available "adult" specimens from Río Verde, San Luis Potosí (*planiceps*, locality Q) and from White Sands, New Mexico (*canescens*, sample O, previously known as *leucophea*) are of age-group V, comments on size of these groups must be tentative. However, woodrats from White Sands appear to be nearly the same size as other specimens from New Mexico. The holotype of *planiceps* is similar in size to other specimens of *N. micropus* from Mexico.

On the basis of the four adult specimens (one male, three females) of *N. angustipalata* examined, it appears that individuals of this species are much larger than those of *N. micropus* from all localities in Mexico. The only areas from which specimens of *N. micropus* compare favorably in size to individuals of *angustipalata* are localities D and L. The external measurements of *angustipalata* far exceed those of all samples of *micropus*, and measurements of lengths of all or parts of the skull are generally larger. In measurements of breadth, however, several samples of *micropus* are larger than *angustipalata* (see table 13 for comparative measurements).

Comparisons of sequence of means and subset relationships from SS-STP computations including the 13 samples of *N. floridana* and 14 of *N. micropus* together, reveal that *floridana* generally is the larger (see Table 12 and Figs. 15-20). Samples of *floridana* from northwestern *(campestris)* and north-central *(attwateri)* Kansas and those from southeastern Texas *(rubida)* are larger on the average in most dimensions than samples of *micropus*. Samples of *attwateri* from southeastern Kansas and from both localities in Texas usually are larger than samples of *micropus;* however, in some

dimensions, samples of *micropus* from south-central Kansas and coastal southern Texas are larger than one or more of the *floridana* samples. Specimens of *micropus* from the above two localities and from localities in western Kansas and northern Oklahoma are usually larger than samples of *baileyi, campestris* from Colorado, and *attwateri* from northeastern Kansas and eastern Oklahoma. Specimens of *micropus* from Colorado, extreme southwestern Kansas, southwestern Oklahoma, and northern Texas are nearly equal in size to specimens of the last-mentioned samples of *floridana.* The *micropus* from southern and western localities are consistently smaller than woodrats of either species from other localities. The single exception is tail length in *N. m. micropus,* which exceeds that of all other samples of *N. micropus* and most samples of *N. floridana.* Woodrats from the panhandle of Texas, southwestern Texas, and non-coastal southern Texas are intermediate in size between specimens from farther to the south and west and those from localities to the north and east.

The general trends noted above are less well marked in certain dimensions than others; for example, least interorbital constriction is broader in all samples of *floridana* females than in any sample of *micropus* females. The only samples of *micropus* that occasionally average larger than *N. angustipalata* are those from south-central Kansas and southern coastal Texas. However, certain samples of *floridana* (*rubida, campestris* from Kansas, and *attwateri* from north-central Kansas) are larger than *angustipalata* in many dimensions.

In conclusion, univariate analyses indicate that the range of size variation within the species *micropus* exceeds that in the populations of *floridana* studied. Also, variation in *micropus* tends to be clinal and relatively consistent geographically. The single major exception is the large size of specimens from coastal southern Texas. Specimens of *micropus* from western and southern localities generally are smaller than those from northern and eastern localities, but those from coastal Texas are larger on the average than all samples of *micropus* from contiguous localities and larger than most samples from northern parts of the range of the species. This phenomenon could have resulted from one or more of three distinct possibilities. The samples from this locality consisted of less than 10 individuals of each sex, and the apparent large size of these woodrats might be the result of sampling error. I consider this possibility relatively unlikely, however, because large size was evinced by specimens of both sexes. The probability of sampling error involving two samples from the same locality is much lower than when only one sample is involved. Secondly, specimens of *floridana* from southern Texas are large; possibly the large size of *micropus* from contiguous localities is the result of introgression of genetic material from *floridana.* Thus, the robustness of animals from coastal Texas perhaps should be interpreted as evidence for hybridization. Thirdly, there is the possibility that whatever selective forces have resulted in large individuals of *floridana* in southern Texas also are operating on adjacent populations of *micropus,* resulting in the unexpected large size. Evaluation of the latter two possibilities is difficult and must remain speculative until additional data are available. If hybridization is the answer, it might be expected that specimens of *floridana* from southern Texas would be slightly smaller than, instead of slightly larger than, specimens from northern Texas and southern Oklahoma. However, it also must be remembered that certain qualitative cranial characters discussed previously indicated that specimens of *floridana* from localities in southern Texas were relatively more *micropus*-like than are those in most other populations of *floridana.*

Multivariate Analyses of Mensural Characters

Moss (1968) and Sokal and Michener

(1967) have shown that standardization of character states to equally weight characters greatly influences the clustering of OTU's in correlation phenograms and further tends to reduce the degree of isolation of "aberrant" OTU's. The distance phenogram usually is less influenced by standardization of character states. Comparisons by correlation and by distance augment one another, and must be considered simultaneously in the interpretation of phenograms. Correlations are relatively independent of size (totally independent with unstandardized character states) and cluster OTU's primarily on the basis of relative proportions. On the other hand, distances are less dependent on relative proportions, and cluster primarily on the basis of absolute differences between the numerical values of characters. For example, when Moss (1968:38) multiplied continuous characters by a factor of two to create hypothetical "giant" OTU's and compared original and "giant" OTU's using unstandardized data, the normal and "giant" OTU's clustered in the correlation phenogram at the 1.0 level. However, in the distance phenogram based on unstandardized data, there was complete separation of normal and "giant" OTU's with comparable clustering within each major cluster. Standardization of the data resulted in a high frequency of group clustering (a cluster of normal OTU's joined its respective cluster of giant OTU's) in the correlation phenogram, but the distance phenogram was altered very little by standardization.

As previously mentioned, character states were standardized for all computations by CLSNT. In most cases I have illustrated distance phenograms, and in all cases the clustering relationships of correlation phenograms are discussed to emphasize proportional relationships and absolute differences among the woodrats. When woodrats from grouped localities were compared using all of the available characters, both correlation and distance phenograms are presented. A certain amount of distortion results in the clustering process from a multidimensional correlation or distance matrix to a two-dimensional phenogram. The coefficients of cophenetic correlation, calculated to express correlation between the original matrices and the resultant phenograms, are given beyond for all phenograms. This coefficient is normally about 10 percent higher for distance phenograms than for correlation phenograms. Rohlf (1968) discussed various relationships between results of cluster analyses and those of principal components. He recommended (1968:254) that "numerical taxonomic studies should use both cluster analyses and 3-D models in order to extract and present as much information as is possible from the raw data." In all cases, I have analyzed principal components in conjunction with cluster analyses. Additionally, for each projection of OTU's onto the three principal components, a minimally interconnected network (Cavalli-Sforza and Edwards, 1967) was computed from the among-OTU distance matrix. When the number of OTU's was low, these have been included on the 3-D drawings. Models are presented as perspective drawings; thus, with respect to the left rear corner of a square platform, the viewer is 0.3 units (one unit is equal to the length of one side of the platform) to the right, 3.0 units toward the front, and at a height (the third principal component) even with the OTU projected farthest from the platform.

Neotoma floridana.—A correlation phenogram was computed from among-OTU correlations for *Neotoma floridana* females using means of the four external and 10 cranial dimensions as character states; the coefficient of cophenetic correlation is 0.714. The 13 OTU's (corresponding to the 13 grouped localities shown in figure 8) cluster into five major groups, which are separated by correlations of zero or negative values. Clusters grouped females as follow: 1) localities 1 (*N. f. baileyi*) and 10 (*N. f. attwateri* from southeastern Oklahoma); 2) localities 2 and 3 (*N. f. campestris*); 3) local-

ities 4 *(campestris)*, 5, 6, and 7 (*attwateri* from Kansas); 4) localities 8, 11, and 12 (*attwateri* from western Oklahoma and Texas); and 5) localities 9 (*attwateri* from northeastern Oklahoma) and 13 (*N. f. rubida* from southeastern Texas). The coefficient of cophenetic correlation between the distance phenogram and the respective matrix is 0.831 for the 13 samples of *floridana* females. As shown in figure 21, four major clusters emerged; the least distance between two major clusters is 1.35.

The proportional relationships of *campestris* females indicate that specimens from Colorado and Nebraska are most like other *campestris* from western Kansas; but because of differences in size, they are placed with *attwateri* in the distance phenogram. The large size of females from north-central Kansas (locality 5) results in the separation of these rats from other *attwateri* females in the distance phenogram. The correlation in size between sample means of *attwateri* females from northeastern Oklahoma and those of *rubida* from southeastern Texas was unexpected.

The correlation phenogram for *floridana* males has a coefficient of cophenetic correlation of only 0.699. Four major clusters are separated from each other by correlations of –0.02 or less. *N. f. campestris* from localities 2 and 3 are in the same cluster with *baileyi*. The second cluster includes *attwateri* from Kansas, *campestris* from locality 4, and *attwateri* from the western sample in Oklahoma. The two samples of *attwateri* from eastern Oklahoma (9 and 10) are placed in the third cluster with samples 12 (southern locality of *attwateri* in Texas) and 13 *(rubida)*. The sample of *attwateri* from locality 11 is alone in the fourth group, but anastomoses with cluster three before these join the first two clusters. The distance phenogram, which has a coefficient of cophenetic correlation of 0.816, has four clusters separated by a distance of 1.25 or more (Fig. 21).

The most noteworthy differences in the two phenograms for *floridana* males

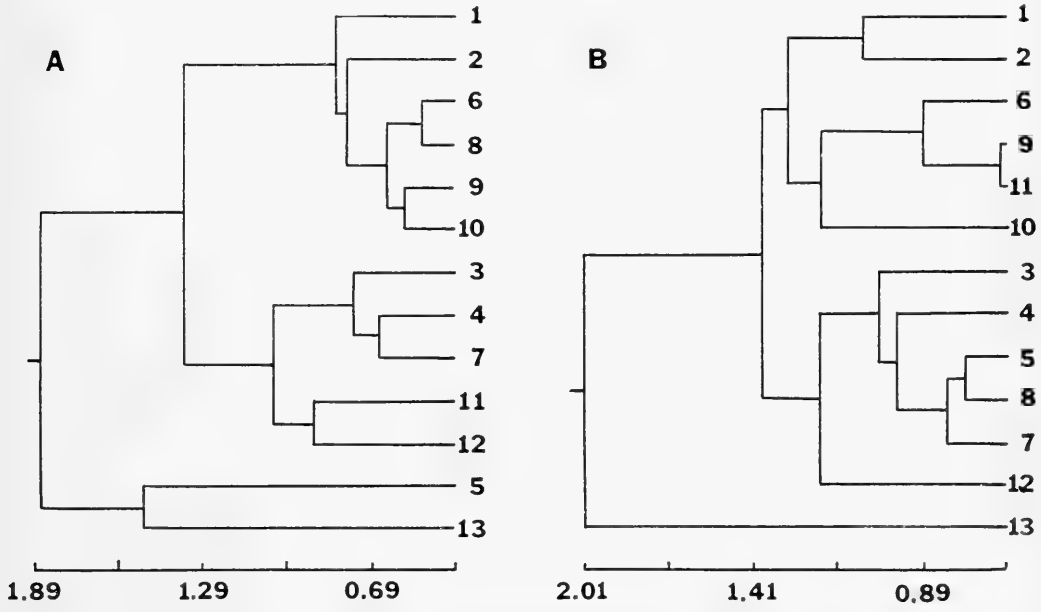

FIG. 21. Phenograms of UPGMA cluster analyses based on distance coefficients comparing standardized means of 14 mensural characters for 13 grouped localities of *Neotoma floridana:* A—females; B—males. See text for coefficients of cophenetic correlation and see figure 8 for geographic areas included within the coded localities.

involves the placement of rats from localities 3, 11, and 13. Based on correlations, sample 3 is most like samples 1 and 2, sample 11 is most distinctive, and sample 13 is similar to sample 12. When the emphasis is on differences (distance), sample 3 is most like the larger *attwateri,* sample 11 is similar to sample 9 and other small *attwateri;* sample 13 is unlike any other sample.

The first three principal components account for 84.4 percent and 78.1 percent of the total variation for females and males, respectively. Percent variation in each component for females and males, respectively, is 63.4 and 48.6 in the first, 14.5 and 15.8 in the second, and 6.5 and 15.7 in the third. The 3-D perspective drawings of projections of OTU's (the 13 samples) onto the first three principal components are shown in figure 22 for both sexes.

The 3-D projection for females is reminiscent of the cluster relationships seen in the distance phenogram; the same four basic groups obtain. Samples 5 and 13 are relatively isolated. Large *campestris* (3 and 4) and large *attwateri* (7, 11, and 12) are situated relatively close, and *baileyi* and smaller *campestris* are near the samples of small *attwateri.* The minimally connected network shows the three samples of *campestris* (2-4) interconnected and connecting to the cluster of smaller-sized females through sample 2 and the cluster of larger-sized females through sample 4. Within the cluster of "small" rats, *baileyi* is most distinct and is connected to the rest of the samples in the cluster through sample 10.

The 3-D projection of *floridana* males also bears a strong resemblance to the respective distance phenogram. In the projection, sample 1 *(baileyi)* connects through sample 2 to the cluster of large *attwateri* and *campestris.* The group of smaller *attwateri* connects to the "large" group through sample 8. *N. f. rubida* is farthest separated from other OTU's and connects to the group of larger rats through sample 12, which is connected to sample 8. Thus, sample 8 appears to be more or less intermediate, serving to interconnect the various clusters.

On the basis of mensural characters, sample 13 *(rubida)* is the only sample that clearly and consistently is distinct. The females in sample 5 (north-central Kansas) evince distinct differences from either *attwateri* or *campestris,* and appear to be nearly as distinct as *rubida;* this relationship is not seen in the comparison of males. The three samples of *campestris* do not form a closely allied group. In *attwateri,* a tendency exists toward one cluster of smaller woodrats and a second of larger woodrats. Geographically, however, localities from which specimens of the two "groups" originated are such that populations of "small" and "large" rats are interspersed. Animals from locality 12 (previously the only locality from which specimens were assigned *attwateri*) are much like members of the "large" group of other *attwateri* (previously *osagensis*) and do not resemble *rubida.*

Neotoma micropus and *Neotoma angustipalata.—Neotoma angustipalata* is treated with samples of *N. micropus* in all CLSNT analyses. These two taxa were combined because, on geographic grounds, it appeared that *angustipalata* might be a subspecies of *micropus* (Hooper, 1953:10; Alvarez, 1963:453) and that *N. angustipalata* and *N. m. planiceps* might best be considered as a single taxon.

The coefficient of cophenetic correlation between the correlation phenogram and matrix for the 15 samples of *N. micropus* and one sample of *N. angustipalata* females is 0.835. Two major clusters are formed. The first consists of one subcluster of samples A (Colorado and Cimarron County, Oklahoma), F (Texas panhandle) and E (New Mexico) and a second subcluster that joins the first at a correlation of 0.05. This subcluster includes samples J (Big Bend area of Texas), K (non-coastal southern Texas), H (southwestern Oklahoma), I (northeastern Texas), B (southwestern Kansas and adjacent Oklahoma panhandle), D

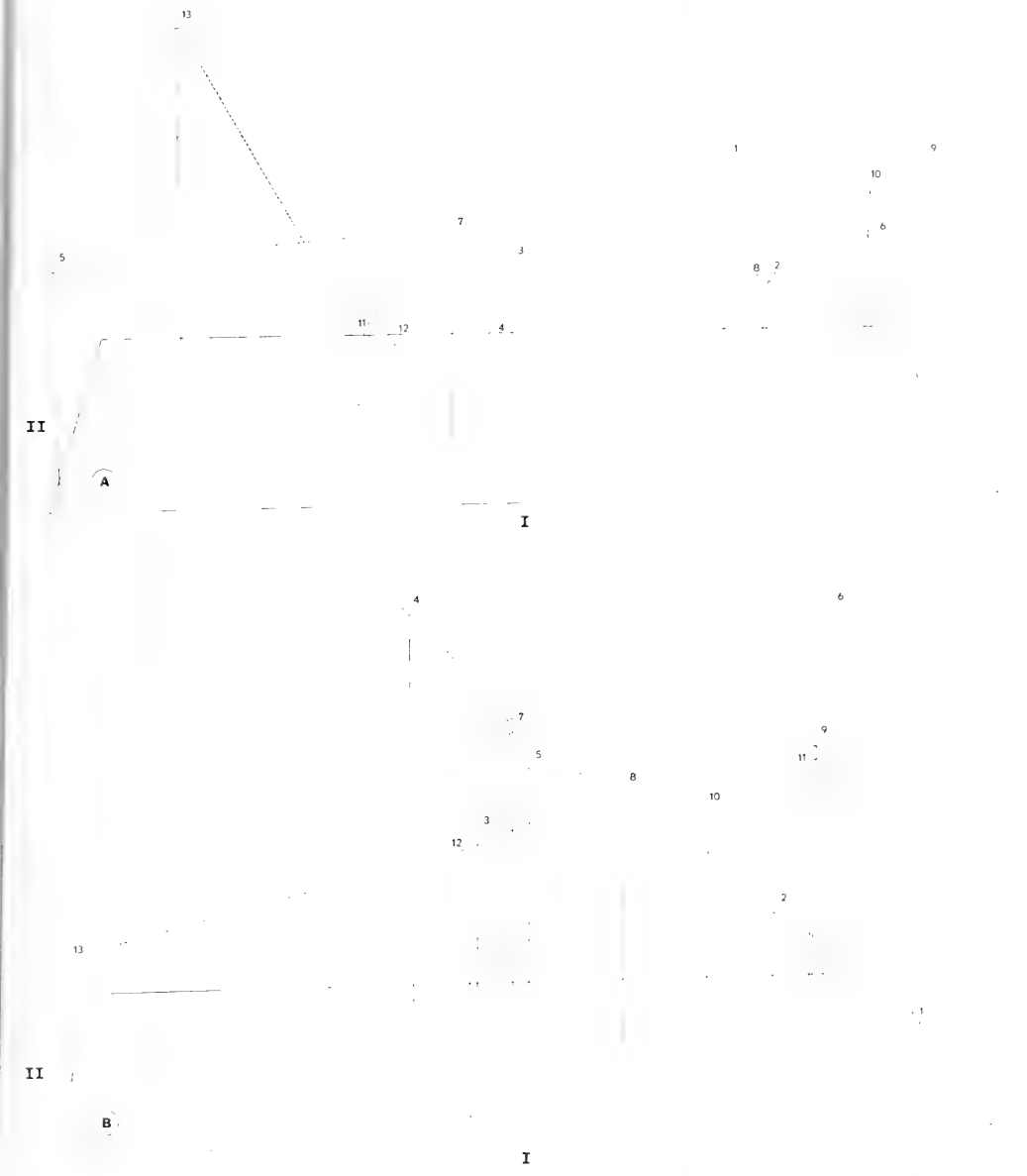

FIG. 22. Three-dimensional perspective drawings of the projections of 13 samples (OTU's) of *Neotoma floridana* onto the first three principal components based on correlation among 14 mensural characters: A—females; B—males. Dashed lines between OTU's illustrate the minimally interconnected networks computed from the respective among-OTU distance matrices. See text for percentages of variation in each component and figure 8 for geographic areas included within the coded localities.

(south-central Kansas), C (south-central Kansas just west of locality D and adjacent Oklahoma panhandle), and G (northwestern Oklahoma south of locality D). The second major cluster is composed of samples L (southern coastal Texas), R (*N. angustipalata*), M (Coahuila and Nuevo León), N (*N. m. micropus* from northern Tamaulipas) and P (*N. m. micropus* from southern Tamauli-

pas). In essence, this phenogram places all samples of *N. m. canescens* except two (M and L) in a single major cluster that is not highly correlated internally. The other major cluster includes an array of taxa including *N. angustipalata,* both samples of *N. m. micropus,* and two samples (one of large woodrats and the other of small woodrats) of *N. m. canescens.*

The distance phenogram (Fig. 23) for *micropus* and *angustipalata* females has a correlation of 0.820 with the distance matrix. If a distance of 1.25 or greater is considered to separate major clusters, four were computed. The pattern of clustering seen in the distance phenogram corresponds quite well to the taxonomic arrangement of these two species. That is, *angustipalata* appears most distinct and is recognized at the specific level, and the two samples of *N. m. micropus* are distinct from those of other *micropus,* but closer to them than to *angustipalata.* The most variable subspecies, *canescens,* consists of two groups that correspond, with a few exceptions, to the previously recognized boundaries of *N. m. canescens* and *N. m. micropus.* Nevertheless, both clusters include samples of woodrats previously assigned to the two different names.

The coefficient of cophenetic correlation for the correlation phenogram of 17 samples of *micropus* males and one sample of *angustipalata* males is relatively high (0.849) for a correlation phenogram. Of the three major clusters (separated by a correlation of –0.05 or less), one contains the two samples from New Mexico (E and O); the second, joins

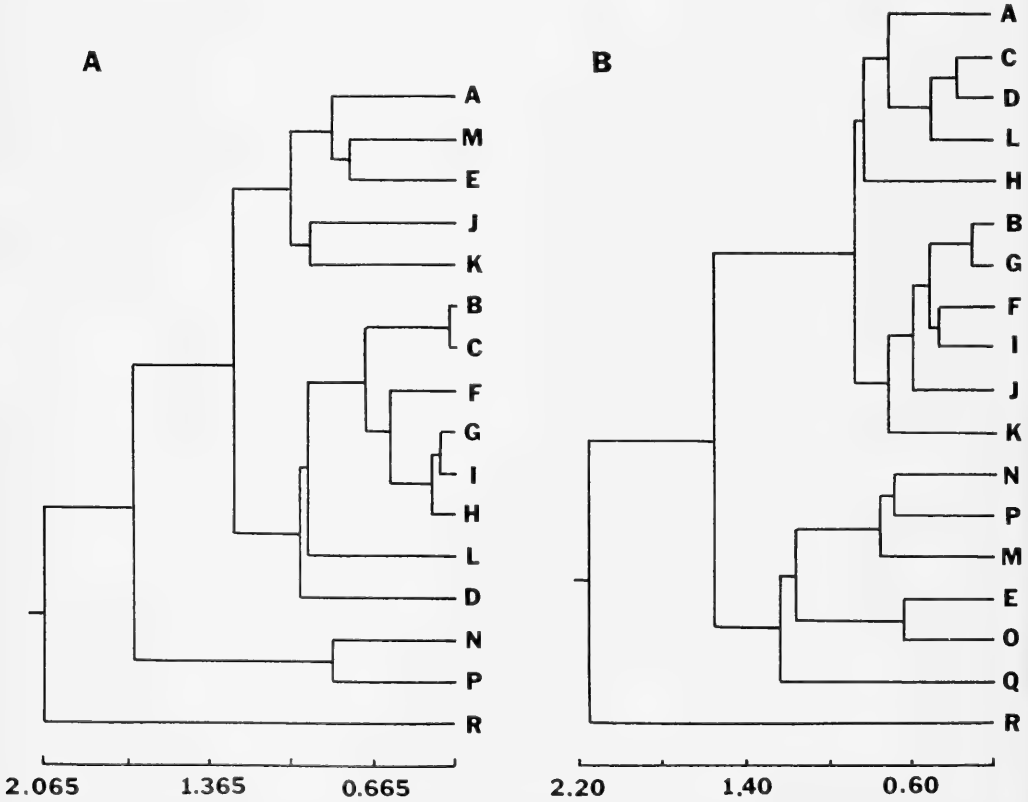

FIG. 23. Phenograms of UPGMA cluster analyses based on distance coefficients comparing standardized means of 14 mensural characters for 16 (females) and 18 (males) grouped localities of *Neotoma micropus* (A-Q) and *N. angustipalata* (R): A—females; B—males. See text for coefficients of cophenetic correlation and figure 8 for geographic areas included within the coded localities.

the first before these two join the third, and includes all samples of *canescens* from localities in the United States except E, O, and K. The third major cluster contains two distinct subgroups that join at a correlation of only 0.12. In the first subgroup are samples K and M (both *N. m. canescens*). In the other, samples N and P (both *N. m. micropus*) join at a correlation of 0.62, and Q *(N. m. planiceps)* joins R *(N. angustipalata)* at 0.800. These two couplets anastomose at a correlation of 0.45. This phenogram illustrates the high proportional similarities between *angustipalata* and *planiceps,* the affinities between the two samples of the subspecies *micropus,* and the complete intermixing of samples of *N. micropus* from the northern part of the range where two subspecies previously were recognized.

The distance phenogram for this series of male samples is shown in figure 23. The coefficient of cophenetic correlation between the phenogram and its matrix is 0.840. There is a marked tendency in both phenograms of males for most samples of *N. m. canescens* (exceptions were samples E, O, and M, especially) to cluster together; the two samples of *N. m. micropus* are always more similar to one another than either is to any other sample, but woodrats in sample M appear to be as near *micropus* as *canescens.* The correlation between *N. angustipalata* and *N. m. planiceps* is remarkably high, indicating proportional similarity. Although available material indicates that *angustipalata* is much larger than *planiceps,* it must be remembered that the only known specimen of *planiceps* is a young adult. The similarities of samples O and E from New Mexico are noteworthy because specimens in sample O previously were recognized as a distinct subspecies, *N. m. leucophea.*

Principal components analysis for females extracted a total of 86.2 percent of the variation (components one to three composed of 55.1, 24.3, and 6.8 percent, respectively). The 3-D drawing of OTU's projected onto the first three components is shown in figure 24. Sample R, as expected, is most distinct and isolated from other OTU's, especially on the second component. Sample M serves as the intermediate through which samples of *N. m. micropus* connect with samples of *N. m. canescens.* The latter are separated on the first component (which is highly correlated with size), but were similarly placed on the second component.

The first three components for males contain 56.1, 27.3, and 7.6 percent of the total variation, respectively, for a total extraction of 91.0 percent. The 3-D projection (Fig. 24) of OTU's onto these components placed *angustipalata* as the most distinct OTU, connected to *micropus* through sample L. *Neotoma micropus planiceps* is the only other relatively distinct OTU, but it is separated much less on component two than is *angustipalata; planiceps* connects to other samples of *micropus* through sample P. In the projection, as in the distance phenogram, sample M appears to share as many affinities with the subspecies *micropus* as with *canescens.*

The 3-D projections of both sexes elucidate the distinctiveness of *angustipalata,* and to a lesser degree, the distinctiveness of *planiceps.* The affinities of sample L with the northern samples of large *N. micropus* are evident. Likewise, the similarity of the two samples of *N. m. micropus* from Tamaulipas, and the intermediacy of woodrats from Coahuila and Nuevo León between *micropus* and *canescens* are shown. Finally, the projections document the absence of any distinct steps in the clinal variation in samples of *N. m. canescens.*

Simultaneous Treatment of Three Species.—When all samples of *N. floridana, N. micropus* and *N. angustipalata* were treated simultaneously in a multivariate analyses of 14 character states, the results are surprising. The correlation phenogram for the 29 samples of females has a coefficient of cophenetic correlation of only 0.686, and is divided

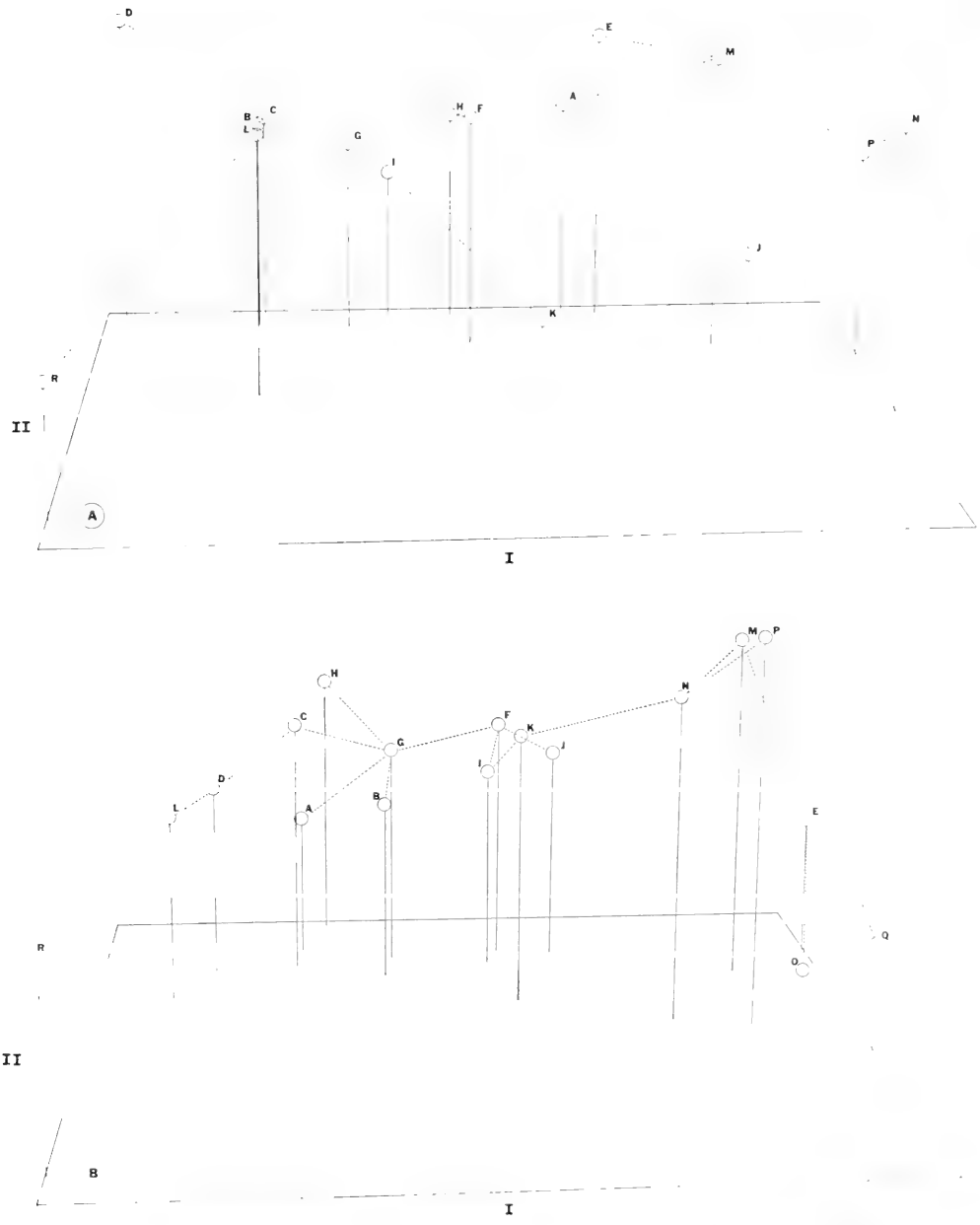

FIG. 24. Three-dimensional perspective drawings of the projections of 16 (females) and 18 (males) samples of *Neotoma micropus* (A-Q) and *N. angustipalata* (R) onto the first three principal components based on correlations among 14 mensural characters: A—females; B—males. Dashed lines between OTU's illustrate the minimally interconnected networks computed from the respective among-OTU distance matrices. See text for percentages of variation in each component, and figure 8 for geographic areas included within the coded localities.

into two primary clusters separated by a negative correlation (–0.25). Most surprising is the intermixing of samples of *micropus* with those of *floridana* and the marked alteration of the clustering relationships seen previously for samples of

floridana. Although clustering of samples of *angustipalata* and *micropus* is not exactly as discussed above, it is noticeably less altered. The first major cluster contains *N. f. rubida*, *N. angustipalata*, the samples of small *N. micropus*, and sample L. The two samples of *N. m. micropus* form a highly correlated couplet (0.78) that anastomoses first with the sample of *angustipalata*. The other major cluster contains the remaining samples of both species arranged into four subclusters. One of these consists only of sample 7 and another is made up of the three samples of smallest *floridana* (*baileyi* and *attwateri* samples 9 and 10). The two remaining subclusters include samples of *floridana* and *micropus* arranged such that neither species appears to be distinct.

Some geographically contiguous samples tend to cluster together and there is a general tendency of samples of each species to cluster in the same subgroups. However, the deviations from these tendencies are so great as to cause this phenogram to bear little resemblance to the classification used herein or to the general conclusions based on univariate analyses.

The placement of OTU's in the distance phenogram for all samples of females (Fig. 25) is more nearly congruent with previously discussed phenograms, 3-D projections, and the classification that I have proposed. Although, some samples of *floridana* and *micropus* appear together in one of the four major clusters, in only one instance is a sample of one species placed more closely to a sample of the other than to a conspecific sample. This exception was sample D. The coefficient of cophenetic correlation between phenogram and matrix is 0.736; the first bifurcation is at a distance of 1.86 and each cluster thereby formed is composed of two major subclusters.

The correlation phenogram for the 31 samples of males closely resembles the two correlation phenograms for males discussed above. It has a coefficient of cophenetic correlation of 0.720 to the correlation matrix. Three clusters are separated from each other by negative correlations. The most distinct of these contains *N. angustipalata* in a couplet with *N. m. planiceps*, *N. f. baileyi* in a couplet with *N. f. campestris* from locality 2, a couplet with the two samples of *N. m. micropus*, and lastly a couplet with two geographically contiguous samples of *N. m. canescens* (K and M). The remaining two clusters are more highly correlated than either is to the first. Samples from the five most southern localities of *N. floridana* (9, 10, 11, 12 and 13) are included in one cluster with sample H (*N. m. canescens* from southwestern Oklahoma). In the third, sample 4 (*campestris*) forms a couplet with sample A (*canescens*) in a subcluster including sample L and northern samples of *canescens*. Samples E, J, and O (*canescens* from New Mexico and adjacent southwestern Texas) form another subcluster with sample 3 (*campestris*). In the remaining subcluster, four samples of *attwateri* (5, 6, 7, and 8) are placed near a sample of *canescens* (I).

Those OTU's that form highly correlated couplets or clusters when treated in the restricted samples usually tend to cluster when the three species are treated simultaneously. Similarly, samples that appear highly distinctive when treated in conspecific groupings usually retain at least partial distinctness when all samples are treated together. However, those samples that are neither especially distinct nor highly correlated when treated conspecifically, usually are unpredictable in their clustering relationships when the number of samples and total amount of variation are increased.

The distance phenogram for 31 samples of males, which has a coefficient of cophenetic correlation of 0.765, is shown in figure 25. Three major clusters separated by a distance of 1.5 or more are evident. The two phenograms for all samples of males of both species indicate the distinctness of *angustipalata* as compared to *micropus* and *floridana*. The size relationships of *micropus* and *flori-*

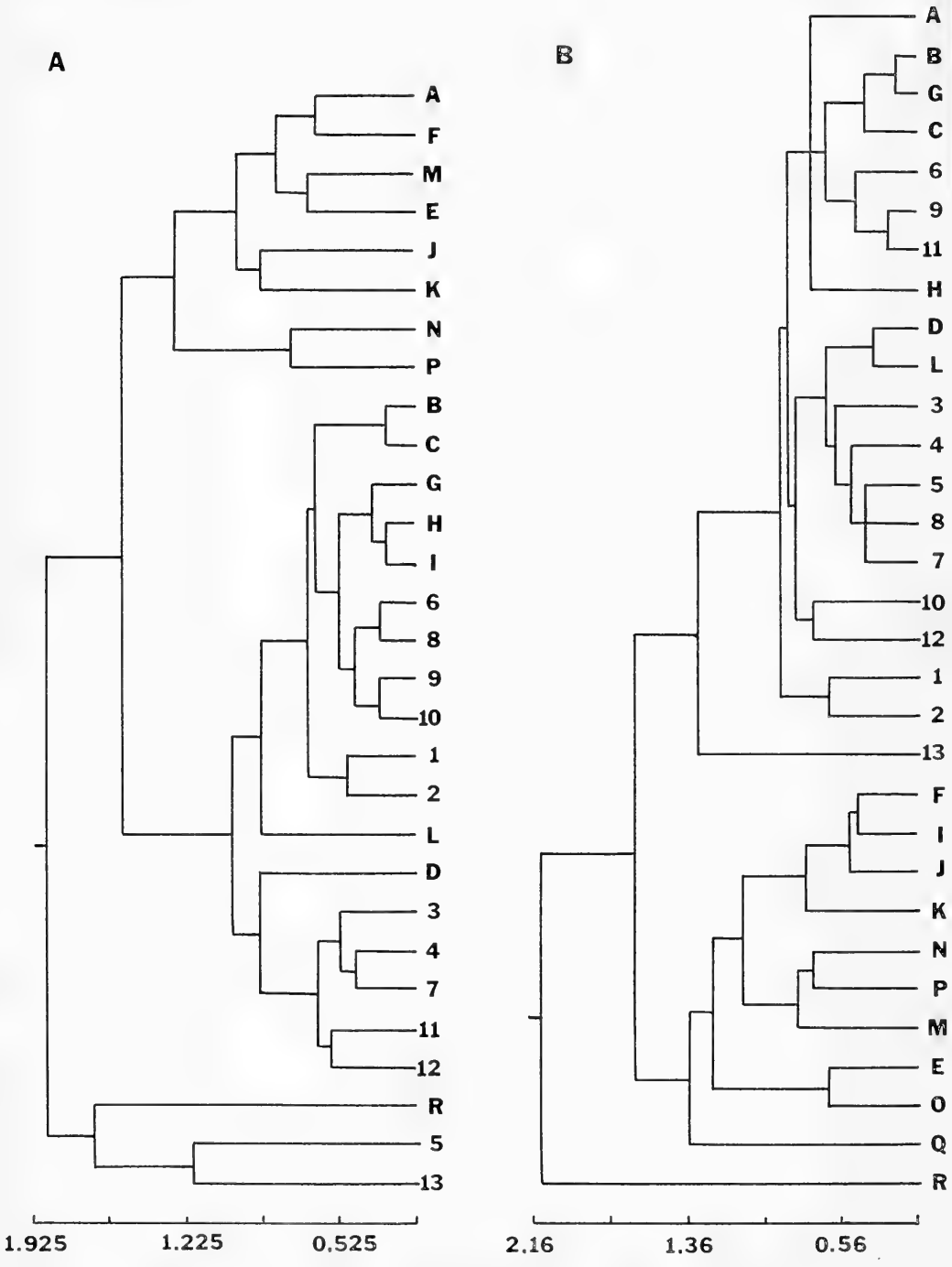

FIG. 25. Phenograms of UPGMA cluster analyses based on distance coefficients comparing standardized means of 14 mensural characters for 29 (females) and 31 (males) grouped localities of *Neotoma floridana* (1-13), *N. micropus* (A-Q), and *N. angustipalata* (R): A—females; B—males. See text for coefficients of cophenetic correlation, and figure 8 for geographic areas included within the coded localities.

dana overlap sufficiently that mensural characters alone do not segregate them into separate major clusters. The larger *micropus* tend to form conspecific group-clusters which are near group-clusters of larger *floridana;* smaller *micropus* tend to cluster separately from samples of smaller *floridana.* On some occasions samples A, F, and K, which are from localities geographically intermediate between large *micropus* and small *micropus,* clustered with the large *micropus* and smaller *floridana;* on other occasions, they clustered with the small *micropus.*

The 3-D projections of all samples of females and of all samples of males are shown separately in figure 26. The minimally connected networks were computed but have been omitted from the drawings to enhance determination of relative positioning of the OTU's. Projection of 29 OTU's on the three components for females results in a more nearly complete separation of samples of *micropus* and *floridana* than is seen in the two phenograms for females. Because each OTU is necessarily connected by the network directly to at least one other OTU and all OTU's are interconnected, it is necessary that at least one connection exist between a sample of *micropus* and one of *floridana.* In this instance two such connections exist. Sample 9 (northeastern Oklahoma *floridana*) connects to sample H (southwestern Oklahoma *micropus*), and sample D (south-central Kansas *micropus*) connects to sample 7 (southeastern Kansas *floridana*). All samples of *N. micropus* are directly or indirectly interconnected without involving a sample of *floridana,* but *floridana* samples 1, 2, 6, 8, 9, and 10 are connected to other samples of *floridana* through a series of samples of *micropus* (9 to H to I to G to C to D to 7). *N. angustipalata* connects only to *N. m. canescens* sample L.

In the 3-D projection of males, only the minimal number (two) of interspecific connections were computed. Sample 9 is connected to sample H to join *micropus* and *floridana. Neotoma angustipalata* joins only to sample 13, *N. f. rubida.* In the unconnected drawing (Fig. 26), it can be seen that several samples of *micropus* overlapped samples of *floridana* on the first component. The connections of these *micropus* samples were G to A, and B to C to D to L. In the 3-D projections for females there are two distinct groups of *floridana* samples. A tendency exists toward a similar separation on the projections for males, but it is less distinctly defined.

Multivariate Analyses of Size, Color, and Qualitative Cranial Characters

Following multivariate analyses of the 14 mensural characters discussed above, similar analyses were conducted using the same 14 mensural characters together with four color reflectance scores and three, scored, qualitative cranial characters. Thus a total of 21 characters was available for each sex of each sample. Instead of analyzing sexes separately as above, the 21 characters for each were pooled and used as 42 characters for each sample. For the two samples composed only of a single male specimen each (O and Q), the 21 characters were treated twice, once with those for males and once with those for females. Measurements of bacula or other characters were not included because data for one or more samples were not available.

The results obtained depict the relationships of the various OTU's in a more comprehensive way than do interpretations based on separate analyses (by sex) of mensural characters alone. However, an understanding of the relationships based only on mensural characters is necessary to understand overall geographic trends in size and to determine relative distinctness or indistinctness of various taxa based solely on dimensions and relative proportions.

Neotoma floridana.—CLSNT based on 42 characters as described above using the 13 samples of *Neotoma floridana* yielded results congruent with the present classification. The coefficient of cophenetic correlation is 0.727 between the

FIG. 26. Three-dimensional perspective drawings of the projections of 29 (females) and 31 (males) samples of *Neotoma floridana* (1-13), *N. micropus* (A-Q), and *N. angustipalata* (R) onto the first three principal components based on correlations among 14 mensural characters: A—females; B—males. See text for percentages of variation in each component and figure 8 for geographic areas included within the coded localities.

correlation phenogram (Fig. 27) and the matrix from which the phenogram was computed. Two major clusters are separated by a correlation of –0.24. This phenogram, which was computed from data on males and females, is remarkably unlike the correlation phenogram discussed above for *floridana* females. Despite several minor alterations, it resembles the correlation phenogram of *floridana* males. The relatively high correlation between *N. f. attwateri* and *N. f. rubida* is indicative of proportional similarity of the two, and possibly reflects intergradation between the two in southeastern Texas. The two samples of *N. f. campestris* from western localities (2 and 3) are also relatively highly correlated. Characteristics of *campestris* from locality 4 are more highly correlated with those of *attwateri* than with other samples of *campestris*. In this phenogram, *balieyi* appears more like *campestris* than *attwateri*.

The distance phenogram (Fig. 27) for *floridana* is characterized by several major shifts in the positioning of OTU's relative to that seen in the correlation phenogram. These shifts affect primarily the non-*attwateri* samples; samples 6, 8, 9, and 10 remain relatively close together and samples 7 and 11 remain together. Sample 12, which is highly correlated to 13, is placed with two other

samples of *attwateri*, 7 and 11, in the distance phenogram. Samples 4 and 5 are removed from a correlation cluster with the "large" *attwateri* samples and placed with sample 3. Sample 3 is clustered with samples 1 and 2 in the correlation phenogram. These two samples (1 and 2) remain together, but are separated by an appreciable distance (1.15). Sample 13 *(rubida)* is the most distinct sample in the distance phenogram. The coefficient of cophenetic correlation for this phenogram is 0.769.

The first five principal components were extracted in computations involving 42 characters. The percent variation in these is 36.6, 22.6, 12.2, 9.8, and 5.1 for a total of 86.3 percent; 71.4 percent of the variation is in the first three components. The 3-D projection of the 13 OTU's on the first three components (Fig. 28) and the minimally connected network (not figured) indicate that sample 7 is intermediate between other samples in many respects; five independent subgroups interconnect by direct attachment to sample 7. One subgroup consists only of sample 5 (sample 5 and 7 are the two most distant directly-connected samples of *attwateri*) and another only of sample 11. A third subgroup includes sample 12 relatively close and sample 13 at a considerable distance. Another includes the four samples of small-sized *attwateri* and the last includes the three samples of *campestris* and one of *baileyi*. The latter "lineage" is especially interesting because neither the correlation nor the distance phenogram placed the three samples of *campestris* together. Moreover, the sequence of the connections is 4 to 3 to 2 to 1; geographically this corresponds east-west for the three samples of *campestris*. The significance of the apparent relationship between *baileyi* and *campestris* will be discussed below with respect to zoogeographic history.

Neotoma micropus and *Neotoma angustipalata*.—The correlation phenogram for the 18 samples of *N. micropus* and *N. angustipalata* (Fig. 29) has a coefficient of cophenetic correlation of 0.815 and consists of three major clusters. Placement of the five samples of small

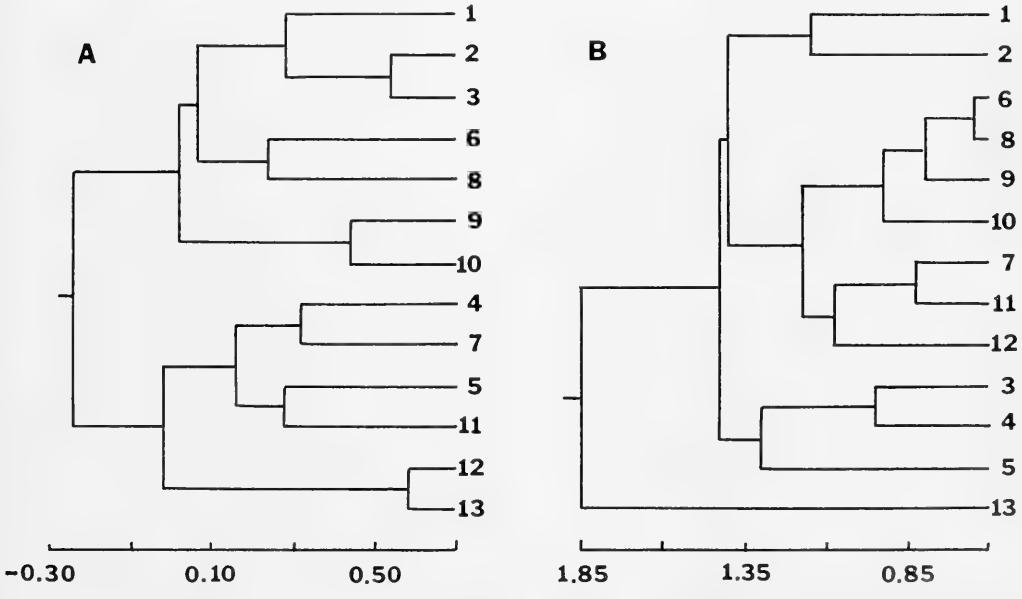

FIG. 27. Phenograms of UPGMA cluster analyses based on correlation (A) and distance (B) coefficients comparing standardized means of 42 mensural, color, and scored cranial characters for 13 geographic localities of *Neotoma floridana*. See text for coefficients of cophenetic correlation, and figure 8 for geographic areas included within the coded localities.

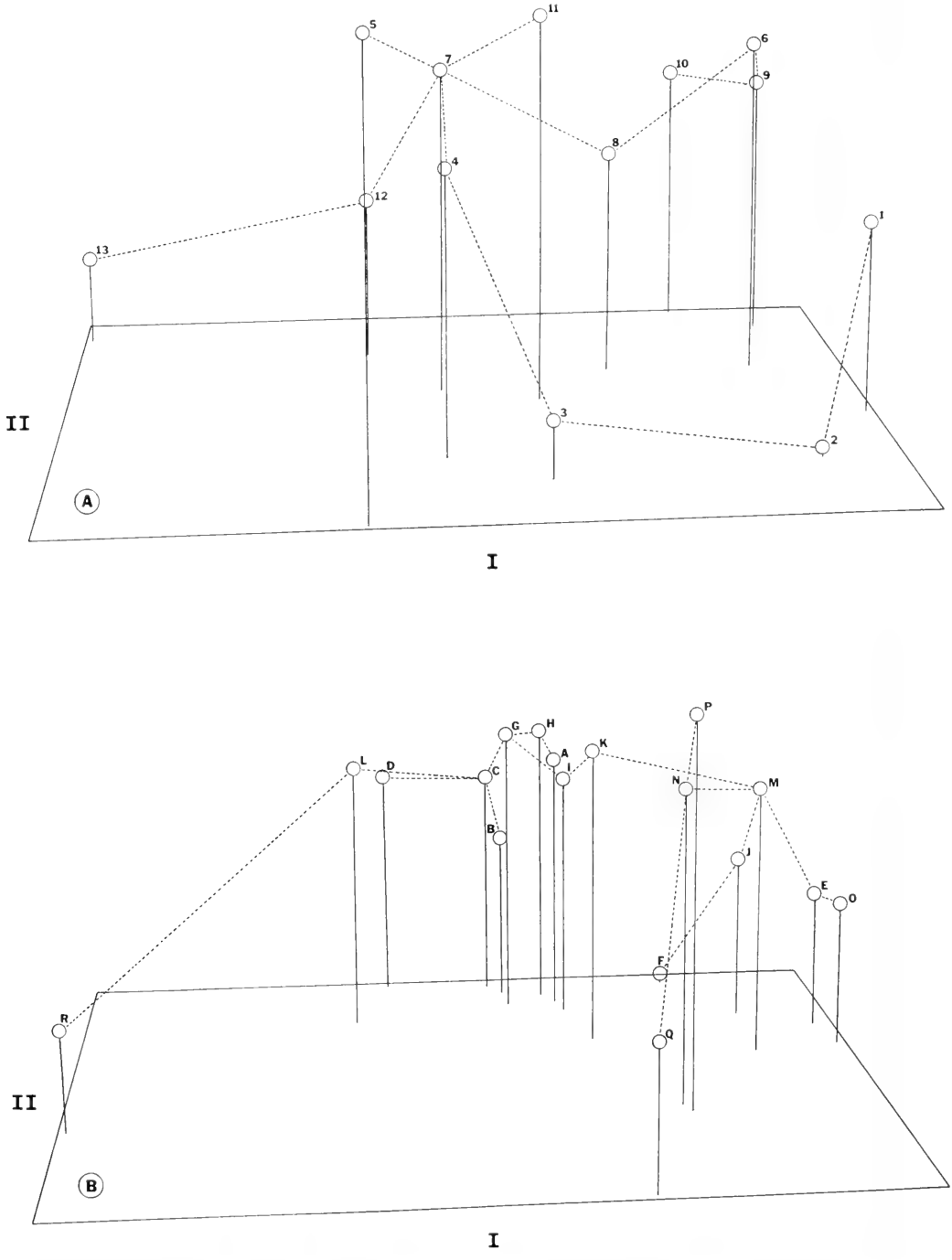

FIG. 28. Three-dimensional perspective drawings of the projections of 13 samples (OTU's) of *Neotoma floridana* (A) and 18 samples (OTU's) of *N. angustipalata* and *N. micropus* (B, compare with Fig. 30) onto the first three principal components based on correlations among 42 mensural, color, and scored cranial characters. Dashed lines between OTU's illustrate the minimally interconnected networks computed from the respective among-OTU distance matrices. See text for percentages of variation in each component, and figure 8 for geographic areas included within the coded localities.

and pallid woodrats from New Mexico, western Texas, Coahuila, and Nuevo León in a single cluster seems reasonable on an *a priori* visual basis. The intermediacy of specimens from locality K is indicated by the low correlation (0.16) between that sample and other samples from eastern and northern localities. As in other phenograms reflecting both correlation and distance, samples N and P *(N. m. micropus)* cluster separately from samples of *N. m. canescens*. Although specimens of *canescens* from locality L and specimens of *angustipalata* do not resemble each other in general appearance, these two samples are similar proportionally. However, as previously discussed, they do not cluster together when distances are emphasized.

The distance phenogram (Fig. 29) for these 18 samples of woodrats is somewhat unique in that there are few small group-clusters anastomosing to form larger clusters; instead, there is a high incidence of individual OTU's sequentially joining clusters composed of less distinct OTU's. The coefficient of cophenetic correlation between the phenogram and the distance matrix is 0.891.

The distinctness of *angustipalata* is again substantiated by the distance phenogram, and *N. m. planiceps* appears more distinct than indicated by results of other analyses. It must be remembered, however, that the latter "sample" consists of a single young adult male. This consideration is especially important because characters of that one specimen have been used for both males and females. Nevertheless, the results indicate

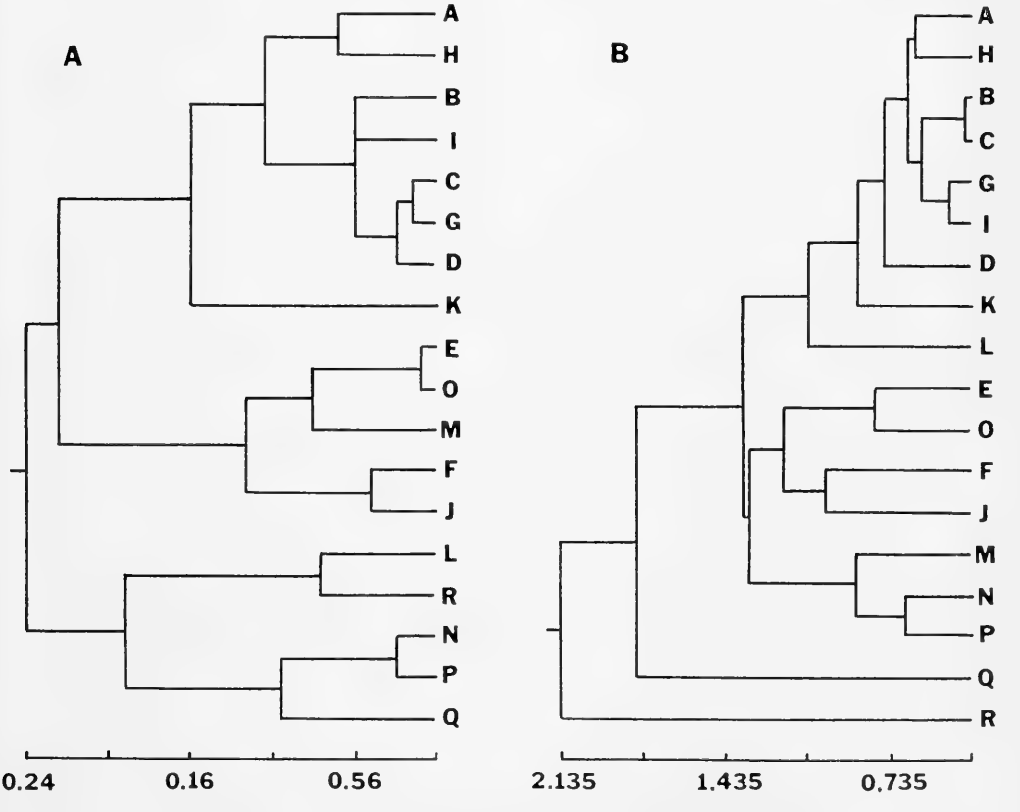

FIG. 29. Phenograms of UPGMA cluster analyses based on correlation (A) and distance (B) coefficients comparing standardized means of 42 mensural, color, and scored cranial characters for 18 geographic localities of *Neotoma micropus* (A-Q) and *N. angustipalata* (R). See text for coefficients of cophenetic correlation, and figure 8 for geographic areas included within the coded localities.

that *planiceps* is not especially similar to samples of either *N. m. micropus,* or *N. m. canescens* and should be recognized as a distinct subspecies until more specimens are available. Also, *planiceps* did not cluster with *angustipalata* as has been seen in some other analyses.

Clustering relationships indicate that there is slight morphological basis for recognizing two subspecies (as has been done in the past) for the woodrats that I have considered collectively under the name *N. m. canescens.* Of the six samples most closely clustered, three previously were assigned to one subspecies and three to another. Furthermore, placement of samples F, J, and K in the various phenograms and 3-D projections together with results of univariate analyses clearly indicate that any subspecies boundary merely would divide the woodrats into two groups from some arbitrarily selected place within a series of partially discordant clines.

Principal components analysis of these 18 samples considered 87.2 percent of the total variation when five components were extracted. Percents of variation in the first five components considered sequentially are 37.2, 30.3, 9.5, 5.7, and 4.5. When projected onto the first three components (Fig. 28), which contain 77 percent of the total variation, the results are similar to those seen in the distance phenogram. The impression of close relationship among the six samples of *N. m. canescens* from northern and eastern localities in the range is maintained; samples D, L, and K connect directly to this "cluster" but do not connect directly to each other. Sample R *(angustipalata)* constitutes the most distinctive OTU and connects only to sample L. Sample M, which serves as an "intermediate", connects to sample K, then serves to connect samples E and O on one "lineage", F and J on a second, and N on a third. Sample N connects first to sample P and at a much greater distance to sample Q *(planiceps).*

The placement of OTU's and the connections shown by the minimally connected network of the 3-D projection for *N. micropus* is congruent with the nomenclatorial arrangement of these woodrats proposed here. Figure 30 illustrates the placement of OTU's on the first and second components better than can be seen in the 3-D drawing (Fig. 28). This figure represents a two-dimensional scatter-diagram of the OTU's on these two components; the three-dimensional minimally interconnected network has been added together with the distance coefficients from the original distance matrix for all directly connected OTU's. In viewing this figure it should be noted that discrepancies between apparent and computed distances separating OTU's are accounted for in the third dimension, which is illustrated in figure 28.

Neotoma angustipalata, recognized as a distinct species, is well separated to the left and to the front of the plotting surface on figure 30. Furthermore, *angustipalata* is not connected to any of the samples of *micropus* from geographically contiguous localities. *N. m. planiceps* is well separated from all other OTU's, especially on the second component, and connects only to a sample of *N. m. micropus* from adjacent Tamaulipas. The two samples of *N. m. micropus* are closely placed on the first and second principal components and are situated in a position nearly intermediate between the nearest OTU's, representing *canescens* and *planiceps.* They connect directly to *planiceps* and to the sample of *canescens* from adjacent Nuevo León and Coahuila. The remaining OTU's all representing samples of *canescens,* are placed in a single "cluster", showing the trend toward smaller individuals in the southwestern parts of the range (samples E, O, J, and M) and the intermediacy of samples F and K.

Simultaneous Treatment of Three Species.—The correlation phenogram that was computed when the 42 character states of the 31 samples (all three species) of woodrats were treated simultaneously is shown in figure 31. This phenogram has a coefficient of cophe-

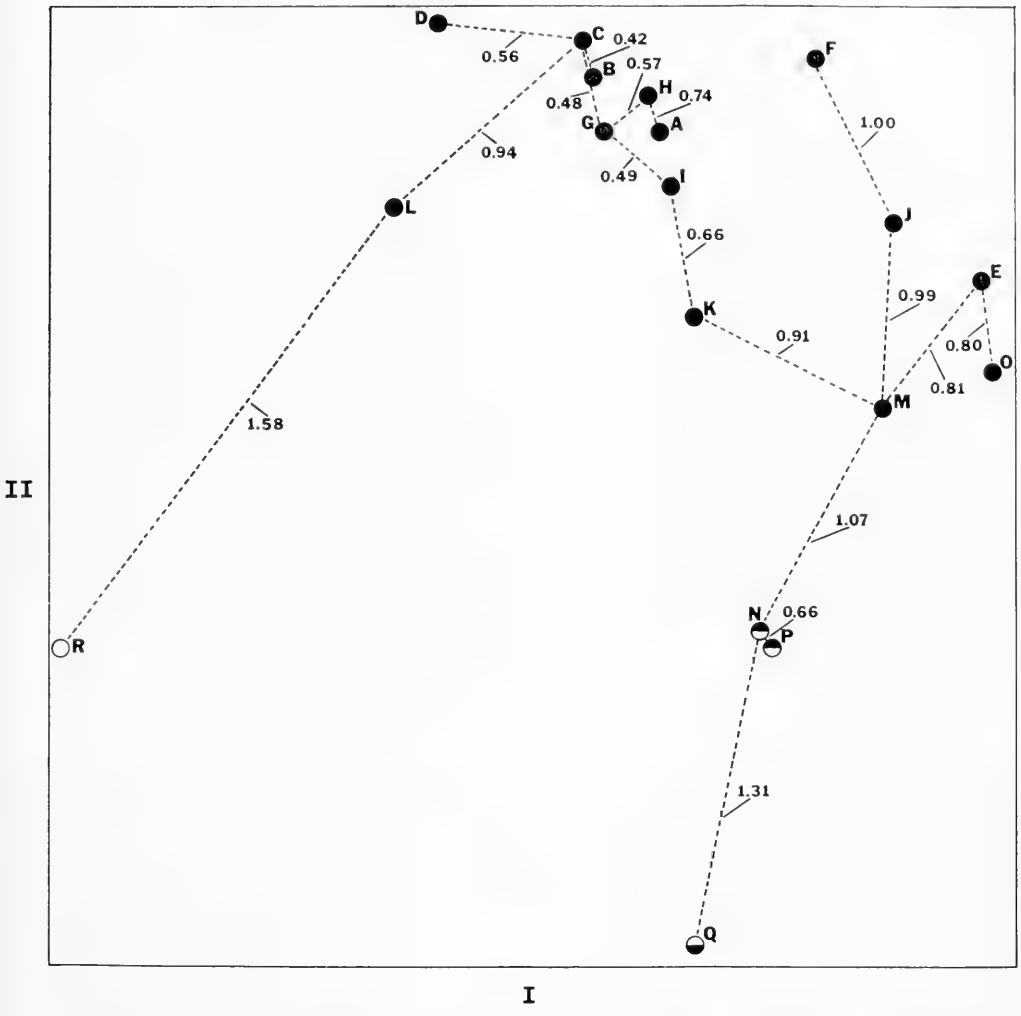

FIG. 30. Two-dimensional drawing of the projections of 18 samples (OTU's) of *Neotoma micropus* (A-Q) and *N. angustipalata* (R) onto the first two principal components based on correlations among 42 mensural, color, and scored cranial characters. Dashed lines between OTU's illustrate the minimally interconnected networks computed from the among-OTU distance matrices. Distance coefficients from the distance matrix are given for each pair of directly connected localities. See text for percentage of variation in each component, and figure 8 for geographic areas included within the coded localities (nominal taxa are shown with distinctive symbols). This figure should be compared with figure 28B.

netic correlation of 0.863 with the correlation matrix. The major separation at a correlation of –0.325 separated all samples of *N. floridana* into one cluster and all samples of *N. micropus* with the single sample of *N. angustipalata* into the other. This phenogram corresponds well with results seen in 3-D projections and in distance phenograms for both species, with the obvious exception of the placement of *N. f. rubida*.

The distance phenogram (Fig. 31) for computations on samples of the three species simultaneously has a coefficient of cophenetic correlation of only 0.714 to the distance matrix. This is unusually low compared to the coefficient (0.863) for the correlation phenogram and ma-

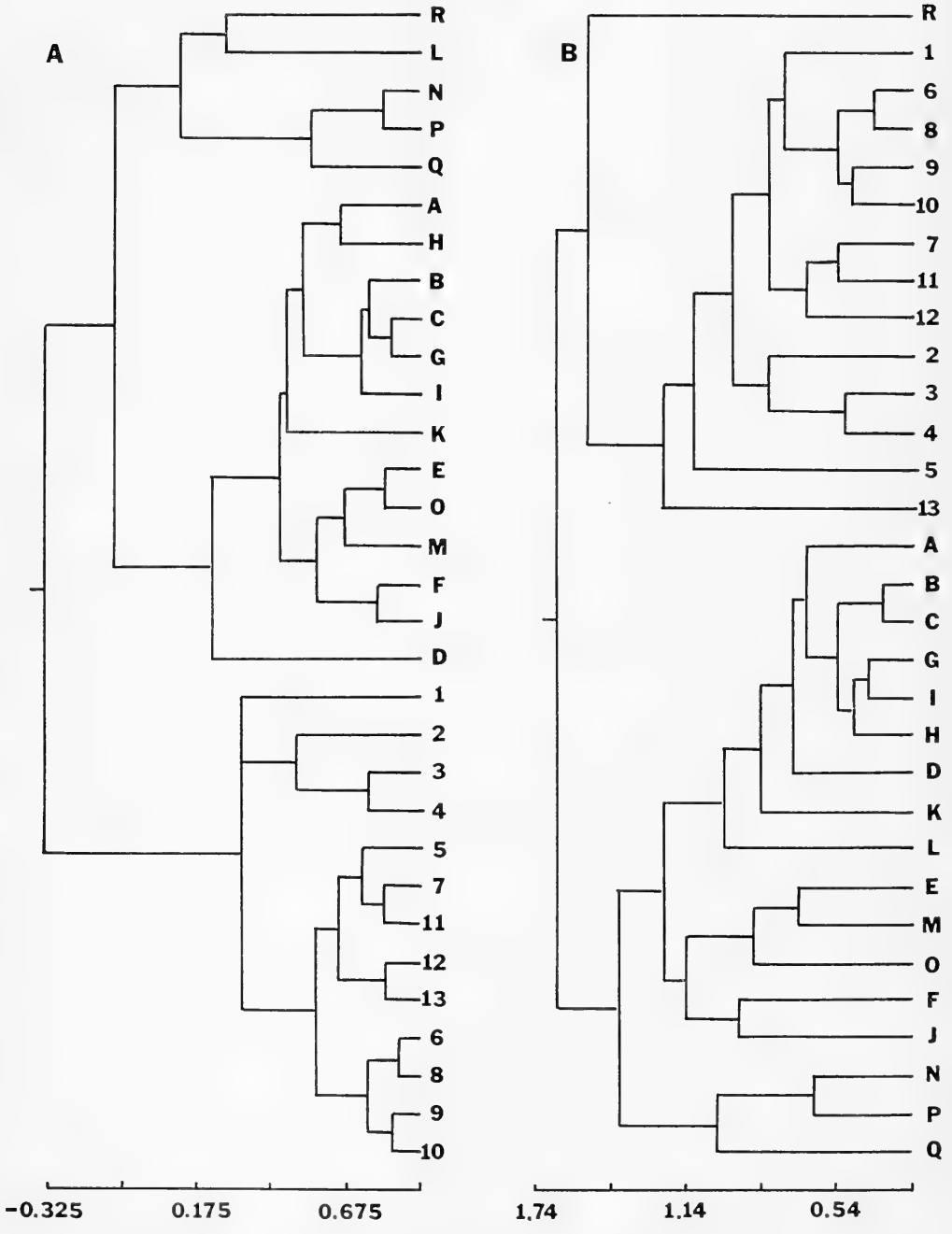

FIG. 31. Phenograms of UPGMA cluster analyses based on correlation (A) and distance (B) coefficients comparing standardized means of 42 mensural, color, and scored cranial characters for 31 geographic localities of *Neotoma floridana* (1-13), *N. micropus* (A-Q), and *N. angustipalata* (R). See text for coefficients of cophenetic correlation, and figure 8 for geographic areas included within the coded localities.

trix; normally the highest coefficient is for distance. Four major clusters are seen in the distance phenogram. At the first bifurcation, all samples of *micropus* are placed together in two clusters. *Neotoma angustipalata* forms a third "cluster" by itself that connects at a distance of 1.53 to the fourth major cluster (composed of the 13 samples of *N. floridana*). Within the *floridana* cluster, two OTU's (5 and 13) are relatively distinct; this was expected for sample 13 *(rubida)* but I anticipated that sample 5 (*attwateri* from north-central Kansas) would cluster either with other samples of *attwateri* or with samples of *campestris.* The three samples of *campestris* form a distinct cluster, and *baileyi* appears relatively distinct, but joins the samples of smaller *attwateri* before they are joined by the samples of larger *attwateri.*

Of the two major clusters of *N. micropus,* one consists of the 14 samples of *N. m. canescens* and the other of the two samples of *N. m. micropus* along with *N. m. planiceps.* The two samples of *N. m. micropus* join at a distance of 0.63, and *planiceps* joins that couplet at a distance of 1.02. In the distance phenogram shown in figure 29, *canescens* from locality M appears more like samples of *N. m. micropus* than like other samples of *canescens;* in the large phenogram, sample M is placed with other samples of *canescens.* In both phenograms, the small, pallid woodrats from New Mexico, western Texas, and adjacent Mexico tend to form a relatively homogeneous and distinct subgroup. This relationship is seen also when OTU's are projected onto principal components. I considered the possibility (see introductory remarks in the account of *N. micropus* above) of applying the available name *N. m. leucophea* to those woodrats from localities E, F, J, M, and O. However, there are no indications of well marked "steps" in clines of variation, and no apparent past or present geographic or physiographic barriers. Because there seems to be no way to designate a meaningful boundary between the two potential taxa, this arrangement was rejected.

Principal components analysis on the character correlation matrix extracted 50.1, 15.9, 7.8, 6.6, and 3.9 percent of the variance for the first five principal components, respectively. Of this, 73.8 percent is in the first three components. A three-dimensional drawing of the 31 OTU's projected onto the first three components is shown in figure 32. The minimally connected network has been omitted from the 3-D projection but is given in figure 33, which shows two two-dimensional scatter diagrams wherein the 31 OTU's are projected onto components one and two (33A) and one and three (33B). The three drawings considered simultaneously show undistorted spatial relationships of the OTU's on the principal components and further elucidate the congruency between the results of these analyses and the nomenclatorial arrangement I have applied to the woodrats.

Samples of *micropus* and *floridana* are completely separated on the first component, although *micropus* sample L nearly overlaps *floridana* samples 1 and 2. Also on the first component, *angustipalata* is placed with *floridana* and widely separated from *micropus. Neotoma floridana rubida* is placed to the left of other samples of *floridana* on that component, and the samples of small southwestern *N. m. canescens* are placed to the right of the samples of larger northern and eastern *canescens.*

On the second component, samples of *N. f. campestris* are separated from other samples of *floridana.* Sample 5 (*attwateri* from north-central Kansas) is between samples of *campestris* and those of other *attwateri,* but on a tangent relative to the first component. This sample of *attwateri* (5) and the sample of *baileyi* (1) both are connected to other samples of *attwateri,* but not to samples of *campestris* or to each other. In part, this projection implies that *baileyi* might best be considered as the same taxon as *attwateri* (*baileyi* is the oldest available name and would be the valid name for all if this

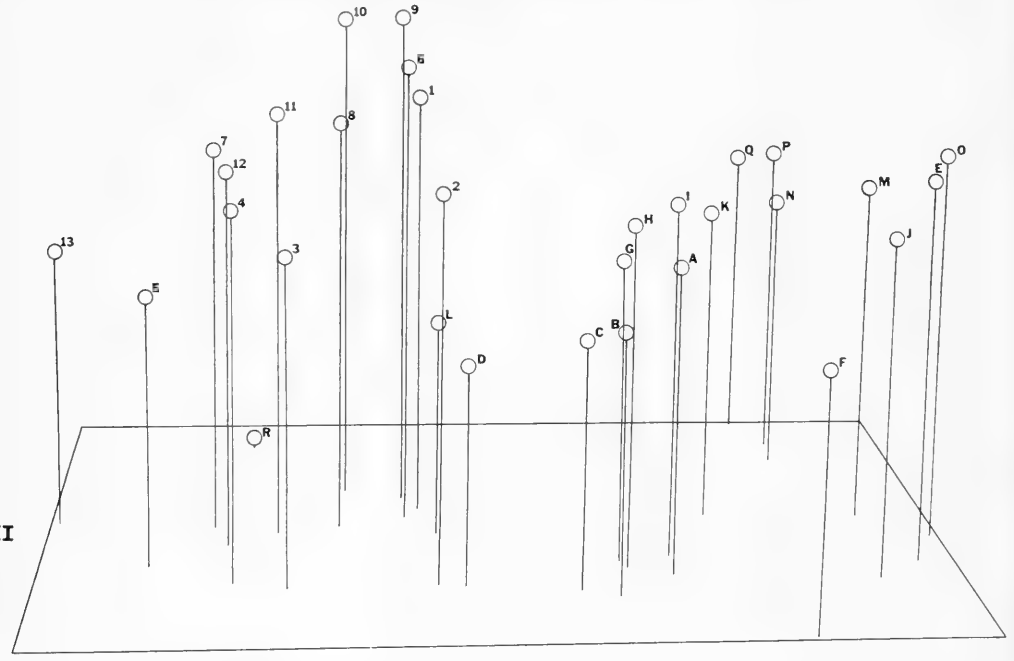

FIG. 32. Three-dimensional perspective drawing of the projections of 31 samples (OTU's) of *Neotoma floridana* (1-13), *N. micropus* (A-Q), and *N. angustipalata* (R) onto the first three principal components based on correlations among 42 mensural, color, and scored cranial characters. See text for percentages of variation in each component, and figure 8 for geographic areas included within the coded localities. This figure should be compared with figure 33.

was done). *Neotoma angustipalata* is distinctly separated from samples of *floridana* on the second component. When samples of *N. micropus* are considered, it can be seen that the second component separates samples P and N (*N. m. micropus*) and sample Q (*planiceps*) in one direction and sample E (*canescens* from the Texas panhandle) in the other; remaining samples are similarly placed on these two components.

The third component further separates *angustipalata* from all samples of *floridana* and clearly demonstrates the distinctiveness of *micropus* samples D and L from *floridana* samples 1, 2, 6, and 9. On both the first and second components, these six samples are placed in relatively close proximity. From the distance matrix, it can be seen that the separation between D and 2 is 1.15, that between L and 8 is 1.04, that between L and 6 is 1.05, and that between L and 2 (which appear especially close on the 3-D projection) is 1.16. In the minimally connected network, only two interconnecting lines (the minimal number) connect OTU's of different species. *Neotoma angustipalata* is connected to *N. f. attwateri* sample 7 at a distance of 1.58, and *N. m. canescens* sample D is connected to *N. f. attwateri* sample 8 at a distance of 0.94.

With the exceptions of a relatively high degree of distinctiveness in *attwateri* sample 5, the apparent affinities of *baileyi* with *attwateri*, and the relative distinctiveness of samples of *canescens* from southwestern localities, the classification I have employed is in accord with the results of this principal components analysis. It clearly shows that *angustipalata* is phenetically distinct and that *floridana* and *micropus* are morphologically distinct and should not be considered conspecific. The distinctiveness of

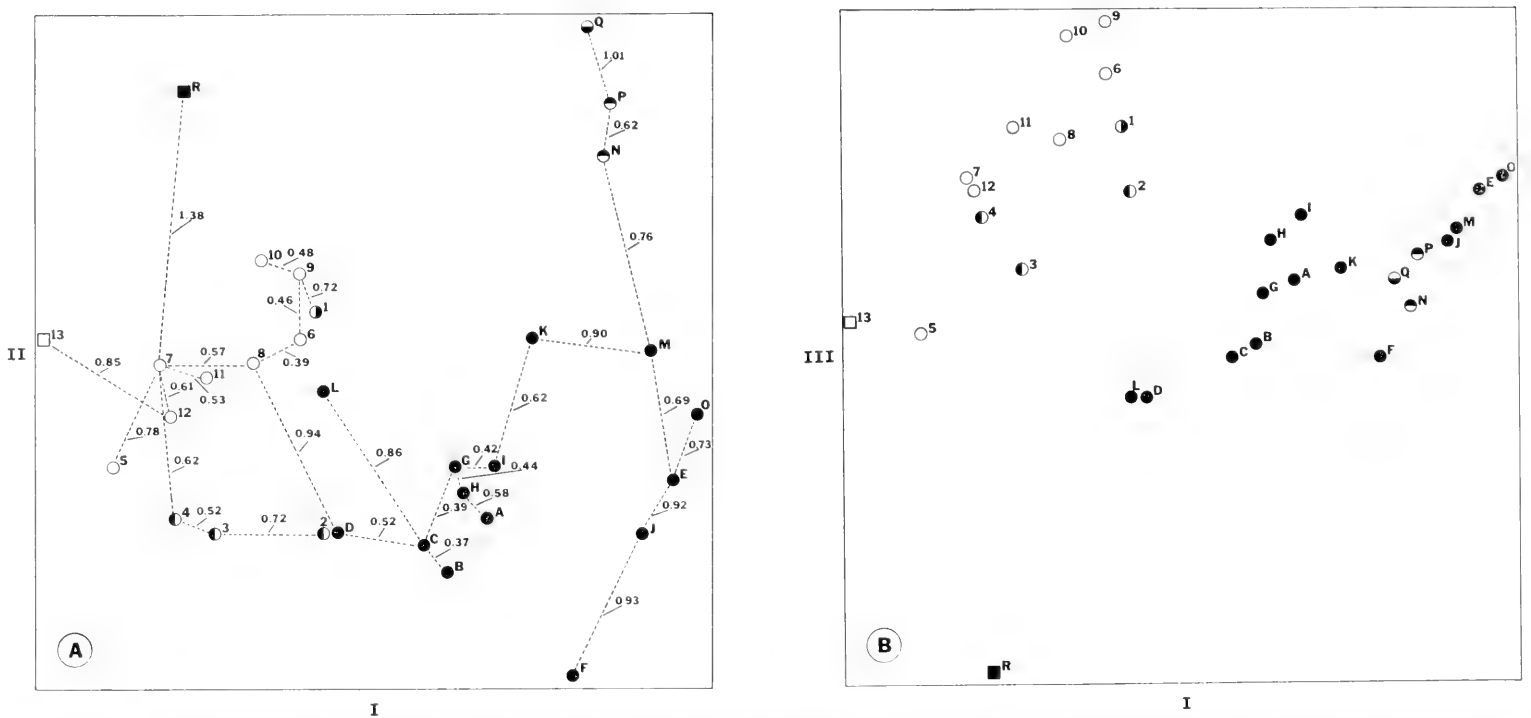

FIG. 33. Two-dimensional drawings of the projections of 31 samples (OTU's) of *Neotoma floridana* (1-13), *N. micropus* (A-Q), and *N. angustipalata* (R) onto the first and second (A), and first and third (B) principal components based on correlations among 42 mensural, color, and scored cranial characters. The dashed lines between OTU's on A illustrate the minimally interconnected networks computed from the among-OTU distance matrix. Distance coefficients from the distance matrix are given (A only) for each pair of directly connected localities. See text for percentage of variation in each component, and figure 8 for geographic areas included within the coded localities (nominal taxa are shown with distinctive symbols). This figure should be compared with figure 32.

N. f. campestris and *N. f. rubida* as compared to contiguous samples of *N. f. attwateri* can be seen also. Similarly, *N. m. micropus* and *N. m. planiceps* are shown to be clearly distinct from *N. m. canescens.* There appears to be some basis for recognition of another name *(N. m. leucophea)* for specimens from New Mexico, western Texas, and adjacent Mexico; the question that arises is basically a matter of one's concept of the limits of a subspecies.

Were *Neotoma floridana baileyi* and *N. f. attwateri* geographically contiguous, I would consider them a single taxon. However, *baileyi* clearly is isolated, and has been shown to share nearly equal affinities with *campestris.* Furthermore, it is relatively unique with respect to qualitative cranial characters. Therefore, I think it best to continue to recognize *baileyi* as subspecifically distinct. To consider those rats from locality 5 (north-central Kansas) as a new subspecies on the basis of their uniqueness in the distance phenogram and 3-D projection just discussed would be, in my estimation, a gross error. The sample from that area is small and there is no reason to believe that the population of woodrats there represents a truly distinctive evolutionary unit. It is possible that the large size and apparent distinctiveness of woodrats from the narrow zone of secondary intergradation between *campestris* and *attwateri* reflect some effect (possibly heterosis) of recent hybridization.

There is some basis for naming as a distinct subspecies those large and relatively distinct populations (L) of *micropus* from southern coastal Texas. They are different from woodrats in adjacent Tamaulipas (and herein are assigned to different subspecies), but study and statistical analysis of all available specimens from southern Texas indicate that the pattern of variation to the north and west from coastal Texas is clinal and that woodrats from locality K (non-coastal southern Texas) show varying degrees of intermediacy between those from locality L and those from localities J, I, and M.

Discriminant Function Analysis

Discriminant function analysis has been employed by Lawrence and Bossert (1969) to distinguish dog-coyote hybrids; these authors (1967) also were able to identify skulls of wild canids with this relatively sophisticated technique. Anderson (1969:44) conducted a preliminary discriminant analysis to distinguish specimens of *Neotoma micropus* and *N. albigula;* he found that members of the two species could be separated better in this way than by factor analysis.

I have used discriminant function analysis (MULDIS) to compare individual specimens of woodrat taxa as follows: *Neotoma floridana baileyi* with *N. f. attwateri; N. f. campestris* with *N. f. attwateri; N. f. campestris* with *N. m. canescens;* and *N. f. attwateri* with *N. m. canescens.* In some cases, specimens from geographically intermediate samples, suspected hybrids, or laboratory-bred hybrids were included as a third group for comparison with reference samples. In one instance, only the reference samples were compared. These analyses were conducted to determine: 1) if the nominal taxa are sufficiently and consistently distinctive at the level of the individual in the 10 cranial dimensions, four color reflectance scores, and three scored qualitative characters so that discriminant analysis could distinguish members of the different taxa by differentially weighting characters to accentuate existing differences; 2) if known hybrids between *floridana* and *micropus* could be distinguished by use of the discriminant technique; 3) if discriminant scores of suspected hybrid individuals would be similar to those of known hybrids; and 4) if a series of discriminant multipliers could be calculated from identified reference samples so that future material could be identified by multiplying the values of the same 17 characters by the discriminant multipliers and then summed to compare discriminant scores. The characters used in these analyses have been described previously.

Males and females of Groups VI-VIII were treated together. In addition to the calculations of values previously mentioned, MULDIS also computed the "best" placement of each individual in the original reference samples and indicated the number, if any, that would "best" have been included in the other reference sample.

In comparisons of *N. f. baileyi* and *N. f. attwateri*, 18 specimens of *baileyi* from several localities within the range of the subspecies were compared with 36 specimens of *attwateri* from localities 6-10. Because *baileyi* is geographically isolated, there are no suspected natural hybrids or geographic intermediates and discriminant scores for a "test" sample of laboratory hybrids were not computed. Although there is no overlap between the discriminant scores of the two subspecies (Fig. 34), one specimen of *attwateri* is more like the reference specimens of *baileyi* than like other specimens of *attwateri*. The mean and range (in parentheses) of discriminant scores from *attwateri* and *baileyi*, respectively, are 14.20 (12.32-16.85) and 18.87 (17.47-20.92). When the single "wrongly placed" specimen of *attwateri* was removed, the upper extreme of that sample was reduced to 15.82. From the list of discriminant multipliers computed for these two taxa (Table 14), it can be seen that measurements of interorbital constriction, breadth of the rostrum, length of the nasals, and morphology of the sphenopalatine vacuities best serve to distinguish *baileyi* from *attwateri*. Only condylobasilar length and length of maxillary toothrow were weighted at especially low levels.

These results indicate that *baileyi* and *attwateri* are generally distinguishable at the level of the individual, but that a few individuals of one taxon may closely resemble members of the other morphologically. As previously discussed, most skulls of *baileyi* can be identified by the three scored cranial characters included in the discriminant function analysis. Of these, only one (sphenopalatine vacuities) was weighted relatively high. Reflectance values were computed by analysis of variance and SS-STP to be significantly different between *baileyi* and *attwateri*, but for some reason, probably because of the high within-group variance, these scores are not weighted noticeably higher than cranial dimensions.

A frequency histogram showing separation of the reference samples of *N. f. campestris* and *N. f. attwateri* together with the projection of four specimens from locality 5 (all from Ellsworth County, Kansas) is shown in figure 35. No overlap between the two samples is observed and all specimens are "best" considered in the sample with which they were originally placed. The mean and extreme (in parentheses) discriminant scores for the 36 specimens of *attwateri* (localities 6-10) and 27 specimens of *campestris* (localities 2-4), respectively, are 13.64 (11.05-15.32) and 18.66 (16.35-20.66). The discriminant multipliers calculated for the comparisons are shown in table 14. That for rostral breadth is especially high and those for reflectance of blue and green are relatively high. Color reflectance was expected to be heavily weighted, considering the differences in color between members of the two subspecies. Several characters are weighted relatively low, especially condylobasilar length.

Within the *attwateri* reference sample, there is a slight but noticeable tendency for the discriminant scores of specimens from localities farthest from the range of *campestris* to be least like those of *campestris*. Furthermore, within the *campestris* reference sample there exists an obvious tendency for specimens from locality 4 (adjacent to the range of *attwateri*) to cluster toward the *attwateri* reference sample. The specimen of *campestris* (KU 119700) with the second lowest discriminant score (17.11) is from a locality in Russell County, Kansas, only one mile west of the Russell-Ellsworth County boundary, which I have considered the general line of demarcation between the two races. Discriminant

TABLE 14. Discriminant multipliers computed for each of 17 characters by discriminant function analyses of reference samples of the four pairs of woodrat taxa indicated.

Character	Discriminant Multipliers			
	N. floridana baileyi and *N. floridana attwateri*	*N. floridana campestris* and *N. floridana attwateri*	*N. floridana campestris* and *N. micropus canescens*	*N. floridana attwateri* and *N. micropus canescens*
Greatest length of skull	0.655	−0.308	−0.035	0.301
Condylobasilar length	−0.097	0.010	0.168	−0.498
Zygomatic breadth	−0.340	−0.095	−0.687	0.391
Least interorbital constriction	0.989	−0.698	1.865	−0.965
Breadth at mastoids	0.331	0.212	0.089	−0.012
Length of rostrum	−0.112	−0.070	0.100	0.482
Breadth of rostrum	1.587	2.837	−0.061	1.176
Alveolar length of maxillary toothrow	0.071	0.184	−0.560	0.299
Length of palatal bridge	−0.175	−0.240	0.319	−0.283
Length of nasals	−1.350	0.168	−0.258	−0.363
Morphology of anterior palatal spine	0.204	0.305	0.870	−0.267
Morphology of posterior margin of palate	0.451	0.293	−0.587	0.697
Morphology of sphenopalatine vacuities	0.962	−0.614	−1.190	0.944
Reflectance of red	0.346	0.795	0.055	−0.106
Reflectance of blue	0.645	1.887	−0.632	0.871
Reflectance of green	0.556	1.321	0.111	−0.191
Reflectance total	−0.168	0.954	0.099	0.000

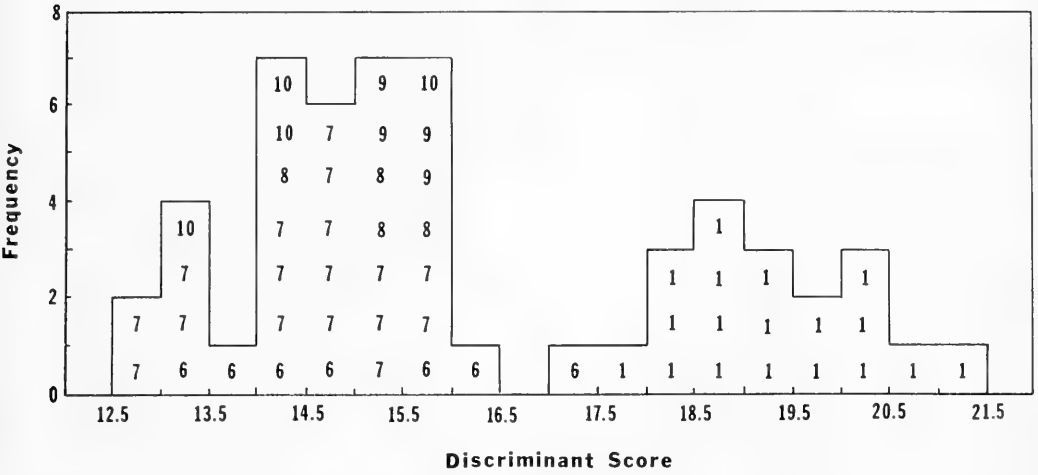

FIG. 34. Frequency histogram of discriminant scores computed by discriminant function analysis comparing individuals of *Neotoma floridana attwateri* (6-10) and *N. f. baileyi* (1). See figure 8 for geographic area of origin, indicated by numerals on the histogram, of each specimen.

scores of two of four specimens from just east of this line are intermediate between the extremes of the two reference samples. Although the scores of the other two are within the extremes for *attwateri*, they are near the *campestris* side of the histogram.

As determined by these analyses, *N. f. campestris* and *N. f. attwateri* are consistently distinct at the level of the individual. The area of presumed secondary intergradation apparently includes both Russell and Ellsworth counties, Kansas, because specimens from this area tend to have convergent, albeit distinct, discriminant scores. Additional specimens from the relatively narrow zone of contact between the two taxa might reveal

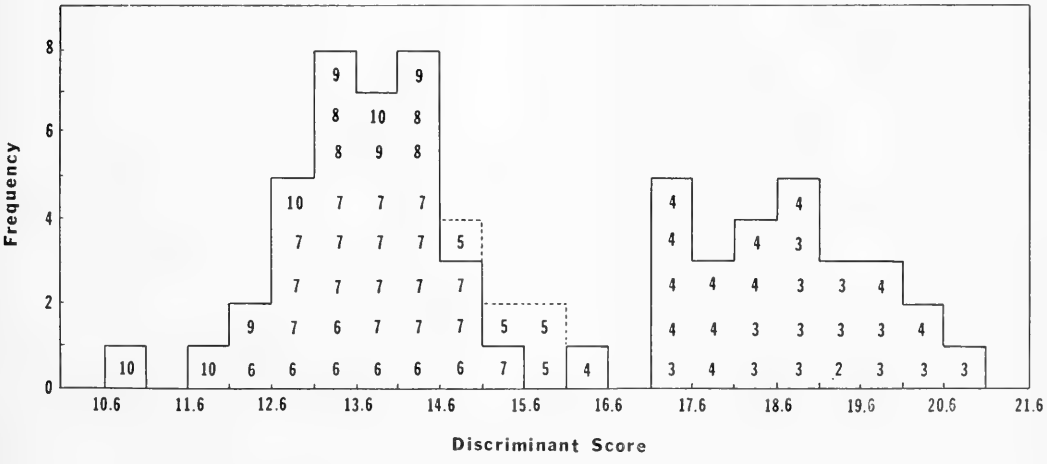

FIG. 35. Frequency histogram of discriminant scores computed by discriminant function analysis comparing *Neotoma floridana attwateri* (5-10) and *N. f. campestris* (2-4). Solid lines enclose individuals that were included in the two reference samples, whereas dashed lines enclose individuals of *attwateri* (5) from a geographically intermediate area whose scores were computed on the basis of discriminant multipliers computed during comparison of the reference samples. See figure 8 for geographic area of origin, indicated by numerals on the histogram for each specimen.

overlap of discriminant scores on the histogram between the two reference samples.

The histogram showing frequency of discriminant scores for 41 *Neotoma micropus canescens*, 27 *Neotoma floridana campestris*, and 11 laboratory-bred hybrids is shown in figure 36. Mean and extreme (in parentheses) scores for *canescens* and *campestris* are, respectively, –12.33 (–14.20 - –9.31) and –5.53 (–7.82 - –3.80). In each reference sample, one individual has a discriminant score that approaches the scores of the other species, but in both instances the specimens are "best" included with the conspecific reference sample. With these two individuals included, the reference samples are separated by 1.49 units, whereas without them the separation would have been 3.71 units. As noted above, specimens of *campestris* from locality 4 tend to have scores that are more like those of *attwateri* than are the scores of specimens from localities 2 and 3. A similar relationship is not observed when *campestris* is computed against *canescens*. Discriminant multipliers computed for the 17 characters are given in table 14. One cranial dimension, interorbital constriction, is weighted especially heavily. This undoubtedly results from the previously discussed (see account of qualitative cranial characters) differences in the morphology of the interorbital region. All three scored cranial characters are weighted relatively heavily, but only morphology of the sphenopalatine vacuities is given an absolute multiplier value greater than unity, indicating that differences in the vacuities between the two races are more consistent (less variance) than differences in the anterior spine and posterior margin of the palate. Reflectance of red and green and the summation of all reflectance readings are weighted low, but the reflectance value for blue is computed an above average discriminant multiplier.

Discriminant scores were computed for 11 laboratory-bred hybrids and projected onto the histogram. Of five individuals of the first filial generation (F1), two have scores in the same frequency

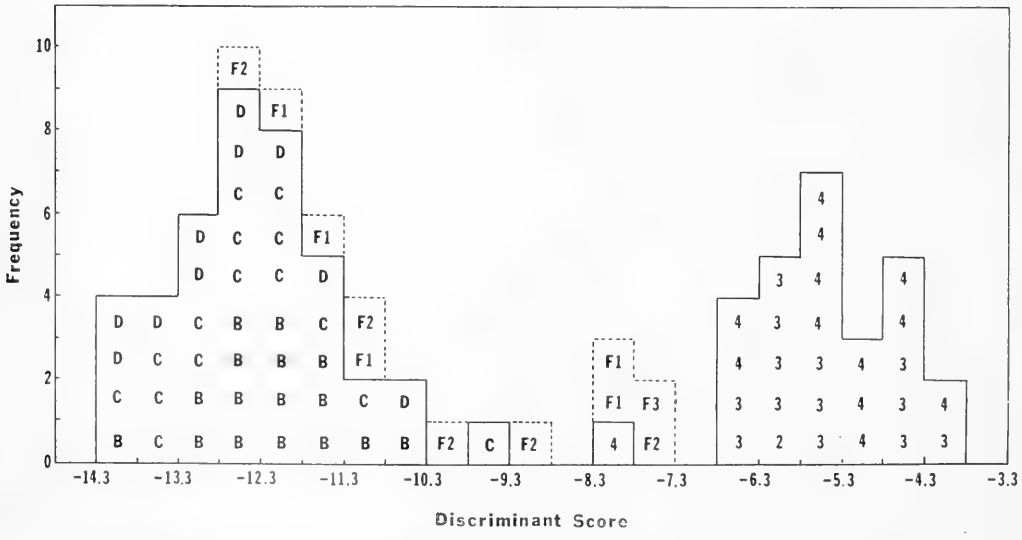

Fig. 36. Frequency histogram of discriminant scores computed by discriminant function analysis comparing *Neotoma floridana campestris* (2-4) and *N. micropus canescens* (B-D). See figure 35 for significance of solid and dashed lines. F1 and F2 indicate laboratory-bred hybrids between the two taxa of the first and second filial generations, respectively. F3 denotes a back-cross individual whose non-hybrid parent was an *N. f. campestris*. See figure 8 for geographic area of origin, indicated by numerals and letters on the histogram, for other specimens.

class as the "aberrant" individual of *campestris* discussed above. The other three have scores between the extremes of the *canescens* reference sample. These results are somewhat surprising, because I had expected F1 hybrids would fall in the 3.7 unit zone between the two reference samples. Considering the results of discriminant analysis of F1 hybrids, the scores of specimens from the second filial generation (F2) are about as expected. Again there is a tendency for the scores to be more like those of *canescens* than those of *campestris*. The range of variation is slightly greater than that of F1's, and the range of variation is less than that seen for the two reference samples. Only one adult (of 30 weeks of age or more) back-cross individual was available. This woodrat (F3), the progeny of an F1 hybrid mated to a *campestris*, has a discriminant score of –7.52, which placed it within the *campestris* range on the histogram.

The separation between *N. f. campestris* and *N. m. canescens* is adequate to demonstrate that the two can be distinguished by discriminant analysis. In the absence of the two extreme individuals, the separation would have been relatively great considering the small number of characters used and the close relationship of the two species. However, larger samples probably would show that the two specimens discussed are not "aberrant," but rather near the extremes of discriminant scores of the two taxa compared.

Reference samples of 36 *N. f. attwateri* from localities 6-10 and 41 *N. m. canescens* from localities B-D were used to compute discriminant multipliers in comparisons of these two taxa. Mean and extreme (in parentheses) dicriminant scores for individuals of the reference samples were 12.77 (10.29-14.98) for *attwateri* and 19.54 (17.34-21.56) for *canescens*. All individuals of both samples were computed to be in the "correct" sample; when discriminant scores were plotted on a frequency histogram (Fig. 37), none of the members of either reference sample had deviate scores resulting in placement in a class disjunct from other classes of the species.

As shown in table 14, rostral breadth again is weighted relatively heavily. Other characters that appear to differ consistently between the two taxa are interorbital constriction, sphenopalatine vacuities, and color reflectance of blue. The summated reflectance score (total) was given a multiplier value of 0.0, and thus was of no use in distinguishing individuals of *N. f. attwateri* and *N. m. canescens*. Mastoid breadth also was shown to be of little value in distinguishing members of the two taxa. Discriminant scores of 40 woodrats from a variety of sources were computed and projected onto the frequency histogram (Fig. 37) with scores of specimens in the two reference samples. This test group is composed of the following specimens: 1) 12 laboratory hybrids of the first filial (F1) generation; 2) six hybrids of the second filial (F2) generation; 3) two back-cross hybrids resulting from the mating of F1 hybrids with *micropus* (M3); 4) eight specimens that I had previously identified as *micropus* (S1) from the locality of sympatry of the two reference taxa (3 mi S Chester, Major Co., Oklahoma); 5) four specimens that I had previously identified as *floridana* (S2) from the locality of sympatry; 6) five specimens previously identified as natural hybrids from that locality (S3); 7) and three specimens from 8.9 mi S Aledo (14 mi SW Fort Worth), Parker Co., Texas (T), that did not appear to be typical representatives of *floridana*.

Six of the F1 hybrids have discriminant scores between the extremes of the scores of the parental species, as was expected for all. Five of the other six have scores that were near the lower end of the range of *N. m. canescens*, but the score of the sixth is like that of typical *canescens*. Most F1 hybrids apparently tend to be intermediate in the 17 characters employed, but somewhat more like *micropus* than *floridana*. Second generation hybrids (F2) are, on the aver-

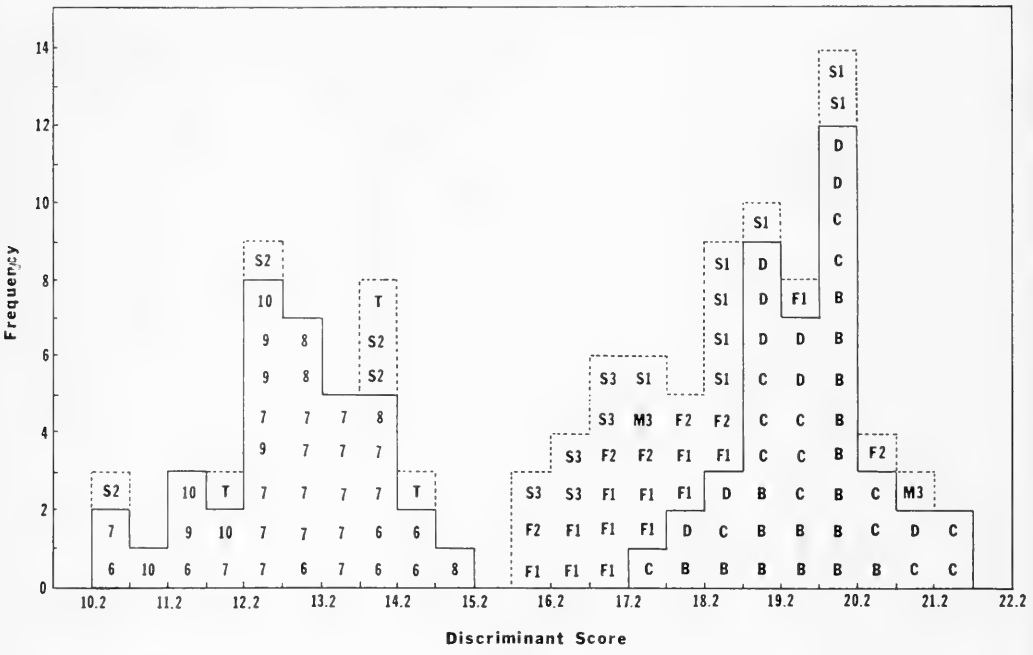

FIG. 37. Frequency histogram of discriminant scores computed by discriminant function analysis comparing *Neotoma floridana attwateri* (6-10) and *N. micropus canescens* (B-D). See figure 35 for significance of solid and dashed lines and see figure 8 for geographic area of origin, indicated by symbols on the histogram, for most specimens. Those not included in figure 8 and their identifying symbols (in parentheses) are as follows: laboratory-bred hybrids between the two taxa of the first and second filial generations (F1 and F2, respectively); laboratory-bred back-cross hybrids whose non-hybrid parent was *N. m. canescens* (M3); specimens from 3 mi S Chester, Major Co., Oklahoma, that had been identified previously as *N. micropus*, *N. floridana*, or hybrids (S1, S2, and S3, respectively); and specimens from 8.9 mi S Aledo, Parker Co., Texas, that were suspiciously atypical in color (T).

age, slightly more *micropus*-like than are F1 hybrids, and also are more variable. The score of one approaches the upper extreme of *micropus* scores; that of another approaches the most *micropus*-like *floridana* scores. None overlapped the scores of *floridana*. One of the two back-cross specimens (M3) demonstrates no perceptible affinities for *floridana*, but the score of the other is similar to those of F1 hybrids.

Considering animals from natural populations, the three suspiciously-colored specimens from Parker County, Texas, all have discriminant scores typical of *floridana*. The scores of two are above the mode for the *floridana* reference sample and one is near the upper extreme; none could be identified as "hybrid" or "intergrade" on the basis of discriminant scores. The scores of seven of the specimens from the area of sympatry that had been identified as *micropus* (S1) are typical of the scores of reference *micropus*. The score of the eighth (17.68), however, is larger than that of only one individual in the *micropus* reference sample, and thus similar to scores of laboratory-bred F1 hybrids. All four of the specimens identified as *N. floridana* (S2) have scores within the extremes of reference *floridana*. One, in fact, is near the lower limit for *floridana*, but two others have scores slightly above the mode. Of greatest interest is the placement on the histogram of scores of the five specimens identified as natural hybrids; all have scores between the extremes of the

two reference samples and are in frequency classes with known F1 and F2 hybrids.

These results show that laboratory reared hybrids between *N. floridana* and *N. micropus* tend to have discriminant scores intermediate between those of non-hybrids, but when not intermediate they are more like *micropus* than *floridana*. Second generation hybrids again appear to be more variable and also more *micropus*-like than F1 hybrids. Backcross hybrids, as expected, tend to be either intermediate or more like their non-hybrid parent. Woodrats from the known area of sympatry in northern Oklahoma may be similar to members of either species, or they may be intermediate. Results of discriminant function analysis further substantiate conclusions by Spencer (1968) and by me that the two species interbreed at the locality of sympatry. In addition, it can be seen that identifications based on visual analysis of pelage and cranial characteristics are highly reliable, as indicated by results of discriminant function analysis. Although the series of specimens from Parker County, Texas, near the western edge of the range of the species in northern Texas, are suspiciously grayish, specimens from that locality are either typical *floridana* or at least much more like *floridana* than *micropus*.

It appears that discriminant function analysis is a sophisticated statistical tool that has tremendous potential in studies of geographic variation, especially in locating zones of marked morphological change (see Rees, 1970, for comparable results in studies of white-tailed deer), and for distinguishing natural hybrids. However, the observed tendency for *floridana-micropus* F1 and F2 hybrids to be more like *micropus* than *floridana* indicates that hybrids of known ancestry (laboratory-bred) should be used as "controls" whenever possible in discriminant analyses to determine where natural hybrids likely will score relative to the scores of the parental species.

NON-MORPHOLOGICAL CHARACTERS

COMPARATIVE REPRODUCTION

In view of the emphasis placed on "reproductive isolation" in the biological species concept (Mayr, 1965:19), studies of reproductive patterns and habits constitute a major aspect of investigations of closely related taxa. It has been suggested (erroneously I think) that evidence of hybridization among animals having internal fertilization implies conspecificity. As presently understood, laboratory experiments in hybridization merely provide an indication of the presence, absence, or efficiency of isolating mechanisms, especially postmating mechanisms (see Mayr, 1963:92). Brand and Ryckman (1969) demonstrated a clear understanding of this concept in their interpretations of studies on *Peromyscus*. Hybridization in natural habitats is more often indicative of conspecificity, but as stated by Mayr (1969:195) "allopatric forms that hybridize only occasionally in the zone of contact are full species." In fact, populations that have diverged morphologically during isolation often hybridize when geographic contact is reestablished until such time as selection has established isolating mechanisms or reinforced incipient mechanisms (Key, 1968). Premating isolating mechanisms, such as habitat isolation, clearly are tenuous forms of isolation, but they may be sufficiently effective to prevent loss of species integrity as a result of hybridization. The emphasis on reproductive isolation would seem better placed on the abilities of taxa to maintain their respective specific integrities rather than on the production of hybrids. Nevertheless, studies of hybridization both in the laboratory and the field often serve as immensely useful indicators of animal relationships.

Breeding Cages.—Two cages were

constructed especially for breeding woodrats in the laboratory. Each was 60 by 60 by 18 inches with a ½-inch plywood floor and hinged top. The sides and top were of ½-inch hardware cloth secured on the inside of a wooden frame. Two other cages constructed for other purposes were found to be excellent breeding cages. These were 60 by 18 by 18 inches with ½-inch plywood floors and sides, and with hinged tops of hardware cloth on wood frames. Internally, these cages were constructed so that removable hardware cloth partitions on wood frames could be inserted at one-foot intervals. The partitions had sliding metal doors allowing woodrats to be separated or penned together easily and without handling. When these four cages were in use, an upright rack of four metal cages, 48 by 24 by 18 inches, frequently was converted into two "two story" breeding cages by replacing the metal trays that served as the floor of the upper and third (from the top) cages with trays 24 by 24 inches. Attempts to breed woodrats in unconverted cages, 48 by 24 by 18 inches, and the smaller 24 by 24 by 18 inch cages never were successful and often resulted in death of one of the rats.

Recognition of Breeding Readiness.—External indications of breeding condition for both sexes were described by Rainey (1956:605-609) for *Neotoma floridana*, and by Raun (1966:14-17) for *N. micropus*. In breeding males the testes become noticeably enlarged and scrotal; the swollen convoluted cauda epididymis forms a conspicuous bulge (Linsdale and Tevis, 1951:354), and the skin of the scrotum appears thinner, more darkly pigmented, and less haired than in nonbreeding males. In both the field and the laboratory it was noted that these characteristics are somewhat more easily discernible in breeding *floridana* males than in breeding *micropus* males. Also in *floridana*, the testes often descend farther into the scrotal sac than do the testes of *micropus* males. Healthy adult laboratory males of both species had apparently viable sperm in the epididymides and testes throughout the year, even when the testes were abdominal and reduced in size. In sexually inactive females, the vulva is imperforate and cornified, the clitoris is small and white or pinkish, and the teats are small. Breeding females are easily distinguished by a turgid, perforate vagina and an enlarged, vascularized clitoris.

Age at Sexual Maturity.—Both male and female woodrats born early in spring usually appear to be in breeding condition by late summer. The testes of young males are smaller than those of adults and the cauda epididymis protrudes less; both the epididymides and testes contain sperm. Several attempts were made to place first-year males of *micropus* with adult breeding females, but each attempt was necessarily terminated to prevent the male from being killed. A first-year *floridana* male was placed with an adult female *floridana* from 8 August until 4 September 1967; although the two were compatible, they were never observed to display sexual interest nor to copulate; no litter resulted. The same male sired several litters during the 1968 and 1969 breeding seasons.

In late summer of 1968, two first-year females of each species were placed with adult males of their own species for more than two weeks each, but no young was born to either. One of three subadult female *N. f. baileyi* (Table 15), obtained in late August of 1968, was nursing three young judged to be less than two weeks of age; the other two females were neither pregnant nor lactating. At least occasional females bear young in the natural environment late in the season of the year in which they are born. Brown (1969:538) found that female *Neotoma mexicana* born in the first litters of spring (April and May) normally produce litters in June and July, often while still at least partially in juvenile pelage. This clearly is not the case in either *N. floridana* or *N. micropus*. Young of both sexes born as late as August were consistently successful breeders in the

laboratory by March of the following year.

Breeding Seasons.—As indicated by age composition of samples of *N. micropus* and as reported by Raun (1966:14), breeding takes place throughout the year in southern populations of the species, with only a slight tendency for seasonality. Females in northern populations of *micropus* (Spencer, 1968:45, and Finley, 1958:486; Tables 15 and 16) apparently begin breeding in December and January, produce at least two and probably three litters before July, and some females have an additional litter and possibly two between early August and the end of October. *Neotoma floridana* in Kansas (Tables 15 and 16; Rainey 1956:609-613) begin breeding in February and females bear their first litters in March or April and their second in May or June. Most females are appreciatively less active reproductively in July, then have an additional litter in August or September with occasional litters being born as late as October. As indicated in tables 15 and 16, the first litter of female *N. f. baileyi* is born in April, a second in June, and a third in July or August. I doubt that *baileyi* produces litters after mid-September, but available data do not preclude the possibility. Late summer and autumn breeding in both species may involve mostly young females born earlier that year.

Estrous Cycle.—Techniques described by Chapman (1951:269) and Zarrow *et al.* (1964:36-37) for determination of estrus by examination of cells lining the vagina were attempted early in my

TABLE 15. Reproductive status of adult and subadult *Neotoma floridana* and *N. micropus* females captured in Nebraska, Colorado, Kansas, and Oklahoma from September, 1966 to April, 1969.

Locality (county)	Date captured	Age	Date litter born	Number progeny born		Number progeny collected with female		Remarks
				♂♂	♀♀	♂♂	♀♀	
			Neotoma floridana baileyi					
Cherry	31 Mar.	Adult	13 Apr.	2	2			
Cherry	31 Mar.	Adult	9 Apr.	2	2	--	--	--
Cherry	31 Mar.	Adult	--	--	--	--	--	No litter born
Cherry	31 Mar.	Adult	26 Apr.	2	2		--	
Cherry	31 Mar.	Adult	6 Apr.	2	1	--	--	--
Cherry	31 Mar.	Adult	--	--	--	--	--	Died 17 Apr.; had 3 resorbing embryos
Cherry	31 Mar.	Adult	16 Apr.	1	3	--	--	--
Cherry	24 Aug.	Subadult	--	--	--	--	--	No litter born
Cherry	24 Aug.	Adult	--	--	--	--	--	Killed 29 Aug.; had 4 embryos × 45 mm.
Cherry	24 Aug.	Subadult	--	--	--	--	--	Killed 29 Aug.; not pregnant
Rock	21 Aug.	Subadult	--	--	--	1	2	Killed 29 Aug.; not pregnant
Rock	22 Aug.	Subadult	--	--	--	--	--	Killed 29 Aug.; not pregnant
			Neotoma floridana campestris					
Logan	29 Aug.	Adults (2)	--	--	--	--	--	No litters born
Logan	29 Aug.	Subadult	--	--	--	--	--	Died 8 Sept.; not pregnant
Ness	4 Sept.	Subadult	--	--	--	--	--	Killed 4 Sept.; not pregnant

TABLE 15.—Continued.

Locality (county)	Date captured	Age	Date litter born	Number progeny born ♂♂	Number progeny born ♀♀	Number progeny collected with female ♂♂	Number progeny collected with female ♀♀	Remarks
Ness	4 Sept.	Subadult	--	--	--	--	--	Killed 13 Sept.; not pregnant
Finney	5 Sept.	Subadult	--	--	--	--	--	Killed 5 Sept.; not pregnant
Finney	5 Sept.	Adults (2)	--	--	--	--	--	Killed 5 Sept.; neither pregnant
Finney	5 Sept.	Subadults (5)	--	--	--	--	--	Killed 13 Sept.; none pregnant
Finney	5 Sept.	Adults (4)	--	--	--	--	--	Killed 13 Sept.; none pregnant
Hodgeman	8 Sept.	Adult	--	--	--	--	--	Killed 13 Sept.; not pregnant
Ellis	18 Dec.	Adults (9)	--	--	--	--	--	No litters born
Ellis	18 Dec.	Adults (2)	--	--	--	--	--	Killed 18 Dec.; neither pregnant
Ellis	19 Dec.	Adults (2)	--	--	--	--	--	Killed 21 Dec.; neither pregnant
Russell	21 Dec.	Adult	--	--	--	--	--	Killed 21 Dec.; not pregnant
Russell	21 Dec.	Adults (4)	--	--	--	--	--	Killed 13 Jan.; none pregnant
Russell	21 Dec.	Adult	--	--	--	--	--	No litter born
			Neotoma floridana attwateri					
Major	31 Jan.	Adult	10 Feb.	2	0	--	--	--
Major	31 Jan.	Adult	--	--	--	--	--	No litter born
Douglas	3 Mar.	Adult	10 Mar.	2	1	--	--	--
Douglas	10 Mar.	Adult	6 Apr.	1	3	--	--	--
Douglas	10 Mar.	Subadult	--	--	--	--	--	No litter born
Douglas	10 Apr.	Adult	--	--	--	0	2	Killed 11 Apr.; not pregnant
Major	7 June	Adult	--	--	--	--	--	Killed 7 June; had 4 embryos × 25 mm
Ellsworth	24 Sept.	Subadults (2)	--	--	--	--	--	Killed 24 Sept.; neither pregnant
Ellsworth	14 Oct.	Adult	--	--	--	--	--	Killed 14 Oct.; not pregnant
Ellsworth	14 Oct.	Subadult	--	--	--	--	--	Killed 14 Oct.; not pregnant
Ellsworth	14 Oct.	Subadults (2)	--	--	--	--	--	Killed 7 Nov.; neither pregnant
Douglas	18 Oct.	Adults (2)	--	--	--	--	--	No litters born
Douglas	7 Nov.	Subadults (2)	--	--	--	--	--	No litters born
Ellsworth	21 Dec.	Adults (2)	--	--	--	--	--	Killed 2 Jan.; neither pregnant
			Neotoma micropus canescens					
Major	31 Jan.	Adults (3)	--	--	--	--	--	No litters born
Haskell	24 Feb.	Adult	--	--	--	0	2	No litter born
Haskell	24 Feb.	Adult	--	--	--	0	2	No litter born

TABLE 15.—Concluded.

Locality (county)	Date captured	Age	Date litter born	Number progeny born		Number progeny collected with female		Remarks
				♂♂	♀♀	♂♂	♀♀	
Haskell	24 Feb.	Adult	--	--	--	--	--	Aborted 3 embryos on 3 Mar.
Haskell	24 Feb.	Adult	3 Mar.	2	1	--	--	--
Haskell	24 Feb.	Adult	29 Feb.	2	2	--	--	--
Haskell	24 Feb.	Adult	--	--	--	--	--	No litter born
Barber	9 Mar.	Adult	11 Mar.	3	0	--	--	--
Barber	10 Mar.	Adult	13 Mar.	3	0	--	--	--
Barber	10 Mar.	Subadult	--	--	--	--	--	No litter born
Haskell	6 Apr.	Adult	--	--	--	0	2	Killed 11 Apr.; not pregnant
Haskell	6 Apr.	Adult	--	--	--	1	1	Killed 11 Apr.; not pregnant
Haskell	6 Apr.	Adult	--	--	--	1	2	Killed 11 Apr.; not pregnant
Baca	8 Apr.	Adult	--	--	--	1	1	No litter born
Baca	8 Apr.	Adult	--	--	--	--	--	No litter born
Baca	18 May	Adult	--	--	--	2	1	No litter born
Baca	18 May	Adult	--	--	--	2	2	No litter born
Baca	18 May	Adult	--	--	--	1	3	No litter born
Baca	18 May	Adult	4 June	2	2	2	2	--
Baca	18 May	Adult	24 May	3	0	0	1	--
Baca	18 May	Adult	31 May	4	0	--	--	--
Baca	18 May	Adult	--	--	--	--	--	No litter born
Meade	5 June	Adult	--	--	--	2	1	No litter born
Haskell	6 June	Adult	--	--	--	2	0	No litter born
Haskell	6 June	Adult	--	--	--	2	1	No litter born
Haskell	6 June	Adult	17 June	1	1	1	1	--
Haskell	6 June	Adult	13 June	1	2	--	--	--
Haskell	6 June	Adult	24 June	3	1	--	--	--
Haskell	6 June	Adult	29 June	2	1	--	--	--
Major	6 June	Adults (2)	--	--	--	--	--	No litters born
Barber	4 July	Subadults (3)	--	--	--	--	--	Killed 19 June; none pregnant
Barber	4 July	Adult	--	--	--	--	--	Killed 19 July; not pregnant
Haskell	11 Aug.	Subadults (2)	--	--	--	--	--	Killed 16 Aug.; neither pregnant
Haskell	11 Aug.	Adult	--	--	--	--	--	Killed 16 Aug.; not pregnant
Stevens	11 Aug.	Adult	--	--	--	0	2	Killed 19 Aug.; not pregnant
Hamilton	7 Sept.	Adults (2)	--	--	--	--	--	Killed 13 Sept.; neither pregnant
Hamilton	7 Sept.	Subadult	--	--	--	--	--	Killed 13 Sept.; not pregnant
Haskell	24 Sept.	?? (6)	--	--	--	--	--	No litters born
Barber	22 Oct.	?? (7)	--	--	--	--	--	No litters born
Haskell	13 Nov.	?? (2)	--	--	--	--	--	No litters born
Meade	25 Nov.	Adults (3)	--	--	--	--	--	No litters born

study. Some rats did not seem to be affected by the daily handling and continued to cycle as described by Chapman (1951:271); other individuals became hyperactive, lost weight, were difficult to handle, and the vagina became cornified and inactive. My limited observations on females that continued to cycle agree in general with the four- to six-day estrous cycle described by Chapman *(loc. cit.)* for *N. floridana,* and no meaningful differences were observed in the cycles of females of the two species or of an F1 hybrid female.

Zarrow *et al.* (1964:39) described a technique for monitoring the estrous cycle of female white rats (genus *Rattus*) by measuring daily activity of cycling females in activity cages. This technique also was tested, but variation in the activity between females far exceeded that of daily activity of any individual female. Some females averaged in excess of 8000 revolutions per day whereas others never recorded more than 500 revolutions and averaged less than 200 revolutions. Activity of two first-year adult virgin females (one *floridana,* the other *micropus*) for the 20-day period from 12 to 31 March 1968 is shown in figure 38. This particular example is slightly atypical because the *floridana* was more active than the *micropus.* Normally *floridana* females turned fewer revolutions of the wheel than did *micropus* females. Both rats were removed from the activity cage the morning of 31 March and were caged with an adult male of their species until 12 April. The female *floridana* gave birth to a litter of five young on 6 May but no litter was born to the *micropus* as a result of that attempted mating. Females removed from an activity cage and placed with males at the peak of activity, which would be expected to correspond with estrus, did not demonstrate greater mating success than other females. The peaks in activity generally followed three- to six-day cycles for both species and probably were associated, at least in part, with the estrous cycle. However, the technique did not give reliable and precise data on the estrous cycles of the two species, and therefore was discontinued early in the 1968 breeding season.

Behavioral Aspects of Breeding.— Several behavioral differences were noted that probably affected breeding success in the laboratory. Certain rats did not seem to adapt to captivity and

TABLE 16. Reproductive data recorded on specimen labels of adult and subadult *Neotoma floridana, N. micropus,* and *N. angustipalata* females.

Number	Date	No Embryos	Pregnant (Number Embryos)	Number Young	Lactating
		N. floridana baileyi from Nebraska			
78376	15 May	X	---	---	---
4311/ 5034 USNM	16 June	---	---	4	X
73386	15 July	---	4	---	---
		N. floridana campestris from Nebraska			
50185	15 August	X	---	---	---
51612	1 November	X	---	---	---
72600	24 November	X	---	---	---
		N. floridana campestris from Colorado			
37098	21 May	X	---	---	X
37100	22 May	---	4	---	X
34747	23 November	X	---	---	---
		N. floridana campestris from Kansas			
4986	25 August	-	---	---	X

TABLE 16.—Concluded.

Number	Date	No Embryos	Pregnant (Number Embryos)	Number Young	Lactating
		N. floridana attwateri from Kansas			
654	9 March	---	---	---	X
53846	10 March	---	3	---	---
78998	12 October	X	---	---	---
16111	1 November	X	---	---	---
68578-80	13 November	X	---	---	---
22628	29 November	X	---	---	---
		N. floridana attwateri from Oklahoma			
4191	19 October	---	---	4	X
		N. floridana attwateri from Texas			
1037 FWCM	February	X	---	---	---
23391 TCWC	27 September	---	---	---	X
51718	22 October	X	---	---	---
3848 TCWC	27 October	X	---	---	---
971 FWCM	24 November	X	---	---	---
		N. micropus canescens from Kansas			
69605	15 June	---	---	---	X
13994	7 July	---	---	---	X
38919	21 July	X	---	---	---
38914	22 July	X	---	---	---
98190	30 November	X	---	---	---
		N. micropus canescens from New Mexico			
79088	14 June	---	3	---	---
		N. micropus canescens from Oklahoma			
74550-51	1 December	X	---		---
		N. micropus canescens from Texas			
56834	22 August	---	2	---	---
56835	22 August	---	---	---	X
51719	30 October	X	---	---	---
		N. micropus canescens from Coahuila			
36324	31 March	---	---	---	X
36329	31 March	X	---	---	---
56710	5 December	X	---	---	---
56712	9 December	---	2	---	---
		N. micropus micropus from Tamaulipas			
56910	17 May	---	---	---	X
56912	19 May	X	---	---	---
56914	19 May	---	2	---	---
56915	21 May	---	2	---	---
56918	22 May	X	---	---	---
56960-63	7 June	X	---	---	---
56954	10 June	---	2	---	---
56955-56	10 June	X	---	---	---
89135	13 November	X	---	---	---
89137-39	13 November	X	---	---	---
89141-42	13 November	X	---	---	---
89144	13 November	X	---	---	---
		N. angustipalata from Tamaulipas			
58865	21 May	X	---	---	---
8138 UNAM	11 July	---	1	---	---

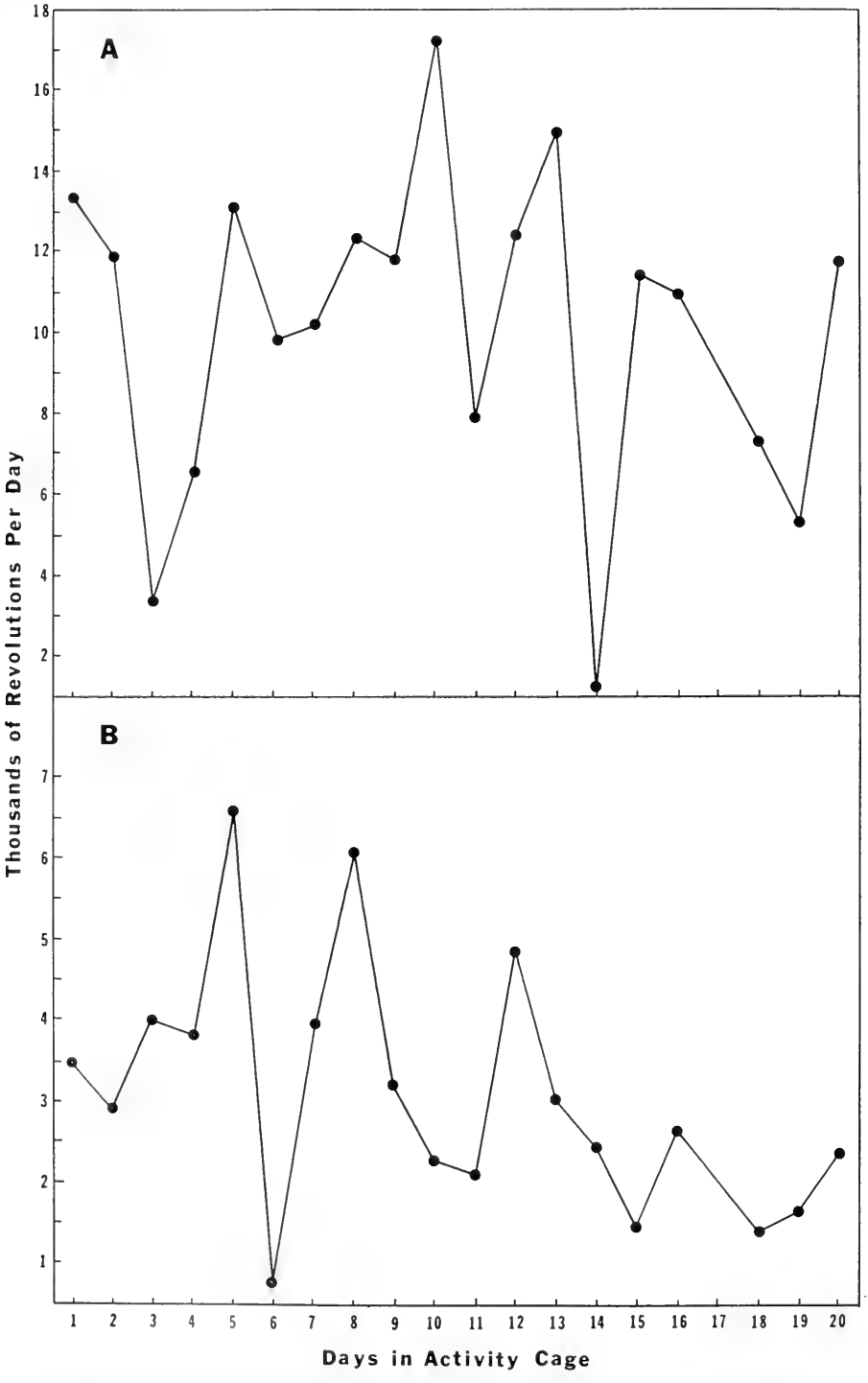

FIG. 38. Daily activity of non-pregnant first-year female woodrats from March 12-31: A—*Neotoma floridana attwateri;* B—*N. micropus canescens.*

conditions of the laboratory; these individuals never became accustomed to handling and either would dash about the cage or cower defensively in a corner when the cage door was opened. When placed in a breeding cage these rats behaved in the same manner, initially and whenever an investigator was in the animal rooms. Although most were not especially good breeders, some did breed and successfully rear litters. Wood (1935: 106) observed similar behavioral patterns and resultant lowered reproductive success in certain individuals of *Neotoma fuscipes*. This type of behavior was never observed in a *N. floridana* that had been in the laboratory for as long as one week. It was prevalent in *N. m. canescens* that were collected in Haskell County, Kansas, and Baca County, Colorado. The habitat from which these animals were obtained is open grassland with practically no cover additional to structures built by the rats. Possibly such behavior is genetically based and has selective advantage for woodrats living in open areas.

When a male and female were placed together they generally spent some time sniffing each other, especially the ventral dermal gland (Howell, 1926:16) and genitalia. This was often followed by sparring or fighting. If the female established dominancy she generally pursued the male relentlessly, biting the tail and lumbar region of his back; if the two were left together, the male eventually was killed. If the male established dominancy, the fighting usually did not last long and such matchings frequently resulted in the birth of a litter. A few males were able to establish dominancy with little or no fighting; these generally were the most successful breeders. Occasional males behaved as described for dominant females and if not removed would kill the female in a relatively short time. Usually these were young and inexperienced males, and in at least one instance, a male *micropus* that behaved in this fashion during his first breeding season was a successful breeder the following year. It usually could be determined within an hour whether or not two rats were compatible; if either was clearly endangered, they were separated. However, most deaths resulted when a pair would appear to be compatible for a period of several hours or even days, after which one, usually the female, would kill the other. In initial attempts to breed woodrats in the laboratory, each breeding cage was supplied with two nest-boxes, an abundance of shredded paper, and occasionally with sticks of wood and pieces of corrugated cardboard. Almost invariably one rat would attempt to hoard all the materials and constant fighting resulted. Later it was discovered that less strife resulted when the rats were not given nest-boxes and when only enough shredded paper was provided for each rat to construct a small cup-shaped nest.

Several investigators (Egoscue, 1957, 1962; Feldman, 1935) left compatible pairs together for the entire breeding season, including that time when young were born and reared. I attempted this only once; on 2 March 1967 a pair of *N. f. campestris* was placed in a "two story" breeding cage (described above). They nested together on the bottom level for several days before the male moved to the upper tray; at that time both seemed normal and no other indication of strife was observed. On 5 April a litter of three newborn young was observed and the male continued to nest unmolested on the upper level. On the morning of 15 April one young was absent and the male was being chased by the female. The male was alive on the following morning, but severely wounded. He was removed from the cage, treated for the wounds, and placed in a separate cage where he recuperated.

The recuperative powers of both species are remarkable. On separate occasions a male of each species was so severely wounded by a female that the skin of the lower back was completely missing, exposing large areas of muscle from the middle of the back to the base

of the tail. Both males were treated regularly with disinfectant and both survived. The new skin was largely scar tissue, and hair was sparse on the back of the *micropus* but dense and normal on the *floridana,* albeit a "line" of demarcation always was visible surrounding the scar.

Breeding Performance in the Laboratory.—Tables 17 and 18 summarize laboratory breeding performances of females and males, respectively. The tabulated results are qualified, as follows: 1) An attempted mating was "successful" if at least one live progeny resulted; 2) Matings were attempted only between adult woodrats that appeared externally to be in breeding condition; 3) No attempts prior to 1 February or after 1 September are included; 4) Attempts to breed woodrats born earlier the same summer are excluded; 5) Matings attempted in cages other than the three types of breeding cages described above are excluded; and 6) A mating attempt was considered only if the two rats were together for at least 24 hours. If two rats remained compatible they were left together for a minimum of six days, which is approximately the length of the estrous cycle, and a maximum of 12 days.

As considered herein, all of the populations of *Neotoma micropus* from which live woodrats were collected for study in the laboratory are of the subspecies *N. m. canescens.* However, the reproductive performance of woodrats from the more open habitats of westerly localities (Baca County, Colorado, and Haskell County, Kansas) was so distinctly different from that of woodrats from the two more easterly localities (Barber and Meade counties, Kansas) that I have considered them separately as "*N. m. canescens* (1)" and "*N. m. canescens* (2)," respectively. Both sexes of *N. m. canescens* (1) were considerably less successful reproductively in the laboratory than any of the other woodrats studied. This probably resulted from the inability of individuals from these two localities to adjust to laboratory conditions.

Females of *N. f. campestris* were also relatively unsuccessful breeders, but males of the race were more successful than males of any other taxon. As discussed above, successful mating attempts generally were those in which the males were dominant. *Neotoma floridana campestris* is the largest of the woodrats studied and members of both sexes generally were able to physically dominate another kind of rat when placed in breeding cages. When two *campestris* were placed together, the female dominated more frequently than did the male.

Members of each of the four races, *N. f. baileyi, N. f. campestris, N. f. attwateri,* and *N. m. canescens,* of the two species studied, were successfully crossed with members of each of the other races at least twice. Reciprocal crosses were successful for five of the six possible mating combinations. No offspring resulted from the four occasions when *baileyi* males were placed with *campestris* females, constituting the only unsuccessful reciprocal cross. Of the four attempts, a male *baileyi* was killed in one and the male was wounded in two of the other three.

Both sexes of the three types of subspecific "hybrids" demonstrated fertility with the exception of female *campestris* X *attwateri.* Only one of five females produced from this cross ever was placed with a male and no progeny were produced; it seems unlikely, however, that females of the cross were infertile. The only female of the cross saved for breeding studies was accidentally killed before a second attempt to mate her could be made.

Of the possible kinds of hybrids involving *micropus* and one of the three subspecies of *floridana,* the fertility of *N. f. baileyi* X *N. m. canescens* females was not tested, but a male of that cross produced a litter of four when mated with a *baileyi* female. The other two kinds of *N. floridana* (*attwateri* and *campestris*) X *N. m. canescens* hybrid

TABLE 17. Reproductive performance of *Neotoma floridana, N. micropus,* and hybrid females in the laboratory.

Males	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
			Neotoma floridana baileyi females					
N. f. baileyi	11	4	36.4	6	8	3.5	3–4	1.27
N. f. campestris	5	5	100.0	10	9	3.8	4	3.80
N. f. attwateri	1	1	100.0	2	1	3.0	3	3.00
N. m. canescens (1)	4	0	0.0	----	----	-	-	0.00
N. m. canescens (2)	3	1	33.3	0	1	1.0	1	0.33
N. f. baileyi X *N. f. attwateri*	1	1	100.0	2	2	4.0	4	4.00
N. f. baileyi X *N. m. canescens*	1	1	100.0	2	2	4.0	4	4.00
TOTAL	26	13	50.0	22	23	3.5	4	1.73
			Neotoma floridana campestris females					
N. f. baileyi	4	0	0.0	----	----	-	----	0.00
N. f. campestris	18	5	27.8	4	10	2.8	3	0.78
N. f. attwateri	5	2	40.0	3	3	3.0	2–4	1.20
N. m. canescens (1)	9	0	0.0	- -	----	----	----	0.00
N. m. canescens (2)	6	2	33.3	2	5	3.5	3–4	1.17
N. f. campestris X *N. f. attwateri*	2	1	50.0	2	1	3.0	3	1.50
N. f. attwateri X *N. m. canescens*	1	0	0.0	----	----	----	----	0.00
TOTAL	45	10	22.2	11	19	3.0	3	0.67
			Neotoma floridana attwateri females					
N. f. baileyi	1	1	100.0	2	1	3.0	3	3.00
N. f. campestris	2	2	100.0	3	2	2.5	2–3	2.50
N. f. attwateri	9	6	66.7	12	10	3.7	3	2.44
N. m. canescens (1)	3	2	66.7	2	2	2.0	2	1.33
N. m. canescens (2)	6	2	33.3	6	1	3.5	3–4	1.17
N. f. attwateri X *N. m. canescens* F_2	1	1	100.0	1	2	3.0	3	3.00
TOTAL	22	14	63.6	26	18	3.1	3	2.00
			Neotoma micropus canescens (1) females					
N. f. baileyi	1	0	0.0	-	----	----	- -	0.00
N. f. campestris	2	1	50.0	3	1	4.0	4	2.00
N. f. attwateri	2	0	0.0	----	- -	----	----	0.00
N. m. canescens (1)	15	0	0.0	----	----	----	- -	0.00
N. m. canescens (2)	5	4	80.0	6	4	2.5	2–3	2.00
N. f. baileyi X *N. f. attwateri*	1	0	0.0	- -	----	- -	----	0.00
TOTAL	26	5	19.2	9	5	2.8	2–3	0.54
			Neotoma micropus canescens (2) females					
N. f. baileyi	4	2	50.0	6	2	4.0	4	2.00
N. f. campestris	6	5	83.3	6	10	3.2	3–4	2.67
N. f. attwateri	6	2	33.3	2	4	3.0	3	1.00
N. m. canescens (1)	10	1	10.0	2	1	3.0	3	0.30
N. m. canescens (2)	8	4	50.0	6	5	2.8	3	1.38
N. f. baileyi X *N. m. canescens*	1	0	0.0	----	----	----	---	0.00
N. f. attwateri X *N. m. canescens*	4	2	50.0	2	1	1.5	1–2	0.75
TOTAL	39	16	41.0	24	23	2.9	3	1.21

TABLE 17.—Continued.

Males	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
			N. f. baileyi X *N. f. campestris* female					
N. f. baileyi X *N. f. campestris*	2	2	100.0	2	2	2.0	2	2.00
			N. f. baileyi X *N. f. attwateri* female					
N. f. baileyi X *N. f. attwateri*	1	1	100.0	1	2	3.0	3	3.00
			N. f. campestris X *N. f. attwateri* female					
N. f. campestris X *N. f. attwateri*	1	0	0.0	----	----	----	----	0.00
			N. f. campestris X *N. m. canescens* females					
N. f. campestris	1	1	100.0	1	1	2.0	2	2.00
N. m. canescens (2)	1	1	100.0	2	1	3.0	3	3.00
N. f. campestris X *N. m. canescens*	6	2	33.3	2	2	2.0	2	0.67
N. f. attwateri X *N. m. canescens*	3	2	66.7	2	3	2.5	2–3	1.67
N. m. canescens X (*N. f. attwateri* X *N. m. canescens*)	1	0	0.0	----	----	----	----	0.00
TOTAL	12	6	50.0	7	7	2.3	2	1.17
			N. f. attwateri X *N. m. canescens* F_1 females					
N. f. attwateri	1	0	0.0	----	----	----	----	0.00
N. f. campestris X *N. m. canescens*	1	1	100.0	0	2	2.0	2	2.00
N. f. attwateri X *N. m. canescens*	6	2	33.3	3	2	2.4	2–3	0.83
TOTAL	8	3	37.5	3	4	2.3	2	0.88
			N. f. attwateri X *N. m. canescens* F_2 females					
N. f. baileyi	1	1	100.0	1	2	3.0	3	3.00
N. f. attwateri X *N. m. canescens* F_2	1	0	0.0	----	----	----	----	0.00
TOTAL	2	1	50.0	1	2	3.0	3	1.50
			N. f. baileyi X (*N. f. baileyi* X *N. m. canescens*) female					
N. m. canescens (1)	1	0	0.0	----	----	----	----	----
			All *Neotoma floridana* females					
N. floridana	63	31	49.2	49	51	3.2	3	1.59
N. micropus	31	7	22.6	10	9	2.7	2–3–4	0.61
Species-hybrids	3	2	66.7	3	4	3.5	3–4	2.33
TOTAL	97	40	41.2	62	64	3.2	3	1.30
			All *Neotoma micropus* females					
N. micropus	38	9	23.7	14	10	2.7	3	0.63
N. floridana	22	10	45.5	17	17	3.4	4	1.55
Species-hybrids	5	2	40.0	2	1	1.5	1–2	0.60
TOTAL	66	21	31.8	33	28	2.9	3	0.92
			All species-hybrid females					
N. floridana	3	2	66.7	2	3	2.5	2–3	1.67
N. micropus	2	1	50.0	2	1	3.0	3	1.50
Species-hybrids	18	7	38.9	7	9	2.3	2	0.89
TOTAL	23	10	43.5	11	13	2.4	2	1.04

TABLE 17.—Concluded.

Males	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
			All non-hybrid females					
Same species	101	40	39.6	63	61	3.1	3	1.23
Other species	53	17	32.1	27	26	3.1	4	1.00
Species-hybrids	8	4	50.0	5	5	2.5	1–2–3–4	1.25
TOTAL	162	61	37.7	95	92	3.1	3	1.15
			All females					
All males	185	71	38.4	106	105	3.0	3	1.14

females demonstrated fertility as did males of all three crosses. One male and one female *floridana* X *micropus* of the second generation were successful when mated to a female and a male *floridana*, respectively, but they did not produce a litter when placed together. Only two attempts were made to mate woodrats that resulted from backcrosses. Neither was successful and the fertility of these woodrats was not established. However, in view of the success of other hybrids, I suspect that backcross progeny were fertile and might have produced young if more attempts to mate them had been conducted.

Gestation.—Published information on the gestation periods of *Neotoma floridana* and *N. micropus* is meager and inconsistent. Knoch (1969:363) observed a range of 33 to 36 days for gestation of three litters of *N. f. attwateri*. The gestation period for *N. f. floridana*, as determined in independent studies, was estimated at 33 to 39 days (Pearson, 1952: 461) and six weeks (Hamilton, 1953: 182). Poole (1940:266) suggested gestational limits of 30 to 36 days for *N. f. magister*. The gestation period of *N. micropus* was calculated to be less than 33 days by Feldman (1935:301). Spencer (1968:25) calculated gestation of two litters of each species (probably *N. f. attwateri* and *N. m. canescens*). Both litters of *floridana* young were born 35 days following copulation; parturition followed copulation by 33 days in one instance and 38 in another for *micropus*. Several hybrid females studied by Spencer *(loc. cit.)* had gestation periods of 34 to 36 days. Additionally, he observed one female each of *floridana* and *micropus* that copulated during post-partum estrus and did not parturiate until 51 and 55 days, respectively, had elapsed. A female *N. m. canescens* collected by Spencer (1968:42) with a litter judged to be less than 10 days of age was not placed with a male until after she produced a litter in captivity 46 days later.

In this study only a single female *(N. f. campestris)* was caged with a male at the time of parturition and a second litter was not observed. Although several females nursing litters at the time of capture (Table 15) later produced second litters without having been placed with males, no litter was produced late enough to indicate an extended period of gestation. The technique of leaving males and females together for several days was not conducive to determination of the gestation period. However, in several instances pairs were separated after a few days because of fighting. Litters born as a result of these matings had relatively narrow gestational limits. The two shortest terms of gestation had maximum durations of 32 days. In one case the female was an *N. f. baileyi* that had been bred to an *N. f. campestris* male, whereas the other was a *floridana* X *micropus* hybrid female mated to a hybrid male of the same cross. The longest gestation calculated had minimal and maximal limits of 37 and 41 days, respectively, and was for an *N. m. canescens* female that had been mated to

TABLE 18. Reproductive performance of *Neotoma floridana*, *N. micropus*, and hybrid males in the laboratory.

Females	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
			Neotoma floridana baileyi males					
N. f. baileyi	11	4	36.4	6	8	3.5	3–4	1.27
N. f. campestris	4	0	0.0	----	----	----	----	0.00
N. f. attwateri	1	1	100.0	2	1	3.0	3	3.00
N. m. canescens (1)	1	0	0.0	----	----	----	----	0.00
N. m. canescens (2)	4	2	50.0	6	2	4.0	4	2.00
N. f. attwateri X *N. m. canescens* F_2	1	1	100.0	1	2	3.0	3	3.00
TOTAL	22	8	36.4	15	13	3.5	3–4	1.27
			Neotoma floridana campestris males					
N. f. baileyi	5	5	100.0	10	9	3.8	4	3.80
N. f. campestris	18	5	27.8	4	10	2.8	3	0.78
N. f. attwateri	2	2	100.0	3	2	2.5	2–3	2.50
N. m. canescens (1)	2	1	50.0	3	1	4.0	4	2.00
N. m. canescens (2)	6	5	83.3	6	10	3.2	3–4	2.67
N. f. campestris X *N. m. canescens*	1	1	100.0	1	1	2.0	2	2.00
TOTAL	33	19	57.6	27	33	3.2	3	1.82
			Neotoma floridana attwateri males					
N. f. baileyi	1	1	100.0	2	1	3.0	3	3.00
N. f. campestris	5	2	40.0	3	3	3.0	2–4	1.20
N. f. attwateri	9	6	66.7	12	10	3.7	3	2.44
N. m. canescens (1)	2	0	0.0	----	----	----	----	0.00
N. m. canescens (2)	6	2	33.3	2	4	3.0	3	1.00
N. f. attwateri X *N. m. canescens* F_1	1	0	0.0	----	----	----	----	0.00
TOTAL	24	11	45.8	19	18	3.4	3	1.54
			Neotoma micropus canescens (1) males					
N. f. baileyi	4	0	0.0	----	----	----	----	0.00
N. f. campestris	9	0	0.0	----	----	----	----	0.00
N. f. attwateri	3	2	66.7	2	2	2.0	2	1.33
N. m. canescens (1)	15	0	0.0	----	----	----	----	0.00
N. m. canescens (2)	10	1	10.0	2	1	3.0	3	0.30
N. f. baileyi X (*N. f. baileyi* X *N. m. canescens*)	1	0	0.0	----	----	----	----	0.00
TOTAL	42	3	7.1	4	3	2.3	2	0.17
			Neotoma micropus canescens (2) males					
N. f. baileyi	3	1	33.3	0	1	1.0	1	0.33
N. f. campestris	6	2	33.3	2	5	3.5	3–4	1.17
N. f. attwateri	6	2	33.3	6	1	3.5	3–4	1.17
N. m. canescens (1)	5	4	80.0	6	4	2.5	2–3	2.00
N. m. canescens (2)	8	4	50.0	6	5	2.8	3	1.38
N. f. campestris X *N. m. canescens*	1	1	100.0	2	1	3.0	3	3.00
TOTAL	29	14	48.3	22	17	2.8	3	1.34
			N. f. baileyi X *N. f. campestris* male					
N. f. baileyi X *N. f. campestris*	2	2	100.0	2	2	2.0	2	2.00
			N. f. baileyi X *N. f. attwateri* males					
N. f. baileyi	1	1	100.0	2	2	4.0	4	4.00
N. m. canescens	1	0	0.0	----	----	----	----	0.00

TABLE 18.—Continued.

Females	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
N. f. baileyi X *N. f. attwateri*	1	1	100.0	1	2	3.0	3	3.00
TOTAL	3	2	66.7	3	4	3.5	3–4	2.33
N. f. campestris X *N. f. attwateri* males								
N. f. campestris	2	1	50.0	2	1	3.0	3	1.50
N. f. campestris X *N. f. attwateri*	1	0	0.0	.	....	....	....	0.00
TOTAL	3	1	33.3	2	1	3.0	3	1.00
N. f. baileyi X *N. m. canescens* males								
N. f. baileyi	1	1	100.0	2	2	4.0	4	4.00
N. m. canescens (2)	1	0	0.0	....	....	. .	....	0.00
TOTAL	2	1	50.0	2	2	4.0	4	2.00
N. f. campestris X *N. m. canescens* males								
N. f. campestris X *N. m. canescens*	6	2	33.3	2	2	2.0	2	0.67
N. f. attwateri X *N. m. canescens*	1	1	100.0	0	2	2.0	2	2.00
TOTAL	7	3	42.9	2	4	2.0	2	0.86
N. f. attwateri X *N. m. canescens* F_1 males								
N. f. campestris	1	0	0.0	....	. .	....	....	0.00
N. m. canescens (2)	4	2	50.0	2	1	1.5	1–2	0.75
N. f. campestris X *N. m. canescens*	3	2	66.7	2	3	2.5	2–3	1.67
N. f. attwateri X *N. m. canescens* F_1	6	2	33.3	3	2	2.5	2–3	0.83
TOTAL	14	6	42.9	7	6	2.2	2	0.93
N. f. attwateri X *N. m. canescens* F_2 males								
N. f. attwateri	1	1	100.0	1	2	3.0	3	3.00
N. f. attwateri X *N. m. canescens* F_2	1	0	0.0	....	....	....	....	0.00
TOTAL	2	1	50.0	1	2	3.0	3	1.50
N. m. canescens X (*N. f. attwateri* X *N. m. canescens*) male								
N. f. campestris X *N. m. canescens*	1	0	0.0	....	. .	....	....	0.00
All *Neotoma floridana* males								
N. floridana	63	31	49.2	49	51	3.2	3	1.59
N. micropus	22	10	45.5	17	17	3.4	4	1.55
Species-hybrids	3	2	66.7	2	3	2.5	2–3	1.67
TOTAL	88	43	48.9	68	71	3.2	3	1.58
All *Neotoma micropus* males								
N. floridana	31	7	22.6	10	9	2.7	2–3–4	0.61
N. micropus	38	9	23.7	14	10	2.7	3	0.63
Species-hybrids	2	1	50.0	2	1	3.0	3	1.50
TOTAL	71	17	23.9	26	20	2.7	3	0.65
All species-hybrid males								
N. floridana	3	2	66.7	3	4	3.5	3–4	2.33
N. micropus	5	2	40.0	2	1	1.5	1–2	0.60
Species-hybrids	18	7	38.9	7	9	2.3	2	0.89
TOTAL	26	11	42.3	12	14	2.4	2	1.00

TABLE 18.—Concluded.

Females	Number matings attempted	Number successful matings	Percent success	Number progeny ♂♂	Number progeny ♀♀	Mean litter size	Mode litter size	Progeny per attempted mating
			All non-hybrid males					
Same species	101	40	39.6	63	61	3.1	3	1.23
Other species	53	17	32.1	27	26	3.1	4	1.00
Species-hybrids	5	3	60.0	4	4	2.7	3	1.60
TOTAL	159	60	37.7	94	91	3.1	3	1.16
			All males					
All females	185	71	38.4	106	105	3.0	3	1.14

a male of the same race. Minima and maxima frequently were 33 to 36 days.

No clearcut differences were observed in gestation periods of the two species either by me or by Spencer (1968). Apparently the gestation period normally fluctuates from 32 to 38 days with a modal duration of 35 days. Post-partum estrus and prolonged gestation apparently occur in both species, but the frequency of this phenomenon is not well known and the physiology associated therewith has not been investigated.

Size of Litters.—Literature pertaining to litter size of *Neotoma floridana* has been summarized by Rainey (1956:613). In most populations that have been studied, females regularly produced litters of one to four; occasional litters of five have been reported. Modal litter size for the species is three and the mean usually is near three. Litter size of *N. micropus* (Asdell, 1964:279) is apparently slightly smaller. Feldman (1935: 301, 302) studied members of this species from Carlsbad, New Mexico; each of 11 litters consisted of two young and in each litter both progeny were of the same sex.

Size of litters born to females of the northern *N. f. baileyi* in the laboratory was slightly greater than those of any of the other woodrats, as evinced both by the mean (3.5) and the mode (four). Litter size of the other two subspecies of *N. floridana* and that of *N. m. canescens* are comparable, having means near 3.0 and modes of three. Two litters born to *N. f. baileyi* X *N. f. campestris* "hybrid" females had only two progeny each. This may indicate some type of partial sterility, but more observations would be necessary to draw meaningful conclusions. The single litter born to an *N. f. baileyi* X *N. f. attwateri* "hybrid" female was the same as the modal litter size (three) of *floridana* females; a male of this cross sired a litter of four when mated to a *baileyi* female.

Litter size of species-hybrids was noticeably lower than that of either of the parental species. Considering all matings involving at least one species-hybrid, modal litter size both of males and of females was only two and the mean for both was 2.4. Because hybrid males sired only four litters with non-hybrid females and hybrid females produced only five litters from matings with non-hybrid males, it was not possible to determine unequivocally from the data whether litters of hybrids are smaller because of partial sterility in both sexes or only in one. However, it can be seen in tables 17 and 18 that no hybrid female produced a litter of more than three young, whereas one hybrid male sired a litter of four when mated to a *floridana* female. Of the 71 litters born as a result of laboratory matings, only two consisted of a single progeny; one of these matings was between a hybrid male and a *micropus* female. Mean litter size of non-hybrid females bred to hybrid males was 2.5 whereas that of the reciprocal was 2.7. Matings involving two hybrid individuals

averaged only 2.3 progeny per litter, possibly indicating that hybrids of both sexes are less fertile than non-hybrids.

Table 15 provides additional information on litter size and seasonal patterns of reproduction. Data presented in table 16 give further information on litter sizes and the reproductive season over a wide geographic area. Litter sizes of *floridana* and *micropus* may vary geographically, with more northerly populations having larger litters. In *N. f. baileyi* the mean was more than 3.5 and the mode was four progeny per litter; these data are based on successful matings in the laboratory, parturiation of previously conceived litters in the laboratory, and embryo counts recorded on specimen labels. All parameters studied indicate that *N. f. campestris, N. f. attwateri,* and northern populations of *N. m. canescens* most frequently have litters of three young each and that the mean usually is near or only slightly greater than three. Southern populations of *canescens* most frequently have litters of two progeny as seen in table 16 and reported by Raun (1966:17) and Baker (1956:286).

The correlation between latitude and litter size of mammals has been observed previously (Lord, 1960, and others) and probably has been best explained by Spencer and Steinhoff (1968), who expanded the theory originally put forth by Lack (1948, 1954). Individuals of northern populations have shorter breeding seasons and can place more progeny in subsequent generations by exerting more "energy" per litter on large litters, whereas those in southern populations are most successful by conserving "energy" expended per litter and producing more litters with each containing fewer individuals. In the woodrats studied, at least, information discussed previously regarding breeding seasons further substantiates the hypothesis.

Sex Ratios at Birth.—Sex ratios of progeny of all rats studied appear to be the typical one to one relationship. The only sample that deviates significantly ($P < 0.05$, tested by Chi-square) is the 26 males to 12 females born to *N. micropus* females that were pregnant when captured; four of 11 litters consisted only of male offspring. However, among young *micropus* collected with adult females there were more females than males and when the two samples are considered together the number of males only slightly exceeds the number of females.

Reproduction in Neotoma angustipalata.—Information on the reproductive habits of *N. angustipalata* is limited. Hooper (1953:9) reported two nursing young collected with a female on 19 May, and an adult female (Table 16) contained a single embryo when obtained in July. Two juveniles (UNAM 2166 and 2167) were collected on 6 October.

Discussion and Conclusions.—Reproductive habits of *N. floridana* and *N. micropus* vary both intra- and interspecifically. In the primary study area, the first litters of *micropus* are born two or three weeks prior to the first litters of *floridana,* but the breeding seasons of the two species are otherwise approximately the same. Laboratory and field observations conducted by me, and Spencer (1968) show that the two species do hybridize, and that hybrid progeny are somatically and reproductively viable. However, hybridization results in partial hybrid sterility, as evinced by reduced litter size. Reproductive isolation is at best incomplete between the two species and they probably will hybridize at all localities of sympatry, at least until selection has had sufficient time to establish and reinforce a mechanism of reproductive isolation. Only a single area of sympatry is presently known and the resultant hybrid zone (see account of *N. m. canescens* above) has not increased in size during the five years that it has been under observation. Furthermore, no conslusive evidence exists to indicate that the hybridization in north-central Oklahoma is introgressive or that introgression has occurred elsewhere along the potential zone of contact between

the two species. Reproductive and distributional evidence indicate that the two species may be in an allopatric phase of speciation as described by Key (1968), wherein dynamic tension zones, such as the mixed population in north-central Oklahoma, are formed prior to establishment of full reproductive isolation.

COMPARATIVE SEROLOGY

The dependency of protein synthesis on genetic control indicates that physicochemical and immunological characteristics of protein macromolecules are phenotypic expressions of the genotype. Comparative study of proteins, therefore, serves as an important means of studying the relationships of animals (Florkin, 1964; Boyden, 1964). Evolutionary rates of serological characters undoubtedly are stochastic (Kirsch, 1969), as are those of most characters.

Starch Gel Electrophoresis of Hemoglobins

Electrophoretically demonstrable variation in mammalian hemoglobins has been the subject of much study recently. In the Carnivora, hemoglobins appear to be relatively stable even at the ordinal level (Seal, 1969), whereas in the Chiroptera variation has been reported at the familial and generic levels (Mitchell, 1966; Valdivieso *et al.*, 1969). Hemoglobin ionographs of primates (Neel, 1961; Ingram, 1963; Hill and Buettner-Janusch, 1964; Sullivan and Nute, 1968) and rodents (Johnson, 1968; Foreman, 1960; and others) have been shown to vary intraspecifically in many taxa. Additionally, Foreman (1964) discovered by tryptic hydrolysis that in the genus *Peromyscus* some electrophoretically identical hemoglobins are chemically distinct.

Birney and Perez (1971) reported multiple hemoglobins in *Neotoma floridana, N. micropus,* and laboratory-bred hybrids of the two species. They observed major bands of four migration rates, designated (from slowest to fastest) 1′, 1, 2, and 3, and several minor bands that were not studied. Based on the number and position of major electrophoretic bands, seven distinctive hemoglobin patterns or phenotypes were described and labeled A through G as follows (Fig. 39): "A" occurred only in *micropus* and consisted of band 1 with a leading diffuse zone that terminated in a minor band at position 3; "B" was observed in both species and in hybrids and consisted of bands 1 and 2 and a leading diffuse zone; "C", observed only in *floridana* and hybrids, was composed of bands 1, 2, and 3; "D" consisted of bands 2 and 3 with a trailing diffuse zone and also was limited to *floridana* and hybrids; "E" was seen only in *micropus* and hybrids and was composed of bands 1′ and 2 with a long leading diffuse zone and a terminal minor band; "F" was observed only in *floridana* and consisted of a heavy band, considered to be band 1, preceded by a short diffuse zone; "G" was observed only in laboratory-bred hybrids and consisted either of bands 1′, 2, and 3 or of all four major bands.

Results of electrophoresing precipitated globins by the urea—veronal method of Chernoff and Pettit (1964) indicated to Birney and Perez (1970) that the electrophoretically demonstrable variation resided in the beta (β) chains of

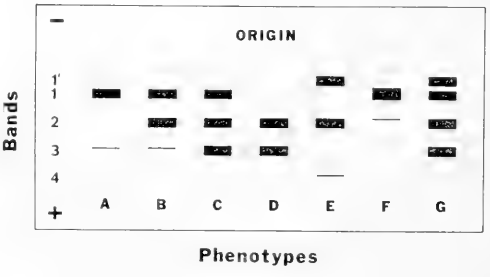

FIG. 39. Diagrammatic representation of electrophoretic patterns (phenotypes) of hemoglobins of *Neotoma floridana* and *N. micropus*. Major bands are represented by solid rectangles and minor bands by horizontal lines. The cathode is indicated by a minus sign and the anode by a plus sign. See Birney and Perez (1971) for photographs of starch gels showing electrophoresed woodrat hemoglobins.

the hemoglobin molecules. They further proposed tentative models that explained the inheritance patterns observed and demonstrated a possible sequence for the evolution of multiple beta loci in the species studied. According to the model, multiple beta loci have arisen by gene duplication so that at least three such loci (probably closely linked) now are present in *floridana* and at least two exist in *micropus*. *Neotoma micropus* may have either a third locus for production of the beta peptides of molecules forming band 1′, or genes producing these peptides may be allelic with those producing the beta peptides seen in band 1. "Alleles" that produce no peptide (termed β° alleles) apparently are present at all beta loci. These non-functional alleles may be either deleted areas on the chromosomes or they may be areas that are physically present but under control of modifier genes, or for other reasons do not contribute a peptide chain. If modifier genes are involved, it is likely that the minor bands result from limited production of the same peptides that form major bands when the β locus involved is fully active.

Materials and Methods.—Studies of hemoglobin samples discussed here were conducted simultaneously with those reported by Birney and Perez (1971). Detailed methods were outlined in that report and are only summarized here. Samples of whole blood were suspended in a trisodium citrate anticoagulate, washed three times in phosphate buffered saline, and lysed in distilled water. Hemoglobin phenotypes were determined by horizontal starch-gel electrophoresis in sodium borate buffer. Gels were sliced and stained in a solution of amido black in water-methanol-glacial acetic acid. The iodoacetimide method described by Riggs (1965) was employed to determine that none of the observed bands resulted from polymerization. Laboratory-bred woodrats are not included in the discussion of hemoglobin variation presented here because they would tend to bias the frequency of various phenotypes in favor of the phenotype(s) of their parents.

Results and Discussion.—Frequencies of the seven hemoglobin phenotypes observed in natural populations of *Neotoma floridana* and *N. micropus* are shown in table 19. At the time ancestral populations of *floridana* and *micropus* constituted a single species, it would appear that only hemoglobin bands 1 and 2 were present. These two bands are common to both species and when they occur together to form phenotype B, the patterns of the two species are essentially indistinguishable. When band 1 occurs without band 2 (phenotypes A and F), it is heavier; the band migrates slightly slower in *floridana,* and has a longer leading diffuse zone in *micropus*. The major band probably is formed by the same, or only slightly modified, peptides. The single banded situation may be the primitive hemoglobin phenotype for the two species, or phenotypes A and F both may have been secondarily derived after the two species were isolated. In any event, it appears that β^1 and β^2 both were present at the time of isolation because both were expressed by some individuals of the two species from every locality from which I have a sample of three or more individuals.

The $\beta^{1'}$ and β^3 alleles apparently originated in populations of *micropus* and *floridana,* respectively, after the two incipient species were geographically isolated. Although both alleles are present in the sample of woodrats from 3 mi S Chester, Major Co., Oklahoma, they have not been observed together elsewhere; $\beta^{1'}$ is not known for *floridana* nor is β^3 known for *micropus*. If the $\beta^{1'}$ allele ever was present in *floridana,* or if β^3 ever was present in *micropus,* they have been lost secondarily or exist in those species in extremely low frequency.

It is not known whether the genes controlling production of the beta chains of molecules forming bands 1 and 1′ are alleles of a single locus or if they occur at separate loci. Similarly, it is not known with certainty what phenotype results

TABLE 19. Frequency, expressed in percent, of seven hemoglobin phenotypes at selected localities of *Neotoma floridana* and *N. micropus*.

Origin of samples	*N*	Hemoglobin Phenotype A	B	C	D	E	F	G
Neotoma floridana baileyi								
Cherry Co., Nebraska	17	....	5.9	52.9	41.2	....	....	....
Rock Co., Nebraska	2	....	....	50.0	50.0	....	....	....
All localities	19	....	5.3	52.6	42.1	....	....	....
Neotoma floridana campestris								
Logan Co., Kansas	3	....	66.7	....	33.3	....	....	....
Finney Co., Kansas	6	....	66.7	....	....	....	33.3	....
Ness Co., Kansas	3	....	100.0	....	....	....	....	....
Hodgeman Co., Kansas	2	....	....	100.0	....	....	....	....
Ellis Co., Kansas	4	....	100.0	....	....	....	....	....
Russell Co., Kansas	17	....	5.9	35.3	58.8	....	....	....
All localities	35	....	40.0	22.9	31.4	....	5.7	..
Neotoma floridana attwateri								
Ellsworth Co., Kansas	4	....	75.0	....	25.0	....	....	....
Douglas Co., Kansas	13	....	76.9	23.1	.	....	....	....
All localities	17	....	76.5	17.6	5.9	..	..	....
Neotoma floridana								
All localities	71	....	39.4	29.6	28.2	....	2.8	....
Neotoma micropus canescens								
Baca Co., Colorado	29	10.3	20.7	....	....	69.0	..	....
Hamilton Co., Kansas	2	50.0	....	....	....	50.0	....	....
Haskell and Stevens cos., Kansas	22	18.2	40.9	....	....	40.9	....	....
Meade Co., Kansas	6	....	50.0	....	....	50.0	....	....
Barber Co., Kansas	13	....	46.2	....	....	53.8	....	....
All localities	72	11.1	33.3	....	....	55.6	..	..
Neotoma from 3 mi S Chester, Major Co., Oklahoma								
Specimens morphologically like *N. micropus*	5	....	40.0	....	....	40.0	....	20.0
Specimens morphologically like hybrids	8	....	12.5	25.0	....	12.5	....	50.0
All specimens	13	....	23.1	15.4	....	23.1	....	38.4

when both genes are present (Birney and Perez, 1971). Therefore, it is not possible to calculate their frequency accurately. Moreover, no *micropus* has been observed that lacked both bands 1 and 1′, but breeding data presented by Birney and Perez indicate that the β° allele also occurs in low frequency at the β^{1}-$\beta^{1'}$ locus(i) in that species, as it does in *floridana*. A crude estimate of the frequency of β^{1} and $\beta^{1'}$ can be calculated by the Hardy-Weinberg formula, if it is assumed that β^{1} and $\beta^{1'}$ are allelic, that when both are present $\beta^{1'}$ acts as a dominant, and that the frequency of the β° allele associated with that locus is sufficiently low to be ignored. By using this formula and following the genetic scheme proposed by Birney and Perez (1971), estimates of the frequency of all other alleles for both species can be calculated as accurately as size of available samples permits (Table 20).

Changes in hemoglobin allele frequency of *Mus musculus* on the Jutland Peninsula appeared to Selander, Hunt, and Yang (1969:384) to be directional from west to east, but in the United States variation apparently is north to south (Selander, Yang, and Hunt, 1969: 285). The frequency of the $\beta^{1'}$ allele in *N. micropus* fluctuates geographically, but no clear picture of the nature of this variation emerges from examination of

the three populations (Table 20) which have sufficiently large samples to warrant calculation of gene frequencies. Some individuals at all localities sampled possess the allele and it probably is widespread in the population. However, it was not found to be fixed at any locality. The β^2 locus is polymorphic at the four western localities sampled, but the β^2 allele may be fixed in eastern populations of the species as indicated by the absence of phenotype A in samples from Meade and Barber counties and in the "hybrid" sample from Oklahoma. The β^2 locus was polymorphic in *N. floridana* at only one locality (Finney County, Kansas), but additional sampling might have yielded animals of phenotype F from other localities.

Two populations of *N. floridana* (*campestris* from Russell County and *baileyi*) appear to have slightly higher frequencies of the β^1 allele and considerably higher frequencies of the β^3 allele than do other populations of the species (Table 20). Of the 17 woodrats from Russell County, 16 were from a single juniper windbreak and all of these had the β^3 allele; hemoglobin of the only animal obtained from another windbreak several miles distant lacked band 3.

None of the 13 individuals of *N. f. attwateri* from Douglas County lacked band 1, but hemoglobin of one of four animals from Ellsworth County (near the *attwateri-campestris* subspecies boundary) did not form the band (Table 19). Frequency of β^3 appears to be low in the sampled populations of *N. f. attwateri,* but the relatively high frequency of this allele in the "hybrid" population from Major County, Oklahoma, indicates that in adjacent populations of *N. f. attwateri* the frequency of this allele is either relatively high or that phenotype G conveys a strong selective advantage.

Presence of hemoglobin phenotype G in several individuals from 3 mi S Chester, Major Co., Oklahoma, clearly indicates that the two species have hybridized at this locality. The phenotype has been observed previously in known hybrids (Birney and Perez, 1971), but not in woodrats of either species from localities of allopatry.

Functional relationships of the dif-

TABLE 20. Frequency of hemoglobin alleles at selected localities of *Neotoma floridana* and *N. micropus*. Localities with samples of less than 10 individuals are not shown separately but are included in totals.

Sample	*N*	$\beta 1'$	$\beta 1$	βo[a]	$\beta 2$	βo	$\beta 3$	βo[b]
Neotoma floridana baileyi								
Cherry County, Nebraska	17	0.00	0.36	0.64	1.00	0.00	0.76	0.24
All localities	19	0.00	0.35	0.65	1.00	0.00	0.77	0.23
Neotoma floridana campestris								
Russell County, Kansas	17	0.00	0.23	0.77	1.00	0.00	0.76	0.24
All localities	35	0.00	0.44	0.56	0.76	0.24	0.37	0.63
Neotoma floridana attwateri								
Douglas County, Kansas	13	0.00	1.00	0.00	1.00	0.00	0.12	0.88
All localities	17	0.00	0.76	0.24	1.00	0.00	0.13	0.87
Neotoma floridana								
All localities	71	0.00	0.47	0.53	0.83	0.17	0.35	0.65
Neotoma micropus canescens								
Baca County, Colorado	29	0.44	0.56	0.00	0.68	0.32	----	----
Haskell and Stevens counties, Kansas	22	0.23	0.77	0.00	0.57	0.43	----	----
Barber County, Kansas	13	0.32	0.68	0.00	1.00	0.00	----	----
All localities	72	0.33	0.67	0.00	0.67	0.33	----	----
Neotoma sp.								
Major County, Oklahoma	13	----	----	----[c]	1.00	0.00	0.32	0.68

[a] See text for assumptions made to calculate frequencies of these alleles for *N. micropus*.
[b] There presently is no evidence that this locus occurs in *N. micropus*.
[c] Frequency of these alleles in this population cannot be calculated.

ferent hemoglobin phenotypes are unknown. The data appear to indicate a poorly defined tendency for animals from arid habitats to have fewer electrophoretic bands (thus fewer kinds of beta polypeptides) than animals from more mesic habitats. Manwell *et al.* (1963) found that hemoglobins of hybrids may have selective advantages over those of either parental species in some birds, but no data are available on this subject for woodrats.

Immunoelectrophoresis of Esterases

It has been shown that injections of whole serum alone stimulate production of a relatively specific antiserum of low antibody titer (Durand and Schneider, 1963), but that whole serum emulsified with complete Freund's adjuvant results in an antiserum of relatively high antibody titer and low specificity (Anthony, 1965). Because adjuvant was used in this study, antisera were of the latter type. A pilot study of precipitin tests (Boyden, 1964, and elsewhere) indicated that either the antisera were not sufficiently specific to distinguish minor differences in woodrat proteins, or that proteins of the closely related woodrats under study had not diverged perceptibly at the sites of antigen-antibody reaction. Anthony (1965) found that precipitin tests were inefficient for comparing closely related races and species of the genus *Canis*.

Micro-immunoelectrophoresis (Schneidegger, 1955) has a distinct advantage over precipitin testing because individual arcs of precipitate are formed. However, Gerber (1968) observed that neither total counts nor weighted scores based on intensity of general protein arcs were reliably indicative of systematic relationships of bats. To reduce the number of arcs to be considered, Anthony (1965) conducted immunoelectrophoresis and differentially stained only for esterases.

Because intra- and interspecific variation in esterases is well known (see Augustinsson, 1961) and because it was desirable to determine if the immune reaction might further elucidate information on the relationships of woodrats, this technique was employed.

Materials and Methods.—Rats were bled by cardiac puncture. Sera were separated by centrifugation and preserved by freezing at –15°C. Antisera against pooled samples of whole sera were prepared in rabbits following the procedure outlined by Gerber and Birney (1968: 413). Antisera obtained following the second series of immunizing injections were used in all reactions. Woodrats from which sera were used for production of antiserum are as follows: *Neotoma floridana baileyi*—15, from Cherry County, Nebraska (A); *N. f. campestris*—8, from Logan and Finney counties, Kansas (B); *N. f. attwateri*—14, from Douglas County, Kansas (F); *N. f. magister*—4, from Giles County, Virginia (G); *N. m. canescens*—16, from Haskell County, Kansas (I); *N. m. canescens*—13, from Barber County, Kansas (K). Serum of each of the above-listed woodrats also was used in reactions with antisera and, in addition, sera of woodrats listed below were reacted against antisera but not used in production of the latter: *N. f. campestris*—14, from Ellis County, Kansas (C); *N. f. campestris*—4, from Russell County, Kansas (D); *N. f. attwateri*—1, from Ellsworth County, Kansas (E); *N. m. canescens*—11, from Baca County, Colorado (H); *N. m. canescens*—7, from Meade County, Kansas (J); *Neotoma* sp.—3, from area of sympatry in Major County, Oklahoma (L). Letters following localities indicate geographic origin of specimens in figure 42 and table 21. All animals used were adults and had been in captivity at least two weeks. An attempt was made to include an equal number of animals of both sexes in each sample, but smaller samples did not always have equal sex ratios.

The sample of *Neotoma floridana magister* was included to serve as a standard for other comparisons and because the taxonomic status of this taxon is unclear; *magister* may be a species dis-

tinct from other populations of *floridana*.

Concentration of protein-nitrogen for immunoelectrophoresis and for injecting rabbits was determined with an Aloe-Hitachi hand protein-refractometer. Serum was diluted to contain one gram per cent protein. Slides for immunoelectrophoresis were prepared by layering three ml of a two percent Ionager solution on each microscope slide. The arrangement of antigen wells and antibody troughs used is shown in figure 40. Electrophoresis was conducted in Michalis' buffer, ionic strength 0.05, pH 8.7, for 35 minutes at 40 volts. Ten lambda of unpooled serum from individual woodrats were placed in each antigen well immediately prior to electrophoresis. Each slide was prepared in duplicate. Following electrophoresis, gel in the precut trough was removed and the trough filled with antiserum. Reactants were allowed to interact in a humidity chamber for 24 hours. Unbound protein was removed by washing the agar slides for two days in three washes of borate-buffered saline, pH 8.6. Salts were removed similarly in three rinses of distilled water. The agar then was dried to a thin film and stained for esterase activity. The staining solution consisted of 40 ml of 0.2 M Tris-maleate and 0.2 M sodium hydroxide adjusted to a pH of 7.0, 1 ml of one per cent α-naphthyl acetate (in acetone), and 20 mg of Fast Blue RR diazonium salt. Reagents were mixed immediately before use and gels incubated in the solution for 20 minutes at room temperature. Stained slides were soaked for 15 minutes in a two per cent glycerol solution to prevent cracking and peeling of the agar.

The size and intensity of the major esterase band (Fig. 41) formed by the antigen of each woodrat against each antiserum was assigned a value on a scale of zero to eight. The minor band was scored similarly on a zero to two scale. Exemplary slides were selected with bands of each value to standardize scoring. The two values for each individual were added together and subjected to a Y + 1 conversion to eliminate zero scores. These values then were averaged for the woodrats from each locality. Because six antisera were used and two bands were considered for each antiserum, a total of 12 values was calculated for specimens from each locality. These values were used as characters and the sample from each locality was treated as an OTU in the CLSNT subroutine discussed previously.

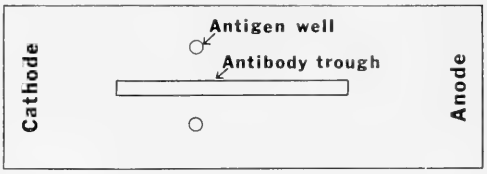

FIG. 40. Diagrammatic representation of microscope slide with Ionagar gel as used for immunoelectrophoresis.

Results and Discussion.—Mean values of scores for size and intensity of esterase bands are shown in table 21. It is immediately apparent that band scores for the population of *N. f. campestris* from Ellis County are highest in every case. Normally, in immunological tests, the homologous reaction is expected to exceed all cross reactions, and cross reactions are considered in terms of percent immunological correspondence to the homologous reaction, which is set at 100. This technique is clearly not applicable in evaluation of the data at hand; even when the population from Ellis County is disregarded, the homologous reaction invariably is exceeded by at least one other cross reaction.

Anthony (1965) found that the immunological response to esterase antigens in cross reactions often surpassed that in reference reactions in studies of dogs. Several variables apparently interact to result in this phenomenon. The number of evolutionarily based changes in esterase molecules at antibody-antigen reaction sites between closely related populations undoubtedly is low, antiserum produced against an emulsion of whole serum and adjuvant is not highly specific, individual subjects have varying concen-

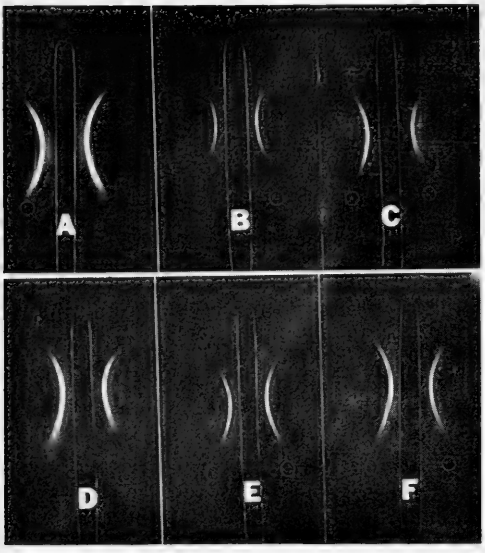

FIG. 41. Examples of esterase bands formed by differentially staining antigen-antibody precipitate in dried Ionagar on microscope slides. The antiserum used was prepared against the serum of *Neotoma floridana campestris*. Separate samples of serum from two woodrats were placed in the wells (left and right) of each slide as follows: A—*N. f. campestris* from locality C; B—*N. f. baileyi* from locality A; C—*N. f. attwateri* from locality F; D—*N. f. magister* from locality G; E—*N. micropus canescens* from locality I; F—*N. m. canescens* from locality K. See accompanying text for explanation of locality codes.

trations of an enzyme in the serum depending on a variety of both intrinsic and extrinsic factors (see, for example, Jones and Bunde, 1970), and the catalytic action of enzymes is often reduced by reaction with corresponding antibodies, especially in antibody excess (Cinader, 1957:373). If the antigen of a given sample contained a sufficient quantity of esterase molecules to stimulate production of a high titer of anti-esterase antibodies of relatively low specificity, and if a related sample contained the same or a similar esterase in greater quantity, the cross reaction would be expected to exceed the reference reaction when the two samples were tested. Therefore, the immune reaction involving single enzymes has severe limitations when comparing closely related taxa.

Nevertheless, Anthony (1965) found that correlations of these kinds of data frequently corresponded well with generally accepted theories of relationships of various breeds of dogs. The correlation and distance phenograms as calculated by CLSNT for the woodrats studied are shown in figure 42. Values for *N. f. campestris* (C) from Ellis County are sufficiently greater than values for other samples that the distance phenogram separates that sample from all others at a distance (2.36) nearly double that (1.24) of the next major separation. Elsewhere in the distance phenogram, the two samples of *N. f. attwateri* appear as a subgroup closely allied to the hybrid sample from Oklahoma, the three samples of *N. m. canescens* from adjacent localities in Kansas form a single subgroup, but samples from the remaining localities do not correspond well with other data concerning relationships.

In the correlation phenogram, which should reflect the relative degree of reactivity (enzyme similarity?) rather than the magnitude of reactions, the Ellis County population is closely coupled with the sample of *N. f. attwateri* from nearby Ellsworth County. The sample of *N. f. attwateri* from Douglas County is next to join that subgroup, followed by the sample from the locality of sympatry. It was expected that the population of *N. f. campestris* (D) from Russell County, which is geographically and morphologically intermediate between those from Ellis and Ellsworth counties, would also be in that subgroup. However, that sample formed a relatively distinct subgroup with the sample of *N. f. magister*, to which it certainly is not closely allied either geographically or morphologically.

The sample of *N. f. baileyi*, and to a lesser extent, the sample of *N. f. campestris* (B) from Logan and Finney counties, Kansas, appear in both phenograms to have esterases more like those of *N. micropus* than like those of other populations of *N. floridana*. This relationship may somehow correspond more

TABLE 21. Mean scores of esterase bands of 12 samples of *Neotoma floridana* and *N. micropus* serum reacted with six antisera. See text for exact localities of origin of woodrats.

Source of antigens	Antisera: *N. f. baileyi* (A)		*N. f. campestris* (B)		*N. f. attwateri* (E)		*N. f. magister* (G)		*N. m. canescens* (K)		*N. m. canescens* (I)	
	Bands: Major	Minor	Major	Minor	Major	Minor	Major	Minor	Major	Minor	Major	Minor
N. f. baileyi (A)	5.90	1.23	3.93	1.03	4.07	1.47	6.27	1.47	4.89	1.07	4.70	1.20
N. f. campestris (B)	5.81	1.31	4.94	1.00	4.56	1.38	6.94	1.50	5.50	1.12	6.81	1.31
N. f. campestris (C)	8.88	2.46	7.45	2.57	7.64	2.36	9.11	2.32	8.27	2.14	8.68	2.71
N. f. campestris (D)	3.88	1.00	4.12	1.00	1.25	1.50	5.38	1.12	2.50	1.12	6.94	1.62
N. f. attwateri (E)	2.50	1.00	2.00	1.00	3.00	1.00	2.00	1.50	2.00	1.00	5.00	2.00
N. f. attwateri (F)	4.79	1.11	3.43	1.00	2.71	1.07	3.64	1.11	3.00	1.12	4.18	1.50
N. f. magister (G)	3.50	1.62	6.00	1.00	1.00	1.75	7.12	1.38	3.62	1.00	7.12	1.00
N. m. canescens (H)	7.50	1.15	5.50	1.00	3.91	1.59	6.86	1.68	6.30	1.00	5.55	1.23
N. m. canescens (I)	6.88	1.44	4.91	1.03	4.17	1.90	7.16	1.69	6.61	1.46	5.98	1.62
N. m. canescens (J)	8.57	2.21	5.21	1.21	3.93	1.64	4.14	1.14	4.83	1.83	6.00	1.29
N. m. canescens (K)	8.08	1.88	5.12	1.31	5.04	1.62	6.31	1.92	6.58	1.81	6.88	1.58
Neotoma sp. (L)	6.00	1.67	3.33	1.00	3.33	1.67	3.67	1.00	5.33	1.00	5.33	2.00

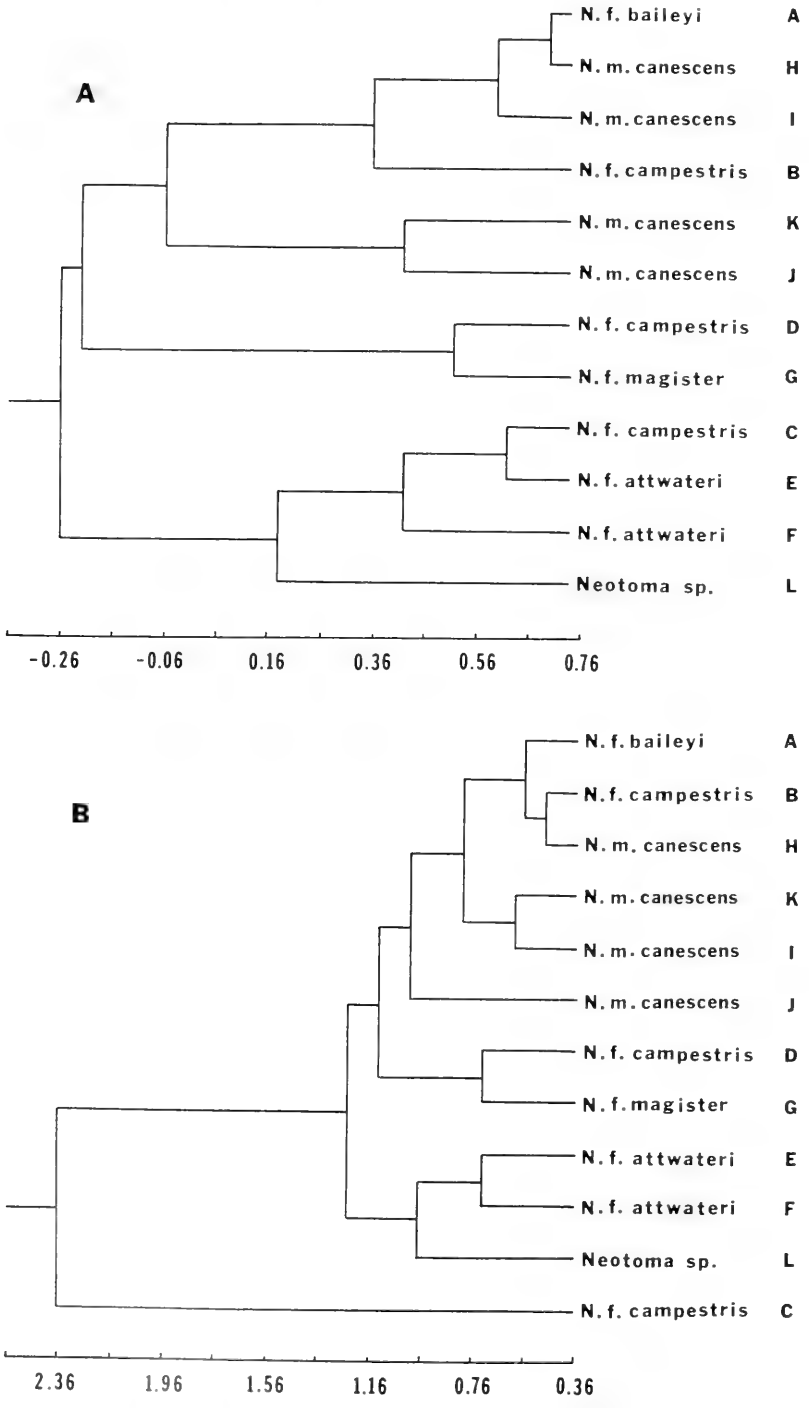

FIG. 42. Correlation (A) and distance (B) phenograms generated from mean scores of size and intensity of precipitated esterase-antibody bands. The coefficient of cophentic correlation of A is 0.792, whereas that of B is 0.895.

to adaptation to arid, relatively harsh environments than to phylogeny. For whatever reason, both phenograms also indicate that, with respect to esterases, the sample of suspected hybrids from Major County, Oklahoma, more closely resembles *floridana* from eastern Kansas than it does western populations of *micropus*. This result is not consistent with characteristics of pelage and skulls of the specimens involved.

The fact that rather well marked differences in the antibody-antigen esterase bands were observed between woodrats of the two species from different localities clearly shows that esterases in woodrats differ qualitatively, quantitatively, or both. However, these data must be interpreted with respect to all other data relating to the supposed relationships of the various populations studied. Additional studies on individual variation of esterases, quantitative variation of the esterases of an individual under various environmental conditions, and antibody specificity to enzymes will be necessary before data such as these can be fully and reliably interpreted with respect to the relationships of mammals.

COMPARATIVE KARYOLOGY

The karyotype of *Neotoma floridana* first was described by Cross (1931), who reported the diploid number as 52. Matthey (1953) verified the diploid number and described two large submetacentric and two large subtelocentric chromosomes in the complement. Mitotic chromosomes of *Neotoma micropus* were described by Hsu and Benirschke (1968); the diploid number was shown to be 52 and the karotype illustrated resembled that reported for *floridana*.

Baker and Mascarello (1960) described the chromosomes of several species of *Neotoma*, and redescribed the karyotypes of both *floridana* and *micropus*. They reported that the number of large biarmed elements varies from one to four in *micropus*, but that females of *floridana* have four biarms and males have three. They concluded that the Y is a medium-sized subtelocentric chromosome in both species. The chromosomal polymorphism in *micropus* was discussed by Baker *et al.* (1970) and shown to be a widespread phenomenon geographically, involving the X chromosomes and one pair of large autosomes.

Materials and Methods.—Preparations of chromosomes were made from cells in bone marrow using a modification of the blaze-dry techniques described by Patton (1967) and Lee (1969). Chromosomes were stained in a saturated solution of crystal violet. Only specimens collected from natural populations are reported. Results discussed below are based on study of at least 10 chromosome spreads from each of 58 woodrats, including specimens of *Neotoma floridana baileyi, N. f. campestris, N. f. attwateri,* and *Neotoma micropus canescens.* Included also are six specimens collected from the area of sympatry between *floridana* and *micropus*—3 mi S Chester, Major Co., Oklahoma.

The maximum number of chromosomes counted in any cell was 52. Some cells had less than 52 chromosomes, but the difference undoubtedly resulted from a loss of chromosomes during preparation. Those having less than 52 chromosomes were not studied or included in the 10 counts. In complete cells, no intraindividual variation beyond that attributable to differential contraction of chromosomes was observed.

Results and Discussion.—A consistent but relatively subtle (and heretofore unnoted) difference exists between the karyotypes of *Neotoma floridana* and *Neotoma micropus,* irrespective of the number of large biarmed elements. In the karyotype of both there is a graded series of 22 pairs of so-called acrocentrics. However, only rarely can chromatin be seen beyond the centromere opposite the arm in metaphase preparations of the acrocentric chromosomes of *micropus,* whereas in *floridana* there is invariably a visable amount of chromatin beyond the

centromeres of at least the larger acrocentrics. These tiny "arms" are evident in the karyotype of an *N. f. attwateri* illustrated by Baker and Mascarello (1969:189) and also were present in the karyotypes of *floridana* studied by me.

If considered to be chromosome arms, these bits of chromatin would increase the Fundamental Number (FN) of the karyotype of *N. floridana*. Only in relaxed spreads of *N. f. campestris*, however, are these "arms" sufficiently large to cause difficulty in determining the number of biarmed chromosomes. Until more information concerning these "arms" is available, I consider it best not to include them in calculations of the FN and have attempted to distinguish such chromosomes from the subtelocentrics that are involved in the polymorphic system. Although it may be misleading to refer to these chromosomes as acrocentrics, I will do so in an attempt to preserve the terminology used by Baker and Mascarello (1969).

In the chromosomal complement of each of the nine female *N. f. baileyi* examined, only two large and distinctly biarmed elements were seen (Fig. 43); in each instance the two biarms were of nearly equal size. Two distinctly biarmed elements (one noticeably larger than the other) also were seen among the chromosomes of each of the four male *baileyi* karyotyped (Fig. 43). There is no chromosome in *baileyi* males that closely resembles the chromosome Baker and Mascarello (1969:189) designated as the Y of *N. f. attwateri*. Therefore, I consider the smaller of these two submetacentric elements as the Y chromosome and the larger as the X. In three male *N. f. attwateri* from Douglas County, Kansas, four biarmed elements were observed (Fig. 44). Three had arms of unequal length and were distinctly larger than the fourth in each instance. The fourth was indistinguishable from the chromosome thought to be the Y in *baileyi*. Each of six *N. f. attwateri* females (two from Ellsworth County and four from Douglas County, Kansas) had four, large, biarmed chromosomes that were indistinguishable from the three larger biarms described for males. The karyotype of these females was like that described by Baker and Mascarello *(loc. cit.)* for five females from Payne County, Oklahoma. Apparently the Y chromosome varies in *attwateri*, but because I examined only three males from a single locality, and Baker and Mascarello studied only two from another locality, it is not possible to determine if the variation is geographic or if it is polymorphic at some localities. Available evidence indicates that the number of large biarmed chromosomes exclusive of the Y is constant in *attwateri* at four in females and three in males.

A small submetacentric chromosome that is indistinguishable from the Y in *baileyi* and in *attwateri* from Douglas County was seen in the karyotypes of three of four *N. f. campestris* males. These animals were from Logan, Finney, and Russell counties, Kansas. The fourth male, from Ness County, Kansas (Fig. 44), lacked such a chromosome, but several "acrocentrics" in the preparation had sufficiently large "arms" beyond the centromere as to be considered subtelocentrics; one of these probably is the Y. Additionally in the Ness County male, there is one large submetacentric, one large subtelocentric, and another large chromosome that may be a subtelocentric. In the karyotype of each of the other three animals there is one large submetacentric chromosome, one distinctly subtelocentric element, and a third large chromosome that probably is a subtelocentric but may be an "acrocentric." The karyotypes of nine female *campestris* all were characterized by two large submetacentrics and either one or two large subtelocentrics. One female from Finney County had two subtelocentrics in all except one of the cells examined; chromosomes in this cell were severely contracted and the two subtelocentrics were indistinguishable from acrocentrics of similar size. The presence of two large submetacentrics in females and one in

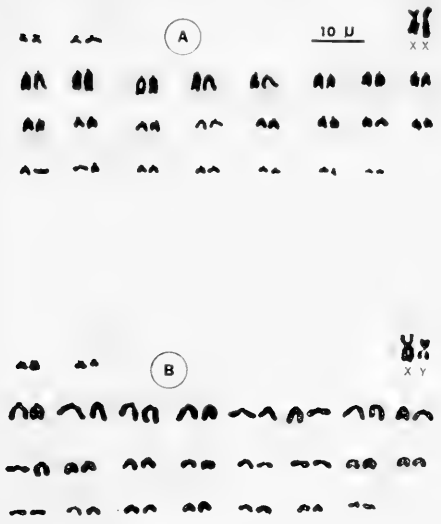

FIG. 43. Karyotypes of a female (A) and a male (B) *Neotoma floridana baileyi* from Rock and Cherry counties, Nebraska, respectively. The scale applies to both karyotypes.

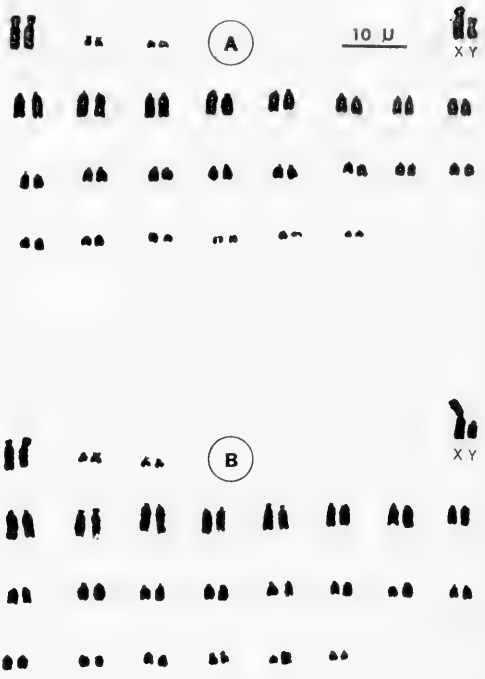

FIG. 44. Karyotypes of a male *Neotoma floridana attwateri* (A) from Douglas County, Kansas, and a male *N. f. campestris* (B) from Ness County, Kansas. The scale applies to both karyotypes.

males indicates that these are the X chromosomes. The presence of one subtelocentric in some females and two in others may represent a polymorphic system the same as, or similar to, that discussed by Baker *et al.* (1970) for *N. micropus*. On the other hand, these observations may be a result of the difficulty in distinguishing large subtelocentrics from the so-called acrocentrics.

A medium-sized subtelocentric chromosome was present in each of the karyotypes of five *N. m. canescens* males (three from Barber County and two from Haskell County, Kansas). This element was not seen in any of the karyotypes of 11 females and undoubtedly is the Y chromosome as shown by Baker and Mascarello (1969) and by Baker *et al.* (1970). Both males from Haskell County had one large submetacentric and one large subtelocentric in addition to the Y chromosome. The three males from Barber County each had one large submetacentric and two large subtelocentrics.

Three of four female *N. m. canescens* from Baca County, Colorado, one of two from Haskell County, Kansas, and four of five from Barber County, Kansas, each had two large submetacentrics and two large subtelocentrics. The karyotypes of these animals were indistinguishable from that illustrated by Hsu and Benirschke (1968) for a *micropus* female. The other three females each had two large submetacentrics, but only a single subtelocentric.

Two males, both identified as hybrids, from the area of sympatry between *floridana* and *micropus* (3 mi S Chester, Major Co., Oklahoma) had karyotypes indistinguishable from those of the three male *N. micropus* from Barber County, Kansas. Four females identified as *micropus* from that locality each had four large biarmed elements. The karyotypes of three of these were indistinguishable from that of *micropus* females having four biarms, but the fourth had two acrocentrics with tiny "arms" as described for *floridana*. The presence of *floridana*-

like acrocentrics in the karyotype of this animal undoubtedly resulted from hybridization of the two species. A female identified as a hybrid had three distinctly biarmed elements, but spreads were not sufficient to determine the presence or absence of "arms" beyond the centromere of large acrocentrics.

The polymorphic system involving the number of large biarmed chromosomes in *N. micropus* reported by Baker and Mascarello (1968) and discussed by Baker *et al.* (1970) probably will be found to exist throughout the range of the species. Baker *et al.* discussed variation in number of biarms in animals from three widely separated localities in Texas and one locality in Oklahoma. The karyotype is now known to be variable at one locality in Colorado and two in Kansas. The only locality from which specimens of *micropus* have been karyotyped and not reported to be polymorphic is 16 km N Ciudad Victoria, Tamaulipas (Hsu and Benirschke, 1968). These animals were of the subspecies *N. m. micropus,* whereas the polymorphic populations all are *N. m. canescens.* However, Hsu and Benirschke (1968) did not indicate if chromosomes of more than two rats (the karyotypes illustrated) from Tamaulipas were examined. Baker *et al.* (1970) discussed the possible origin of polymorphism in *micropus;* apparently it is the result of neither a Robertsonian change (as frequently is seen in mammals) nor of a single pericentric inversion. These authors suggested that both inversions and translocations may be involved in the origin of this system.

The discovery of a submetacentric Y chromosome in some populations of *N. floridana* is of interest. No other species of the genus has been reported to have a submetacentric Y chromosome and, although the karyotype of *N. f. baileyi* was not found to vary, these findings indicate that a previously undescribed polymorphism exists in the Y chromosome of *N. f. attwateri* and *N. f. campestris.* The number of large biarmed chromosomes (exclusive of the Y) has not been found to vary from three in males and four in females for *N. f. attwateri,* but only two biarms were seen in the karyotype of the nine *baileyi* females and only one (exclusive of the Y) in the four *baileyi* males examined. In *N. f. campestris,* the number of large submetacentric chromosomes seems to be constant at two in females and one in males. Although it is difficult to distinguish large subtelocentrics from some "acrocentrics" in rats of this subspecies, apparently the number fluctuates from zero to two. The large biarms in *baileyi* and the large submetacentrics in *campestris* probably are the X chromosomes, but in *attwateri* the X chromosomes cannot be certainly identified.

As shown by Baker *et al.* (1970), the X chromosomes in *micropus* cannot be distinguished with certainty, because polymorphism is involved and also because the relative lengths of the arms in the large, biarmed chromosomes is variable. In the *micropus* examined by me, at least one large submetacentric always was found in males and two such elements were present in females; in the absence of other information these would appear to be the X chromosomes. However, Baker *et al.* (1970) reported two females that had only one large, biarmed chromosome. All males examined by them had at least one biarmed chromosome in addition to the smaller subtelocentric Y. This chromosome probably is the X, but as seen in the two females having only a single biarmed element, at least one X can be an acrocentric in females.

Because of the limited number of animals examined and the chromosomal complexity of this group, a discussion of the evolution of chromosomes in *N. floridana* and *N. micropus* is somewhat premature. However, in *N. floridana* previously reported by Cross (1931), Matthey (1953), and Baker and Mascarello (1969), and in *N. f. attwateri* from northeastern Kansas, the number of biarmed chromosomes was always four in females and three plus the Y in

males. This is also the number of biarms reported for *N. m. micropus* from Tamaulipas and the most common karyotype seen in *N. m. canescens*. It is likely, then, that this is the karyotype from which others have evolved. The number of large biarms is unstable in *micropus* and possibly fluctuates in *N. f. campestris*, but in *N. f. baileyi* the two biarmed autosomes have been replaced by two acrocentrics.

Because the Y chromosome is a medium-sized subtelocentric in all populations of *N. micropus* examined and in all *floridana* that have been examined excepting *baileyi*, some *campestris*, and the *attwateri* from northeastern Kansas, the subtelocentric undoubtedly is the primitive Y chromosome and the submetacentric is derived. If it is eventually found that the lengthened arm of the submetacentric Y was acquired by a translocation of an arm of one of the original biarmed autosomes, then the two polymorphic systems may have a common origin. In any event, the submetacentric Y chromosome evidently was present in at least some *floridana* males prior to the time *baileyi* and *campestris* dispersed to the geographic areas they now occupy. The apparent fixation of this element in *baileyi* is not surprising considering that the subspecies is isolated in a relatively small geographic area. The submetacentric Y probably is commoner than the subtelocentric in *campestris*. Both forms of the Y chromosome are known in *attwateri;* but the relative status of the two is not known.

SUMMARY AND ZOOGEOGRAPHIC CONSIDERATIONS

Neotoma angustipalata, *N. floridana*, and *N. micropus* form a closely related complex of almost entirely allopatric taxa. The distributions of *floridana* and *micropus* are most appropriately termed stasipatric. Key (1968:22) discussed stasipatry as follows: "We could perhaps distinguish a condition of 'stasipatry' as a special case of parapatry in which the zone of overlap is limited by an impairment of the fecundity of freely produced hybrids rather than by ecological factors." The only known locality where the two species occur together (3 mi S Chester, Major Co., Oklahoma) is characterized by the presence of hybrids, identification of which was based on a variety of comparisons with hybrids reared in the laboratory. For example, the electrophoretic pattern of hemoglobins of some animals from the locality of sympatry was otherwise observed only in known hybrids; discriminant function analysis based on 17 characters of specimens of the two groups indicated they were generally intermediate between non-hybrid specimens of the two species; and the karyotype of one animal from the locality in question almost certainly contained chromosomes derived from both species.

There is no reason to believe that *floridana* and *micropus* ever have occurred together without producing natural hybrids or that they will do so in the near future. Although *floridana* generally is an inhabitant of relatively mesic woodland habitats (*N. f. campestris* being a notable exception) and *micropus* generally is associated with arid grasslands, either species probably could expand its range (at least slightly) in the absence of the other (although the existence of a relatively broad hiatus between the distributions of the two species throughout much of the region of potential contact might argue against the latter point). In any event, the two apparently hybridize when in contact and results of laboratory breeding studies strongly suggest some hybrid inviability. By definition, then, "stasipatry" best explains the distributional relationship of these two woodrats.

The distribution of *N. floridana* is not contiguous with that of *N. angustipalata*. *Neotoma micropus* and *N. angustipalata* occupy adjacent geographic

areas, but sympatry is unknown and no evidence of natural hybridization has been uncovered (but, see Alvarez, 1963: 452). To predict how *micropus* and *angustipalata* would act if they were sympatric clearly is speculative; representatives of *angustipalata* are larger than are those of *micropus* from adjacent localities in México and I doubt that the two would hybridize. However, size alone apparently is a relatively inefficient isolating mechanism among woodrats. Morphologically, *angustipalata* is approximately as distinct from both *floridana* and *micropus* as these two species are from each other.

Considering the fact that *floridana* and *micropus* hybridize in the laboratory and also in nature, some systematists might argue that the two are conspecific. However, *micropus* and *floridana* have maintained a high level of specific integrity in the past, apparently are doing so at present, and I predict, after extensive field and laboratory study, that they will continue to do so. Although there obviously is at least some genetic compatibility between *floridana* and *micropus,* the process of speciation between the two is essentially complete, and I regard it as having reached an irreversible point in time. Furthermore, I do not believe that our understanding of the evolutionary history and systematic relationship of these rats would be enhanced by formally placing *micropus* in the specific synonymy of *floridana.* In fact, such an arrangement would suggest that the two intergrade broadly and are more closely related than is the case. If considered as a single species, individuals or populations that should be studied separately might eventually be treated together in research by non-taxonomically oriented biologists, whose research design is partially dependent on decisions by taxonomists.

Despite my convictions that *floridana* and *micropus* should be considered separate species, certain data indicate that hybridization is, or recently has been, introgressive. Analyses of frequency and size of the fork on the anterior palatal spine and of the morphology of the posterior margin of the bony palate indicate that in some instances one or more populations of one species from localities geographically contiguous with populations of the other may have acquired selected genetic material introgressively. This was suggested most strongly by populations of *floridana* in Oklahoma and Texas. Also, specimens of *micropus* from localities adjacent to the range of *floridana* in south-central Kansas and coastal Texas are larger (thus somewhat like *floridana*) than specimens of *micropus* from localities not geographically contiguous with populations of *floridana.* It is possible that each species is selectively acquiring a limited amount of genetic material from the other (Key, 1968; Lewontin and Birch, 1966). However, certain other characters, such as electrophoretic patterns of hemoglobins and analyses of karyotypes, do not indicate introgression. Introgression is extremely difficult to "prove" or "disprove," and in the case of *floridana* and *micropus* elucidation of this phenomenon must await additional data.

The *micropus* species-group established by Burt and Barkalow (1942) is meaningless. The three species studied (*angustipalata, floridana,* and *micropus*) share a common ancestor in the not too distant past and represent a single species-group, the *floridana*-group. Anderson (1969) and Finley (1958) have shown that *N. albigula* is closely allied to *N. micropus* (Burt, 1960; Hooper, 1960), and Anderson (1969) indicated the possibility that *floridana, micropus,* and *albigula* eventually may best be considered a single species. Thus, it would seem that *albigula* and related species (*palatina, nelsoni,* and *varia*—see Hall and Genoways, 1970) also should be included in the *floridana*-group.

When the nomenclatorial arrangements of *floridana* and *micropus* are considered below the level of the species, some conclusions are relatively clearcut, whereas others are somewhat arbitrary.

Among populations of *floridana* studied, total geographic variation was less than that found in *micropus*. *Neotoma floridana baileyi* has certain unique features of the skull, and is relatively less variable than other samples as evinced by the absence of intraspecific variation in chromosomal complement and by lower coefficients of variation in most mensural characters; *baileyi* also has evolved a relatively distinctive pattern of reproduction. In certain aspects, some cranial dimensions and color for example, *baileyi* appears to have its affinities as much with *campestris* as with *attwateri*, but in final multivariate analysis, *baileyi* appeared more like *attwateri* than like *campestris*. As discussed beyond, the probable evolutionary history of these woodrats also suggests that the affinities of *baileyi* are with *attwateri*.

Neotoma floridana campestris is the most distinctive of the western subspecies of *floridana* with respect to color. Statistical analysis of mensural data indicated that in a few instances *attwateri* is larger than *campestris*. Specimens in a sample of *campestris* from Colorado and Nebraska were especially small relative to those in two samples of *attwateri* from localities in Kansas. A tendency was observed for woodrats from the zone of intergradation between *campestris* and *attwateri* to be larger than individuals in adjacent populations of either subspecies and for rats from localities west of this zone to become clinally smaller. Apparently, *campestris* exists in relatively small and semi-isolated populations that occupy discontinuous areas of suitable habitat. One acquires this impression in field study of *campestris* and additional evidence of localized stocks includes: 1) high variability of mensural characters in samples of this subspecies; 2) two of six animals from a semi-isolated population in Finney County, Kansas, had unique hemoglobin; and 3) three males each from different populations had a submetacentric Y chromosome, but a male from a fourth population had a subtelocentric Y chromosome.

Neotoma floridana attwateri, as here recognized, includes those animals previously assigned to *attwateri* and to the subspecies *osagensis*. As indicated above, specimens assignable to *attwateri* from near the range of *campestris* are especially large. Those from southeastern Kansas and southern Texas were next largest among the samples studied, and those from eastern Oklahoma and northeastern Kansas were smallest. The subspecies has not been found to be polymorphic for the number of large biarmed chromosomes, but it is polymorphic in the morphology of the Y chromosome. Three males from northeastern Kansas had a distinct submetacentric Y element, whereas two from near Stillwater, Oklahoma (Baker and Mascarello, 1969), had the more common subtelocentric Y.

Variation in *Neotoma micropus* is more easily definable geographically than that in *N. floridana*, but more difficult to resolve nomenclatorially at the subspecific level. *N. m. planiceps* is known only by the holotype; thus variation within the subspecies is unknown. The holotype is a small woodrat similar in size to other Mexican representatives of the species. Multivariate analyses indicated that *planiceps* is relatively distinct morphologically from both *canescens* and *micropus*. Possibly *N. m. planiceps* and *N. angustipalata* represent a single taxon. The holotype of the former is a young adult and conclusions regarding the affinities of *planiceps* must be regarded as tentative.

The name *N. m. micropus* has been restricted to the brownish, long-tailed woodrats that occur on the coastal plain and Sierra de Tamaulipas in the state of Tamaulipas. An appreciable amount of geographic variation exists even within this restricted area. Woodrats become progressively less brownish and more grayish from south to north in Tamaulipas. Variation in size especially and that in color to a lesser extent forms a sharp step-cline across the lower Río Grande.

However, the zone of contact between *micropus* and *canescens* in western Tamaulipas and eastern Nuevo León is relatively broad; the type locality of *N. m. micropus* (Charco Escondido, Tamaulipas) is in this zone of intergradation, but woodrats from that locality resemble more closely those from coastal Tamaulipas than rats from most of the range of *N. m. canescens.*

Neotoma micropus canescens is the most variable subspecies studied. Specimens from northern and eastern parts of the range are larger than those from southern and western localities, with the exception that specimens from coastal southern Texas are among the largest of the species. The darkest individuals occur in the northeastern parts of the range, but members of the subspecies become progressively paler from east to west. Distributional records of available specimens indicate that a large area in central Texas is not inhabited by *N. micropus.* If true, populations of large woodrats from coastal southern Texas are only circuitously connected geographically with populations of large woodrats to the north. Routes of gene flow between northern and southern populations of large woodrats thus would include populations of smaller western rats. The subspecies *canescens* could be subdivided into five subspecies with some merit as discussed previously. Another logical arrangement might recognize the small pallid woodrats of New Mexico, southwestern Texas, and adjacent México (exclusive of coastal Tamaulipas) as one subspecies *(leucophea)* and restrict the name *canescens* to the large woodrats from the northern and eastern parts of the range of the subspecies as here recognized. However, such an arrangement would not account for intermediacy in size and color of woodrats from southeastern Colorado, the panhandle of Texas, and non-coastal southern Texas. It might also result in an arrangement whereby populations of one subspecies are separated by populations of another.

Neotoma angustipalata is known by too few specimens to permit a meaningful analysis of intraspecific variation. Hooper (1953) commented on the extreme variability in this species and I observed the same phenomenon. More specimens of this enigmatic species are needed.

SUGGESTIONS FOR ADDITIONAL RESEARCH

Many aspects of the biology, and in particular the systematics, of woodrats of the *floridana* species-group (as here defined) need additional study. I have attempted throughout the preceding discussions to indicate these needs, and summarize them here. My study and others (Anderson, 1969; Finley, 1958) demonstrated the importance of continued field and laboratory work on the distributional and systematic relationships of *N. albigula* with both *N. floridana* and *N. micropus.* Especially critical geographic areas include southeastern Colorado, New Mexico, western Texas, the Edwards Plateau, southern Chihuahua, and montane areas of Coahuila.

Additional field work to study the exact distributional relationships of *floridana* and *micropus* is needed in southeastern Colorado, and throughout the area of general contact in Oklahoma and Texas. Sustained search for areas of sympatry and continued study of the one such area now known should result in elucidation of the distinctiveness of the two species and the presence or absence of introgression. Collecting efforts in that area of central Texas not now known to be inhabited by either *Neotoma floridana* or *Neotoma micropus* will elucidate the distributional status of woodrats and potential routes of gene flow in that state. The acquisition of additional specimens of *N. m. micropus* and *N. m. canescens* from Tamaulipas will help to clarify the relationships of these two taxa. Specimens from southern Tamaulipas and San Luis Potosí are needed to assess the systematic status of *N. angustipalata* and *N. m. planiceps* and to better understand the distributional relationship of these

woodrats with adjacent populations of *N. m. micropus* and *N. m. canescens.*

Certain problems requiring a combination of field and laboratory research have been studied, but most still lack definitive solutions. Birney and Perez (1971) presented hypotheses concerning the nature of variation and the mode of inheritance of woodrat hemoglobin, but these hypotheses need to be tested and refined. The chromosomal polymorphism in the number of large biarmed chromosomes first reported for *N. micropus* by Baker and Mascarello (1969), discussed by Baker *et al.* (1970), and observed in *N. floridana* by me needs to be analyzed more intensively from the standpoint of evolution, geographic distribution, and function. Baker and Mascarello (1969: 195) stated that "our results demand . . . introduction of individuals to wild populations different in chromosomal constitutions." I do not believe that such a means of study is necessary or advisable and am strongly opposed to research that might alter natural patterns of evolutionary phenomena in animals. However, studies wherein mating of captive individuals of "different chromosomal constitution" could be followed with analysis of meiosis in progeny would be enlightening. The polymorphism involving the Y chromosome in *N. floridana* should be studied to discern its distribution and origin.

Boice (1969) observed behavioral differences between *N. albigula* and *N. micropus* and Birney and Twomey (1970) reported evidence for physiological divergence of *N. floridana* and *N. micropus.* These areas of research hold promise in their own right and in terms of clarifying the overall systematics of the woodrats of the *floridana* species-group.

ZOOGEOGRAPHIC COMMENTS

Hibbard (1967:128) suggested that "the stock that gave rise to *Neotoma* must have separated off from a generalized cricetine in the Upper Miocene." He considered the extinct genus *Pliotomodon,* named by Hoffmeister (1945) from Pliocene deposits in California, as a specialized side branch related to *Neotoma,* but not in the direct lineage of Recent woodrats. The specimen from the Cumberland Cave Fauna (Pleistocene) named as a distinct genus, *Parahodomys,* by Gidley and Gazin (1933: 356) may represent another such offshoot, but also best may be considered as a member of the genus *Neotoma.*

The three species of *Neotoma* referred to the subgenus *Paraneotoma* by Hibbard (1967) from the Upper Pliocene and Middle Pleistocene of Kansas are more like *N. (Hodomys) alleni* than Recent members of the subgenus *Neotoma.* It is not possible to determine whether *Paraneotoma* is ancestral to Recent *Neotoma* or if the subgenus represents a once widely distributed group of species related to *N. alleni.* Alvarez (1966:9) named *N. magnodonta* from the Middle or Upper Pleistocene of México (state of México) as a member of the subgenus *Hodomys;* thus it clearly is not in the lineage of the *floridana* species-group. The only other fossil named as a distinct species that might relate significantly to the evolutionary history of the *floridana* species-group is *N. ozarkensis,* which was described by Brown (1909:196) from Middle to Late Pleistocene (Conard Fissure) deposits of northern Arkansas. This woodrat may prove to be no more than a subspecies of *floridana;* however, if the specimens are from pre-Wisconsin deposits it is likely that they predate all but the earliest processes of divergence of *floridana* and *micropus.*

These fossil records indicate that the genus *Neotoma* originated in the late Miocene or early Pliocene and evolved during the Pliocene to the extent that presently recognized subgenera were distinct by the beginning of the Pleistocene. There is no evidence that woodrats of the *floridana*-group inhabited the Central Plains during the Yarmouth. *Neotoma (Paraneotoma) taylori* occurred in at least parts of the Great Plains at that time

(Hibbard, 1967; 1970). Hibbard (1963: 209) reported a specimen that he considered more like *floridana* than *micropus* from a late Illinoian fauna in Kansas, and Hibbard and Taylor (1960:175) reported *N. micropus* from the Sangamon of Kansas. These specimens were tentatively identified on the basis of the shape of the posterior triangle of the anterior loop of M1. Semken (1966:151) and Dalquest *et al.* (1969:249) have indicated, and I concur, that this is not a diagnostic character to distinguish the two species. Semken *(loc. cit.)* reported additional material from the late Illinoian that compared favorably with *micropus,* but he elected not to assign the material to either species.

Dalquest *et al.* (1969) reported *N. floridana, N. micropus,* and *N. albigula* from deposits considered to be 11,000 to 8000 years BP. Although I have not examined this material, neither the measurement they used for specific identification (breadth of molar rows) nor any other single measurement taken by me will serve to distinguish Recent specimens of the three species. Furthermore, identification of Recent specimens of the three based on fragmentary skulls and lower jaws would be difficult, especially distinguishing between *floridana* and *micropus.* Possibly *albigula* occurred sympatrically with either *floridana* or *micropus* on the Edwards Plateau in the late Pleistocene, but I question whether *micropus* and *floridana* were in sympatry that early and I cannot conceive of all three species having occurred there simultaneously.

As I interpret these findings they indicate that woodrats of the *floridana*-group occurred on the Great Plains by late Illinoian. They may have diverged from related groups as late as the Illinoian. *Neotoma albigula* and related species also could have diverged from a *floridana*-like stock during the Illinoian, because results of most studies (e.g. Sprague, 1941; Burt and Barkalow, 1942; Burt, 1960; Hooper, 1960) indicate that *micropus* and *floridana* are more alike morphologically than either resembles *albigula.*

With the advance of Wisconsin ice, the basal stock of *floridana* probably retreated southward. *Neotoma albigula* might have been restricted to the Mexican Plateau or to the region of southern California, Arizona, and New Mexico (or both), *micropus* to the lowlands of coastal southern Texas and Tamaulipas, and *floridana* to the southeastern United States, possibly to peninsular Florida (see Sherman, 1952; Blair, 1958). Guilday *et al.* (1964:158) suggested that *N. f. magister* survived Wisconsin glaciation in the southern Appalachian Mountains. In view of the striking morphological and ecological distinctness of *magister* as compared with all other subspecies of *floridana,* I agree with Guilday *et al.* and further suggest that *magister* and *floridana* eventually will be found to represent biological species at least as distinct as *floridana* and *micropus.* However, the status of *magister* is beyond the scope of the present paper and the relationship of this taxon must await detailed field and laboratory study.

Speculation on the distribution in Wisconsin time of *Neotoma angustipalata* and *Neotoma palatina* also is of interest. The affinities of *angustipalata* as shown herein are clearly with *micropus* and *floridana,* but proclivities toward one, more than the other, are lacking. *Neotoma palatina* is thought to be most closely related to *N. albigula. Neotoma angustipalata* has a relatively restricted range in southern Tamaulipas and San Luis Potosí, whereas *palatina* is restricted to the barranca of Río Balaños, associated tributaries, and adjacent uplands. Besides *micropus* and *floridana,* only *angustipalata* and *palatina* are characterized by the absence of a maxillovomerine notch. Possibly this characteristic has evolved twice, but the solid vomerine septum of these four species may be indicative of a pre-Wisconsin common ancestor. *Neotoma palatina* apparently was sufficiently isolated from adjacent populations of *albigula* to effect speciation.

Neotoma angustipalata probably was isolated in montane habitats of the Sierra Madre Oriental during the Wisconsin, whereas *micropus* occurred on the coastal lowlands. Both *angustipalata* and *palatina* represent peripherally-distributed species that have managed to avoid extinction, but for some reason (possibly the presence of adjacent populations of *micropus* and *albigula*, respectively) have been unable to significantly expand their ranges since the recession of Wisconsin ice.

Recent advances in paleobiology, geology, and meteorology have improved understanding of late Pleistocene and Holocene climatic and vegetational patterns on the Great Plains. These data were summarized by Hoffmann and Jones (1970) according to post-Pleistocene chronology and terminology proposed by Bryson *et al.* (1970). During Full-glacial (to approximately 13,000 BP), *floridana* and *micropus* probably were completely isolated in their respective refugia. Following initial isolation, the two incipient species evolved distinctive hemoglobins from the original double-banded phenotype. Differences in chromosomal complements, morphology, and color also have evolved under differential selective pressures since that time. Blair (1958) included *floridana* and *micropus* in a list of mammals and reptiles that previously were isolated into eastern and western populations, but that since have reestablished contact in the forest-grassland ecotone. The barrier that isolated *micropus* and *floridana* along the Gulf Coast of the southeastern United States may have been the Mississippi Embayment, but as discussed by Blair (1958) most species separated by this barrier remain disjunct. During the more equable climate of Late-glacial (13,000 to 10,500 BP), and with northeastward retreat of continental ice (despite minor phases of retreat and readvance), both isolated populations began a northward dispersal. During the more continental climates of the Pre-boreal (10,500 to 9140 BP), Boreal (9140 to 8450 BP), and Atlantic (8450 to 4680 BP), *micropus* and *floridana* reached their present limits of distribution and *floridana* at least occurred somewhat farther north and west of the present range (see Jones, 1964). It probably was during this time that woodrats advanced northward along the Missouri and westward along the Niobrara rivers. The Smoky Hill, Saline, Republican, Arkansas, and possibly other rivers and tributaries served as corridors for *floridana* to disperse across western Kansas into eastern Colorado and southwestern Nebraska. Several late Pleistocene-early Recent records of *floridana* from localities north of the present range are available (e.g., Parmalee and Jacobson, 1959; Bader and Hall, 1960; Parmalee *et al.* 1961). Morphologically, *N. f. baileyi* somewhat resembles *N. f. campestris*, especially those specimens from populations in Colorado and southwestern Nebraska. Possibly there was appreciable north-south gene flow through eastern and central Nebraska during this period. However, I doubt that the Sand Hills region of Nebraska ever was inhabited by *floridana* and the similarities between *baileyi* and *campestris* more likely represent convergence. When all characters are considered, *baileyi* clearly is more closely related to *attwateri* from northeastern Kansas than to *campestris*.

During and following Full-glacial, the Sierra de Tamaulipas may have served as a barrier for the small, brownish, long-tailed woodrats that presently occur there. When populations of *micropus* subsequently dispersed northward, these rats reestablished contact and intergraded with other populations. The result of this intergradation and subsequent selection is the coastal subspecies to which the name *N. m. micropus* is restricted. The evolutionary history of *N. m. planiceps* cannot be understood until the relationships and status of this nominal subspecies are better known. However, *planiceps* apparently is isolated from other populations of *micropus* on the Mexican Plateau at present, but

probably has not been isolated since the Full-glacial.

The Sub-boreal (4680 to 2690 BP) probably was the coolest post-glacial period on the Northern Great Plains. This period was characterized by a southward shift in both the northern and southern limits of the boreal forest. It probably was during this cooler period that *floridana* retreated slightly southward and eastward, leaving the isolated *N. f. baileyi* in the sheltered canyons of the Niobrara River and associated tributaries. Jones (1964) and Hoffman and Jones (1970) suggested that *baileyi* became isolated during a hot, dry post-glacial period. Although that hypothesis remains plausible, it is now thought that the earliest period characterized by hot, dry climate was the Scandic (1690 to 1100 BP); the degree of distinctness exhibited by *baileyi* suggests a longer period of isolation. Rainey (1956) and Jones (1964) discussed the apparent inability of *N. f. attwateri* to extend its range into superficially suitable habitat in southeastern Nebraska; *attwateri* possibly is unable to move farther north because of the severity of the climate, especially in winter. Riparian habitats that appear suitable for habitation by *baileyi* are present in southern South Dakota, but for some reason (possibly the absence of enough shelter during winter) woodrats have not been found there. Perhaps *baileyi* has been able to persist in north-central Nebraska only in specially sheltered areas, the most important element furnished by the canyons of the Niobrara being protection from severe winters rather than a relatively cool environment during hot, dry summers.

The Sub-boreal also may have isolated *N. f. campestris* from *N. f. attwateri*, and the two probably were disjunct for an extensive period. Contact may have been reestablished in the relatively warm moist Sub-Atlantic, broken again during the dryer Scandic, and not reestablished until European man fostered the spread of riparian and other woodland habitats in north-central Kansas. Although the two subspecies appear to have been separated for a lengthy period, they are presently in contact. During the dry Scandic and possibly during other periods as well, it appears that *campestris* was distributed in an unknown number of small isolated populations in disjunct and probably marginal habitats.

Since the time of initial isolation, the submetacentric Y chromosome apparently became fixed in *baileyi*, but the translocation obviously had occurred prior to isolation as it is seen also in *campestris* and in *attwateri* from northeastern Kansas. Origin of the β^3 hemoglobin locus also occurred prior to the time of isolation, because the β^3 allele is seen in all three of the western subspecies of *floridana*. During the warm, wet Neo-Atlantic and since that time, *campestris* probably has dispersed somewhat from the isolated, relict populations of the Scandic, but continues to occur in relatively disjunct, semi-isolated populations.

With the possible exception of *N. m. micropus* and *N. m. planiceps*, I doubt that any of the populations of *micropus* have evolved long in isolation from other members of the species. Variation in size and color both are clinal, the chromosomal polymorphism involving number of large biarmed elements has been observed at localities from which significant numbers of woodrats have been karyotyped (the only exception is *N. m. micropus* from north of Ciudad Victoria, Tamaulipas), and no marked changes in hemoglobin phenotypes were observed in northern populations of the species.

Neotoma micropus and *N. floridana* apparently evolved in the classical manner during the Pleistocene as a result of isolation during glacial advance. Although two species in my estimation, they are closely related, recently evolved, and retain limited genetic compatibility. It is impossible to define precisely at what stage two evolving phena should be called species, but as I understand *floridana* and *micropus* the process of

evolution almost certainly has reached a point in time whereby irreversible differentiation has taken place. Although *micropus* and *floridana* apparently did not evolve exactly according to the stasipatric model (White *et al.*, 1967; Key, 1968), they are stasipatrically distributed today and apparently are continuing the process of speciation in a manner similar to that seen in morabine grasshoppers, for which this model was proposed. That is, the two species are in contact and form a tension zone wherein hybrids with reduced viability are produced. This tension zone undoubtedly shifts slightly within the deciduous forest-grassland ecotone in response to environmental changes. Introgression of a few advantageous genes may be occurring in one or both species as a result of hybridization within the tension zone, but clearly introgression (if it has occurred at all) has been limited and mostly prevented by rigid selection.

LITERATURE CITED

Allen, J. A.

1891. Notes on new or little-known North American mammals based on recent additions to the Collection of Mammals in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist., 3:263-310.

1894a. Cranial variations in Neotoma micropus due to growth and individual differentiation. *Ibid.*, 6:233-246.

1894b. Descriptions of ten new North American mammals, and remarks on others. *Ibid.*, 6:317-332.

Alvarez, T.

1963. The Recent mammals of Tamaulipas, México. Univ. Kansas Publ., Mus. Nat. Hist., 14:363-473.

1966. Roedores fosiles del Pleistoceno de Tequesquinahua, estado de México, México. Acta Zool. Mexicana, 8(3):1-16.

Andersen, K. W., and E. D. Fleharty

1967. Mammalian distribution within biotic communities in northeastern Jewell County, Kansas. Fort Hays Studies, Sci. Ser., 6:v + 1-46.

Anderson, S.

1969. Taxonomic status of the woodrat, *Neotoma albigula*, in southern Chihuahua, Mexico. Misc. Publ., Univ. Kansas Mus. Nat. Hist., 51:25-50.

Anthony, R. L.

1965. Serological, immunoenzymatic and biochemical comparisons among registered breeds of dogs. Unpublished Ph.D. dissertation, Univ. Kansas, 82 pp.

Armstrong, D. M.

1972. Distribution of mammals in Colorado. Monog. Mus. Nat. Hist., Univ. Kansas, 3:x + 1-415.

Asdell, S. A.

1964. Patterns of mammalian reproduction. Comstock Publ. Assoc., Cornell Univ. Press, Ithaca, New York, 670 pp.

Augustinsson, K.

1961. Multiple forms of esterase in vertebrate blood plasma. Ann. New York Acad. Sci., 94:844-860.

Bader, R. S., and J. S. Hall

1960. Mammalian remains from an Indiana cave. Jour. Mamm., 41:111-112.

Bailey, V.

1905. Biological survey of Texas. . . . N. Amer. Fauna, 25:1-222.

1932. Mammals of New Mexico. *Ibid.*, 53:1-412.

Baird, S. F.

1855. Characteristics of some new species of Mammalia, collected by the U.S. and Mexican Boundary Survey, Major W. H. Emory, U.S.A. Commissioner. Proc. Acad. Nat. Sci. Philadelphia, 7:331-333.

1858. Mammals, *in* Reports of explorations and surveys . . . from the Mississippi River to the Pacific Ocean. . . . 8(1): xxi-xlviii + 1-757.

Baker, R. H.

1942. Notes on small mammals of eastern Texas. Jour. Mamm., 23:343.

1951. Mammals from Tamaulipas, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 5:207-218.

1953. Mammals from owl pellets taken in Coahuila, Mexico. Trans. Kansas Acad. Sci., 56:253-254.

1956. Mammals of Coahuila, México. Univ. Kansas Publ. Mus. Nat. Hist., 9:125-335.

Baker, R. J., and J. T. Mascarello

1969. Karyotypic analyses of the genus *Neotoma* (Cricetidae, Rodentia). Cytogenetics, 8:187-198.

Baker, R. J., J. T. Mascarello, and R. G. Jordan

1970. Polymorphism in the somantic chromosomes of *Neotoma micropus* Baird, the plains woodrat. Experientia, 26:426-428.

Bangs, O.

1898. The land mammals of peninsular Florida and the coast region of Georgia. Proc. Soc. Nat. Hist., 28: 158-235.

Berry, R. J., and A. G. Searle

1963. Epigenetic polymorphism of the rodent skeleton. Proc. Zool. Soc. London, 140:577-615.

Birch, L. C., and P. R. Ehrlich

1967. Evolutionary history and taxonomy. Syst. Zool., 16:282-285.

Birney, E. C.

1970. Systematics of three species of woodrats. . . . Unpublished Ph.D. Dissertation, Univ. Kansas, Lawrence.

Birney, E. C., and J. E. Perez

1971. Inheritance of multiple hemoglobins in two species of woodrats, genus *Neotoma* (Rodentia: Cricetidae). Univ. Kansas Sci. Bull., 49:345-356.

Birney, E. C., and S. L. Twomey

1970. Effects of sodium chloride on water consumption, weight, and survival in the woodrats, *Neotoma micropus* and

Neotoma floridana. Jour. Mamm., 51:372-375.

Blair, W. F.
1938. Ecological relationships of the mammals of the Bird Crest Region, northeastern Oklahoma. Amer. Midl. Nat., 20:473-526.
1939a. New mammals from Texas and Oklahoma, with remarks on the status of *Thomomys texensis* Bailey. Occas. Papers Mus. Zool. Univ. Michigan, 403:1-7.
1939b. Faunal relationships and geographic distribution of mammals in Oklahoma. Amer. Midl. Nat., 22:85-133.
1940. A contribution to the ecology and faunal relationships of the mammals of the Davis Mountain Region, southwestern Texas. Misc. Publ. Mus. Zool. Univ. Michigan, 46:1-39.
1943a. Ecological distribution of mammals in the Tularosa Basin, New Mexico. Contrib. Lab. Vert. Biol. Univ. Michigan, 20:1-24.
1943b. Populations of the deer-mouse and associated small animals in the mesquite association of southern New Mexico. *Ibid.*, 21:1-40.
1952. Mammals of the Tamaulipan biotic province in Texas. Texas Jour. Sci., 4:230-250.
1954. Mammals of the mesquite plains biotic district in Texas and Oklahoma, and speciation in the central grasslands. *Ibid.*, 6:235-264.
1958. Distributional patterns of vertebrates in the southern United States in relation to past and present environments. Pp. 433-468 *in* Zoogeography (C. L. Hubbs, ed.). Amer. Assoc. Advance. Sci., 51:x + 1-509.

Blair, W. F., and C. E. Miller, Jr.
1949. The mammals of the Sierra Vieja region, southwestern Texas, with remarks on the biogeographic position of the region. Texas Jour. Sci., 1:67-92.

Boice, R.
1969. Water intake as a function of ease of access in *Neotoma*. Jour. Mamm., 50:605-607.

Booth, E. S.
1957. Mammals collected in Mexico from 1951 to 1956 by the Walla Walla College Museum of Natural History. Walla Walla College Publ., 20:1-19.

Boyden, A. A.
1964. Perspectives in systematic serology. Pp. 75-99 *in* Taxonomic biochemistry and serology (C. A. Leone, ed.). The Ronald Press, New York, x + 728 pp.

Brand, L. R., and R. E. Ryckman
1969. Biosystematics of *Peromyscus eremicus, P. guardia,* and *P. interparietalis*. Jour. Mamm., 50:501-513.

Brown, B.
1909. The Conard Fissure, a Pleistocene bone deposit in northern Arkansas: with descriptions of two new genera and twenty new species of mammals. Mem. Amer. Mus. Nat. Hist., 9:155-208.

Brown, J. H.
1968. Adaptation to environmental temperature in two species of woodrats, *Neotoma cinerea* and *N. albigula*. Misc. Publ. Mus. Zool. Univ. Michigan, 135:1-48.

Brown, J. H., and A. K. Lee
1969. Bergmann's rule and climatic adaptation in woodrats *(Neotoma)*. Evolution, 23:329-338.

Brown, L. N.
1963. Maturational and seasonal molts in Peromyscus boylii. Amer. Midl. Nat., 70:466-469.
1969. Reproductive characteristics of the Mexican woodrat at the northern limit of its range in Colorado. Jour. Mamm., 50:536-541.

Bryson, R. A., D. A. Baerreis, and W. M. Wendland
1970. The character of late-glacial and postglacial climatic changes. Pp. 55-74 *in* Pleistocene and Recent environments of the Central Great Plains (W. Dort, Jr., and J. K. Jones, Jr., eds.). Special Publ., Univ. Kansas Dept. Geol., 3:xii + 1-433.

Burt, W. H.
1954. The subspecies category in mammals. Syst. Zool., 3:99-104.
1960. Bacula of North American mammals. Misc. Publ. Mus. Zool. Univ. Michigan, 113:1-76.

Burt, W. H., and F. S. Barkalow, Jr.
1942. A comparative study of the bacula of wood rats (Subfamily Neotominae). Jour. Mamm., 23:287-297.

Cary, M.
1911. A biological survey of Colorado. N. Amer. Fauna, 33:1-256.

Cavalli-Sforza, L. L., and A. W. F. Edwards
1967. Phylogenetic analysis: models and estimation procedures. Evolution, 21: 550-570.

Chapman, A. O.
1951. The estrous cycle in the woodrat, *Neotoma floridana*. Univ. Kansas Sci. Bull., 34:267-299.

Chernoff, A. I., and N. M. Pettit, Jr.
1964. The amino acid composition of hemoglobin. III. A qualitative method for identifying abnormalities of the polypeptide chains of hemoglobin. Blood, 24:750-756.

Choate, J. R.
1970. Systematics and zoogeography of Middle American shrews of the genus Cryptotis. Univ. Kansas Publ. Mus. Nat. Hist., 19:195-317.

Choate, J. R., and H. H. Genoways
1967. Notes on some mammals from Nebraska. Trans. Kansas Acad. Sci., 69: 238-241.

Cinader, B.
1957. Antibodies against enzymes. Ann. Rev. Microbiol., 11:371-390.

Cockrum, E. L.
1952. Mammals of Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 7:1-303.

Coues, E.
1877. Monographs of North American Rodentia. No. I.—Muridae. Pp. x + 1-264, *in* Monographs of North American Rodentia (E. Coues and J. A. Allen, eds.). Bull. U.S. Geol. Surv. Territories, 11:xii + 1-1091.

Cross, J. C.
1931. A comparative study of the chromosomes of rodents. Jour. Morphol., 52:373-401.

Crowson, R. A.
1965. Classification, statistics and phylogeny. Syst. Zool., 14:144-148.

Dalquest, W. W.
1951. Six new mammals from the state of San Luis Potosí, México. Jour. Washington Acad. Sci., 41:361-364.
1953. Mammals of the Mexican state of San Luis Potosí. Louisiana State Univ. Stud. Biol. Sci. Ser., 1:1-229.
1968. Mammals of north-central Texas. Southwestern Nat., 13:13-21.

Dalquest, W. W., E. Roth, and F. Judd
1969. The mammal fauna of Schulze Cave, Edwards County, Texas. Bull. Florida State Mus., 13:205-276.

Davis, W. B.
1960. The mammals of Texas. Bull. Texas Game Fish Comm., 27:1-252.

Dice, L. R.
1937. Mammals of the San Carlos Mountains and vicinity. Univ. Michigan Studies, Sci. Ser., 12:245-268.

Dice, L. R., and H. J. Leraas
1936. A graphic method for comparing several sets of measurements. Contrib. Lab. Vert. Genetics Univ. Michigan, 3:1-3.

Durand, M., and R. Schneider
1963. Etúde immunoelectrophorétique du sérum de chien et ses relations antigéniques avec les diverses especes de mammiféres. Arch. Inst. Pasteur, 40:91-95.

Egoscue, H. J.
1957. The desert woodrat: a laboratory colony. Jour. Mamm., 38:472-481.
1962. The bushy-tailed wood rat: a laboratory colony. Jour. Mamm., 43:328-337.

Ehrlich, P. R.
1961. Has the biological species concept outlived its usefulness. Syst. Zool., 10:167-176.

Ehrlich, P. R., and R. W. Holm
1963. The process of evolution. McGraw-Hill Book Co., Inc., New York, xvi + 347 pp.

Ehrlich, P. R., and P. H. Raven
1969. Differentiation of populations. Science, 165:1228-1232.

Elliot, D. G.
1899. Description of apparently new species and sub-species of mammals from Oklahoma Territory. Field Columbian Mus. Publ. 37, Zool. Ser., 1:279-282.
1901. A synopsis of the mammals of North America and the adjacent seas. *Ibid.*, 2:xv + 1-471.

Feldman, H. W.
1935. Notes on two species of wood rats in captivity. Jour. Mamm., 16:300-303.

Finley, R. B., Jr.
1958. The wood rats of Colorado: distribution and ecology. Univ. Kansas Publ. Mus. Nat. Hist., 10:213-552.

Fitch, H. S., and D. G. Rainey
1956. Ecological observations on the woodrat, Neotoma floridana. *Ibid.*, 8:499-533.

Florkin, M.
1964. Perspectives in comparative biochemistry. Pp. 51-74 *in* Taxonomic biochemistry and serology (C. A. Leone, ed.). The Ronald Press Co., New York, x + 728 pp.

Foreman, C. W.
1960. Electromigration properties of mammalian hemoglobins as taxonomic criteria. Amer. Midl. Nat., 64:177-186.
1964. Tryptic peptide patterns of some mammalian hemoglobins. Jour. Cell. Comp. Physiol., 63:1-6.

Gabriel, K. R.
1964. A procedure for testing the homogeneity of all sets of means in analy-

sis of variance. Biometrics, 20:459-477.

Gabriel, K. R., and R. R. Sokal
1969. A new statistical approach to geographic variation analysis. Syst. Zool., 18:259-278.

Genoways, H. H.
1971. Systematics and evolution of the spiny pocket mice of the genus *Liomys*. Unpublished Ph.D. Dissertation, Univ. Kansas, Lawrence.

Gerber, J. D.
1968. Electrophoretic and immunologic comparisons of the serum proteins of bats. Unpublished Ph.D. Dissertation, Univ. Kansas, Lawrence.

Gerber, J. D., and E. C. Birney
1968. Immunological comparisons of four subgenera of ground squirrels. Syst. Zool., 17:413-416.

Gidley, J. W., and C. L. Gazin
1933. New Mammalia in the Pliestocene fauna from Cumberland Cave. Jour. Mamm., 14:343-357.

Glass, B. P.
1949. Report on the mammals of the Black Mesa region, Oklahoma. Proc. Oklahoma Acad. Sci., 30:26-30.

Goertz, J. W.
1970. An ecological study of *Neotoma floridana* in Oklahoma. Jour. Mamm., 51:94-104.

Goldman, E. A.
1905. Twelve new wood rats of the genus *Neotoma*. Proc. Biol. Soc. Washington, 18:27-33.
1910. Revision of the wood rats of the genus Neotoma. N. Amer. Fauna, 31:1-124.
1933. New mammals from Arizona, New Mexico, and Colorado. Jour. Washington Acad. Sci., 23:463-473.

Goodwin, G. G.
1954. Mammals from Mexico collected by Marian Martin for The American Museum of Natural History. Amer. Mus. Novitates, 1689:1-16.

Guilday, J. E., P. S. Martin, and A. D. McCrady
1964. New Paris No. 4: a late Pleistocene cave deposit in Bedford County, Pennsylvania. Bull. Natl. Speleol. Soc., 26:121-194.

Hall, E. R.
1926. Changes during growth in the skull of the rodent Otospermophilus grammurus beecheyi. Univ. California Publ. Zool., 21:355-404.
1955. A new subspecies of wood rat from Nayarit, Mexico, with new name-combinations for the *Neotoma mexicana* group. Jour. Washington Acad. Sci., 45:328-332.

Hall, E. R., and W. W. Dalquest
1963. The mammals of Veracruz. Univ. Kansas Publ. Mus. Nat. Hist., 14:165-362.

Hall, E. R., and H. H. Genoways
1970. Taxonomy of the *Neotoma albigula*-group of woodrats in central Mexico. Jour. Mamm., 51:504-516.

Hall, E. R., and K. R. Kelson
1959. The mammals of North America. The Ronald Press Co., 2: viii + 547-1083 + 79.

Hamilton, W. J., Jr.
1953. Reproduction and young of the Florida wood rat, *Neotoma f. floridana* (Ord). Jour. Mamm., 34:180-189.

Hays, H. A.
1958. The distribution and movement of small mammals in central Oklahoma. *Ibid.*, 39:235-244.

Hedges, S. R.
1969. Epigenetic polymorphism in populations of *Apodemus sylvaticus* and *Apodemus flavicollis* (Rodentia, Muridae). Jour. Zool. Soc. London, 159:425-442.

Hibbard, C. W.
1963. A late Illinoian fauna from Kansas and its climatic significance. Papers Michigan Acad. Sci., Arts, Letters, 48:187-221.
1967. New rodents from the late Cenozoic of Kansas. *Ibid.*, 52:115-131.
1970. Pleistocene mammalian local faunas from the Great Plains and central lowland provinces of the United States. Pp. 395-433 *in* Pleistocene and Recent environments of the Central Great Plains (W. Dort, Jr., and J. K. Jones, Jr., eds.). Special Publ., Univ. Kansas Dept. Geol., 3:xii + 1-433.

Hibbard, C. W., and D. W. Taylor
1960. Two late Pleistocene faunas from southwestern Kansas. Contrib. Mus. Paleo. Univ. Michigan, 16:1-223.

Hill, R. L., and J. Buettner-Janusch
1964. Evolution of hemoglobin. Fed. Proc., 23:1236-1242.

Hoffmann, R. S., and J. K. Jones, Jr.
1970. Influence of late-glacial and post-glacial events on the distribution of Recent mammals of the Northern Great Plains. Pp. 355-394 *in* Pleistocene and Recent environments of the Central Great Plains (W. Dort, Jr., and J. K. Jones, Jr., eds.). Special

Publ., Univ. Kansas Dept. Geol., 3:xii + 1-433.

Hoffmeister, D. F.
1945. Cricetine rodents of the Middle Pliocene of the Mulholland Fauna, California. Jour. Mamm., 26:186-191.

Hoffmeister, D. F., and L. de la Torre
1960. A revision of the wood rat *Neotoma stephensi*. *Ibid.*, 41:476-491.

Hooper, E. T.
1938. Geographic variation in wood rats of the species Neotoma fuscipes. Univ. California Publ. Zool., 42:213-246.
1940. Geographic variation in bushy-tailed wood rats. *Ibid.*, 42:407-424.
1941. Mammals of the lava fields and adjoining areas in Valencia County, New Mexico. Misc. Publ. Mus. Zool. Univ. Michigan, 51:1-47.
1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. *Ibid.*, 77:1-255.
1953. Notes on mammals of Tamaulipas, México. Occas. Papers Mus. Zool. Univ. Michigan, 544:1-12.
1960. The glans penis in *Neotoma* (Rodentia) and allied genera. *Ibid.*, 618:1-20.

Howell, A. B.
1926. Anatomy of the wood rat . . . . Monog. Amer. Soc. Mamm., 1:x + 1-225.

Hsu, T. C., and K. Benirschke
1968. An atlas of mammalian chromosomes. Springer-Verlag, New York Inc., 2:62.

Ingram, V. M.
1963. Hemoglobins in genetics and evolution. Columbia Univ. Press, New York, 165 pp.

Jiménez-G., A.
1966. Mammals from Nuevo León, Mexico. Unpublished MS Thesis, Univ. Kansas, Lawrence.

Johnson, M. L.
1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Syst. Zool., 17:23-30.

Jolicoeur, P.
1959. Multivariate geographical variation in the wolf *Canis lupus* L. Evolution, 13:283-299.

Jones, J. K., Jr.
1954. Distribution of some Nebraskan mammals. Univ. Kansas Publ. Mus. Nat. Hist., 7:479-487.
1964. Distribution and taxonomy of Nebraska. *Ibid.*, 16:1-356.

Jones, R. D., and D. E. Bunde
1970. Age and sex differences in the serum proteins of the chinchilla. Jour. Mamm., 51:425-429.

Kellogg, R.
1914. On the retention of *Neotoma campestris* Allen as a separate subspecies from *Neotoma floridana baileyi* Merriam. Kansas Univ. Mus. Nat. Hist. Publ. 1, Zool. Ser., 1:1-6.

Kelson, K. R.
1952. Comments on the taxonomy and geographic distribution of some North American woodrats (genus Neotoma). Univ. Kansas Publ. Mus. Nat. Hist., 5:233-242.

Key, K. H. L.
1968. The concept of stasipatric speciation. Syst. Zool., 17:14-22.

King, J. A. (ed.)
1968. Biology of *Peromyscus* (Rodentia). Special Publ., Amer. Soc. Mamm., 2:xiii + 1-593.

Kirsch, J. A. W.
1969. Serological data and phylogenetic inference: the problem of rates of change. Syst. Zool., 18:296-311.

Knoch, H. W.
1969. The eastern wood rat, Neotoma floridana osagensis: a laboratory colony. Trans. Kansas Acad. Sci., 71:361-372.

Koopman, K. F., and P. S. Martin
1959. Subfossil mammals from The Gómez Farías Region and the tropical gradient of eastern Mexico. Jour. Mamm., 40:1-12.

Lack, D.
1948. The significance of litter-size. Jour. Animal Ecol., 17:45-50.
1954. The natural regulation of animal numbers. Clarendon Press, Oxford, viii + 343 pp.

Lawlor, T. E.
1965. The Yucatan deer mouse, Peromyscus yucatanicus. Univ. Kansas Publ. Mus. Nat. Hist., 16:421-438.

Lawrence, B., and W. H. Bossert
1967. Multiple character analysis of *Canis lupus, latrans,* and *familiaris,* with a discussion of the relationships of *Canis niger*. Amer. Zool., 7:223-232.
1969. The cranial evidence for hybridization in New England Canis. Breviora, 330:1-13.

Lay, D. W., and R. H. Baker
1938. Notes on the home range and ecology of the Attwater wood rat. Jour. Mamm., 19:418-423.

Layne, J. N.
1968. Ontogeny. Pp. 148-253 *in* Biology of *Peromyscus* (Rodentia) (J. A. King,

ed.). Special Publ., Amer. Soc. Mamm., 2:xiii + 1-593.

Lee, M. R.
1969. A widely applicable technic for direct processing of bone marrow for chromosomes of vertebrates. Stain Technol., 44:155-158.

Lewontin, R. C., and L. C. Birch
1966. Hybridization as a source of adaptation to new environments. Evolution, 20:315-316.

Lidicker, W. Z., Jr.
1960. The baculum of *Dipodomys ornatus* and its implication for superspecific groupings of kangaroo rats. Jour. Mamm., 41:495-499.
1962. The nature of subspecies boundaries in a desert rodent and its implications for subspecies taxonomy. Syst. Zool., 11:160-171.

Linsdale, J. M., and L. P. Tevis
1951. The dusky-footed wood rat. Univ. California Press, Berkeley, x + 664 pp.

Long, C. A.
1968. An analysis of patterns of variation in some representative Mammalia. Part I. A review of estimates of variability in selected measurements. Trans. Kansas Acad. Sci., 71:201-227.
1969. An analysis of patterns of variation in some representative Mammalia. Part II. Studies on the nature and correlation of measures of variation. Misc. Publ. Univ. Kansas Mus. Nat. Hist., 51:289-302.

Lord, R .D., Jr.
1960. Litter size and latitude in North American mammals. Amer. Midl. Nat., 64:488-499.

Manwell, C., C. M. A. Baker,
and W. Childers
1963. The genetics of hemoglobins in hybrids—1. A molecular basis for hybrid vigor. Comp. Biochem. Physiol., 10:103-120.

Matthey, R.
1953. Les chromosomes des Muridae. Rev. Suisse Zool., 60:225-283.

Mayr, E.
1963. Animal species and evolution. Harvard Univ. Press, xiv + 1-797.
1965. Numerical phenetics and taxonomic theory. Syst. Zool., 14:73-97.
1969. Principles of systematic zoology. McGraw-Hill Book Co., New York, xi + 428 pp.

McCarley, W. H.
1952. The ecological relationships of the mammals of Bryan County, Oklahoma. Texas Jour. Sci., 4:102-112.
1959. The mammals of eastern Texas. *Ibid.*, 11:385-426.

Mearns, E. A.
1897. Descriptions of six new mammals from North America. Proc. U.S. Natl. Mus., 19:719-721.

Merriam, C. H.
1894a. Abstract of a study of the American wood rats, with descriptions of fourteen new species and subspecies of the genus Neotoma. Proc. Biol. Soc. Washington, 9:117-128.
1894b. A new subfamily of murine rodents—the Neotominae—with descriptions of a new genus and species and a synopsis of the known forms. Proc. Acad. Nat. Sci., Philadelphia, 46:225-252.

Mitchell, H. A.
1966. Multiple haemoglobins in bats. Nature, 210:1067-1068.

Moss, W. W.
1968. Experiments with various techniques of numerical taxonomy. Syst. Zool., 17:31-47.

Murphy, M. F.
1952. Ecology and helminths of the Osage wood rat, Neotoma floridana osagensis, including the description of Longistriata neotoma n. sp. (Trichostrongylidae). Amer. Midl. Nat., 48:204-218.

Neel, J. N.
1961. The hemoglobin genes: a remarkable example of the clustering of related genetic functions on a single mammalian chromosome. Blood, 18:769-777.

Ord, G.
1815. Zoology of North America. *In* Guthrie, W. A new geographical, historical, and commercial grammar; and present state of the several kingdoms of the world. Philadelphia (2nd ed.), 2:291-361.
1818. *In* De Blainville, H. Sur une nouvelle espèce de rongeur de la Floride, par M. Ord de Philadelphie. Bull. Sci. Soc. Philom. Paris, 1818:181-182.

Parmalee, P. W., R. A. Bieri,
and R. K. Mohrman
1961. Mammal remains from an Illinois cave. Jour. Mamm., 42:119.

Parmalee, P. W., and K. W. Jacobson
1959. Vertebrate remains from a Missouri cave. *Ibid.*, 40:401-405.

Patton, J. L.
1967. Chromosome studies of certain pocket

mice, genus *Perognathus* (Rodentia: Heteromyidae). *Ibid.*, 48:27-37.

Pearson, P. G.
1952. Observations concerning the life history and ecology of the woodrat, *Neotoma floridana floridana* (Ord). *Ibid.*, 33:459-463.

Poole, E. L.
1940. A life history sketch of the Allegheny woodrat. *Ibid.*, 21:249-270.

Power, D. M.
1970. Geographic variation of red-winged blackbirds in Central North America. Univ. Kansas Publ. Mus. Nat. Hist., 19:1-83.

Rainey, D. G.
1956. Eastern woodrat, Neotoma floridana; life history and ecology. *Ibid.*, 8:535-646.

Rainey, D. G., and R. H. Baker
1955. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. *Ibid.*, 7:619-624.

Raun, G. G.
1966. A population of woodrats *(Neotoma micropus)* in southern Texas. Bull. Texas Memorial Mus., 11:1-62.

Rees, J. W.
1970. A multivariate morphometric analysis of divergence in skull morphology among geographically contiguous and isolated groups of white-tailed deer *(Odocoileus virginianus)* in Michigan. Evolution, 24:220-229.

Riggs, A.
1965. Hemoglobin polymerization in mice. Science, 147:621-623.

Rohlf, F. J.
1967. Correlated characters in numerical taxonomy. Syst. Zool., 16:109-126.
1968. Stereograms in numerical taxonomy. *Ibid.*, 17:246-255.

Russell, R. J.
1953. Mammals from Cooke County, Texas. Texas Jour. Sci., 4:454-464.

Say, T., and G. Ord
1825. A new genus of Mammalia proposed, and a description of the species upon which it is founded. Jour. Acad. Nat. Sci. Philadelphia, 4(2):345-349.

Scheidegger, J.
1955. Une micro-methode de l'immuno-electrophorese. Intern. Arch. Allergy, 1:103.

Schwartz, A., and E. P. Odum
1957. The woodrats of the eastern United States. Jour. Mamm., 38:197-206.

Seal, U. S.
1969. Carnivora systematics: a study of hemoglobins. Comp. Biochem. Physiol., 31:799-811.

Selander, R. K.
1967. Why there are no subspecies in North American house sparrows. Syst. Zool., 16:286-287.

Selander, R. K., W. G. Hunt, and S. Y. Yang
1969. Protein polymorphism and genic heterozygosity in two European subspecies of the house mouse. Evolution, 23:379-390.

Selander, R. K., S. Y. Yang, and W. G. Hunt
1969. Polymorphism in esterases and hemoglobin in wild populations of the house mouse *(Mus musculus)*. Pp. 271-338 *in* Studies in genetics. (M. R. Wheeler, ed.) Univ. Texas Press, Austin, viii + 339 pp.

Semken, H. A., Jr.
1966. Stratigraphy and paleontology of the McPherson Equus beds (Sandahl Local Fauna), McPherson County, Kansas. Contrib. Mus. Paleo. Univ. Michigan, 20:121-178.

Sherman, H. B.
1952. A list and bibliography of the mammals of Florida, living and extinct. Quart. Jour. Florida Acad. Sci., 15: 86-126.

Smith, H. M.
1965. Phenetic taxonomy: an example of existentialism in science. Syst. Zool., 14:148-149.

Smith, J. D.
1972. Systematics of the chiropteran family Mormoopidae. Misc. Publ. Univ. Kansas Mus. Nat. Hist., 56:1-132.

Sokal, R. R.
1961. Distance as a measure of taxonomic similarity. Syst. Zool., 10:70-79.

Sokal, R. R., and C. D. Michener
1967. The effects of different numerical techniques on phenetic classification of bees of the *Hoplitis* complex (Megachilidae). Proc. Linnean Soc. London, 178:59-74.

Sokal, R. R., and R. C. Rinkel
1963. Geographic variation of alate *Pemphigus populitransversus* in eastern North America. Univ. Kansas Sci. Bull., 44:467-507.

Sokal, R. R., and F. J. Rohlf
1969. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Co., San Francisco, xxi + 776 pp.

Sokal, R. R., and P. H. A. Sneath
1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco, xvi + 359 pp.

Spencer, A. W., and H. W. Steinhoff
1968. An explanation of geographic variation in litter size. Jour. Mamm., 49:281-286.

Spencer, D. L.
1968. Sympatry and hybridization of the eastern and southern plains wood rats. Unpublished Ph.D. thesis, Oklahoma State Univ.

Sprague, J. M.
1941. A study of the hyoid apparatus of the Cricetinae. Jour. Mamm., 22:296-310.

Stickel, W. H., and L. F. Stickel
1948. Mammals of northwestern Texas found in barn owl pellets. *Ibid.*, 29:291-293.

Strecker, J. K.
1924. The mammals of McLennan County, Texas. Baylor Bull., 27(3):1-20.
1929. Notes on the Texas cotton and Attwater wood rats in Texas. Jour. Mamm., 10:216-220.

Sullivan, B., and P. E. Nute
1968. Structural and functional properties of polymorphic hemoglobins from orangutans. Genetics, 58:113-124.

Tilden, J. W.
1961. Certain comments on the subspecies problem. Syst. Zool., 10:17-23.

Valdivieso, D., J. R. Tamsitt, and E. C. Pino
1969. Electrophoretic properties of Neotropical bat hemoglobin. Comp. Biochem. Physiol., 30:117-122.

Warren, E. R.
1910. The mammals of Colorado . . . . G. P. Putnam's Sons, New York, xxxiv + 300 pp.
1942. The mammals of Colorado, their habits and distribution. Univ. Oklahoma Press, Norman, xviii + 330 pp.

Watt, J. C.
1968. Grades, clades, phenetics, and phylogeny. Syst. Zool., 17:350-353.

White, M. J. D., R. E. Blackith,
R. M. Blackith, and J. Cheney
1967. Cytogenetics of the *viatica* group of morabine grasshoppers. I. The "coastal" species. Australian Jour. Zool., 15:263-302.

Wiley, R. W.
1971. Activity periods and movements of the eastern woodrat. Southwest. Nat., 16:43-54.

Wilson, E. O., and W. L. Brown, Jr.
1953. The subspecies concept. Syst. Zool., 2:97-111.

Wood, F. D.
1935. Notes on the breeding behavior and fertility of Neotoma fuscipes macrotis in captivity. Jour. Mamm., 16:105-109.

Zarrow, M. X., J. M. Yochim,
and J. L. McCarthy
1964. Experimental endocrinology . . . . Academic Press, New York, xvi + 519 pp.

AVAILABLE MISCELLANEOUS PUBLICATIONS IN MAMMALOGY

UNIVERSITY OF KANSAS MUSEUM OF NATURAL HISTORY

7. Handbook of mammals of Kansas. By E. Raymond Hall. Pp. 1-303, illustrated. December 13, 1955. Paper bound $1.50 postpaid.

18. Furbearers in Kansas: A guide to trapping. By Howard J. Stains and Rollin H. Baker. Pp. 1-100, 2 plates, 13 figures in text. November 19, 1958. Paper bound 50 cents postpaid.

30. Collecting and preparing study specimens of vertebrates. By E. Raymond Hall. Pp. 1-46, 34 figures in text. May 21, 1962. Paper bound 75 cents postpaid.

34. Habits of the red fox in northeastern Kansas. By William C. Stanley. Pp. 1-31, 3 plates, 3 figures in text. December 21, 1963. Paper bound 25 cents postpaid.

39. The status of deer in Kansas. By Donald D. Anderson. Pp. 1-36. September 28, 1964. Paper bound 25 cents postpaid.

43. Names of species of North American Mammals north of Mexico. By E. Raymond Hall. Pp. 1-16. December 10, 1965. Paper bound 25 cents postpaid.

46. The distributional status of bats in Kansas. By J. Knox Jones, Jr., Eugene D. Fleharty, and Patrick B. Dunnigan. Pp. 1-33, 11 figures in text. May 1, 1967. Paper bound 25 cents postpaid.

49. Natural history of the prairie dog in Kansas. By Ronald E. Smith. Pp. 1-39, 4 plates, 10 figures in text. September 27, 1967. Paper bound 50 cents postpaid.

51. Contributions in mammalogy. A volume honoring Professor E. Raymond Hall. Edited by J. Knox Jones, Jr. Pp. 1-428, 122 figs. July 11, 1969. Paper bound $5.00 postpaid.

54. The dentition of glossophagine bats: development, morphological characters, variation, pathology, and evolution. By Carlton J. Phillips. Pp. 1-138, 49 figs. September 24, 1971. Paper bound $5.00 postpaid.

56. Systematics of the chiropteran family Mormoopidae. By James Dale Smith. Pp. 1-132, 40 figs. March 10, 1972. Paper bound $5.00 postpaid.

58. Systematics of three species of woodrats (genus *Neotoma*) in central North America. By Elmer C. Birney. Pp. 1-173, 44 figs. April 13, 1973. Paper bound $7.50 postpaid.

MONOGRAPHS IN MAMMALOGY

2. Readings in mammalogy. By J. Knox Jones, Jr. and Sydney Anderson. Pp. ix + 586. 1970. Paper bound $8.00 postpaid.

3. The distribution of mammals in Colorado. By David M. Armstrong. Pp. x + 415, 8 pls. Cloth bound $16.00 postpaid.