MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 137

A Systematic Study of the Mexican and Guatemalan Gray Squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae)

BY
GUY G. MUSSER
The American Museum of Natural History

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
NOVEMBER 1, 1968

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN

The publications of the Museum of Zoology, University of Michigan, consist of two series—the Occasional Papers and the Miscellaneous Publications. Both series were founded by Dr. Bryant Walker, Mr. Bradshaw H. Sawles, and Dr. W. W. Newcomb.

The Occasional Papers, publication of which was begun in 1913, serve as a medium for original studies based principally upon the collections in the Museum. They are issued separately. When a sufficient number of pages has been printed to make a volume, a title page, table of contents, and an index are supplied to libraries and individuals on the mailing list for the series.

The Miscellaneous Publications, which include papers on field and museum techniques, monographic studies, and other contributions not within the scope of the Occasional Papers, are published separately. It is not intended that they be grouped into volumes. Each number has a title page and, when necessary, a table of contents.

A complete list of publications on Birds, Fishes, Insects, Mammals, Mollusks, and Reptiles and Amphibians is available. Address inquiries to the Director, Museum of Zoology, Ann Arbor, Michigan 48104.

LIST OF MISCELLANEOUS PUBLICATIONS ON MAMMALS

No. 24. A comparative life history study of the mice of the Genus *Peromyscus*. By ARTHUR SVIHLA. (1932) 39 pp. $0.50

No. 25. The moose of Isle Royale. By ADOLPH MURIE. (1934) 44 pp., 7 pls. $0.70

No. 26. Mammals from Guatemala and British Honduras. By ADOLPH MURIE. (1935) 30 pp., 1 pl., 1 map $0.35

No. 32. Following fox trails. By ADOLPH MURIE. (1936) 45 pp., 6 pls., 6 figs. $1.00

No. 38. Revision of *Sciurus variegatoides*, a species of Central American Squirrel. By WILLIAM P. HARRIS, JR. (1937) 39 pp., 3 pls., (2 colored), 3 figs., 1 map $0.50

No. 39. Faunal relationships and geographic distribution of mammals in Sonora, Mexico. By WILLIAM H. BURT. (1938) 77 pp., 26 maps $0.75

No. 45. Territorial behavior and populations of some small mammals in southern Michigan. By WILLIAM H. BURT. (1940) 58 pp. .....out of print

No. 46. A contribution to the ecology and faunal relationships of the mammals of the Davis Mountain Region, southwestern Texas. By W. FRANK BLAIR. (1940) 39 pp., 3 pls., 1 map $0.35

No. 51. Mammals of the lava fields and adjoining areas in Valencia County, New Mexico. By EMMET T. HOOPER. (1941) 41 pp., 3 pls., 1 map $0.50

No. 52. Type localities of pocket gophers of the Genus *Thomomys*. By EMMET T. HOOPER. (1941) 26 pp., 1 map $0.25

No. 58. A systematic review of the Neotropical water rats of the Genus *Nectomys* (Cricetinae). By PHILIP HERSHKOVITZ. (1944) 88 pp., 4 pls., 5 figs., 2 maps $1.15

No. 59. San Francisco Bay as a factor influencing speciation in rodents. By EMMET T. HOOPER. (1944) 89 pp., 5 pls., 18 maps $1.25

No. 72. Faunal relationships of Recent North American rodents. By EMMET T. HOOPER. (1949) 28 pp. $0.35

No. 73. A study of small mammal populations in northern Michigan. By RICHARD H. MANVILLE. (1949) 83 pp., 4 pls., 6 figs., 1 map $1.25

No. 77. A systematic review of the harvest mice (Genus *Reithrodontomys)* of Latin America. By EMMET T. HOOPER. (1952) 255 pp., 9 pls., 24 figs., 12 maps $4.00
Cloth bound $4.60

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 137

A Systematic Study of the Mexican and Guatemalan Gray Squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae)

BY
GUY G. MUSSER
The American Museum of Natural History

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
NOVEMBER 1, 1968

CONTENTS

PAGE

INTRODUCTION 5

ACKNOWLEDGMENTS 6

MATERIAL AND METHODS 7

Sample Groups 8

Age, Molt, and Sex 10

Measurements and Other Characters 11

MORPHOLOGICAL VARIATION 18

Mensural Characters 18

Pelage Characters 25

GEOGRAPHIC VARIATION AND INTERGRADATION 43

Aureogaster Group 43

Socialis Group 46

Intergradation Between Aureogaster and Socialis Groups 62

RELATIONSHIPS OF *Sciurus aureogaster, C. colliaei, S. variegatoides,* AND *S. yucatanensis* 77

CONCLUSIONS AND QUESTIONS 89

TAXONOMY 93

APPENDIX 99

LITERATURE CITED 109

ILLUSTRATIONS

FIGURE PAGE

1. Distribution of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis* 9
2. Size differences between juveniles and adults 10
3. Sketches illustrating scored gradations of pelage features 14
4. Sketches illustrating scored gradations of pelage features 15
5. Variation in length of head and body and length of tail in *Sciurus aureogaster* .. 19
6. Variation in cranial length in *S. colliaei, S. variegatoides,* and *S. yucatanensis* 23
7. Frequencies of occurrence and diameters of sphenopalatine vacuities in *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis* 26
8. Amount of pigmentation of the crown in *Sciurus aureogaster* 27
9. Color of eye rings in *Sciurus aureogaster* 28
10. Size of postauricular patches in *Sciurus aureogaster* 29
11. Size and color of nape and rump patches in *Sciurus aureogaster* 30
12. Geographic variation in area of nape and rump patches in *Sciurus aureogaster* .. 31
13. Geographic variation in area of nape and rump patches in *Sciurus aureogaster* .. 32
14. Color of underparts in *Sciurus aureogaster* 33
15. Size of shoulder and costal pattern in *Sciurus aureogaster* 34
16. Amount of pigmentation of feet in *Sciurus aureogaster* 35
17. Color of underside of tail in *Sciurus aureogaster* 36
18. Frequency of melanism in *Sciurus aureogaster* 37
19. Distribution of principal body patterns in *Sciurus aureogaster* 38
20. Percentage of 11 "patterns" in 58 samples of *Sciurus aureogaster* 42
21. Gradations in color of underparts in *Sciurus aureogaster* following p. 44
22. Variation in color and pattern of *Sciurus aureogaster* (Aureogaster Group) from Catemaco ..... following p. 44
23. Frequencies of gray and melanistic phases in *Sciurus aureogaster* (Socialis Group) 51
24. Schematic profile of northeastern Oaxaca 63
25. Frequencies of pelage features of *Sciurus aureogaster* in Puebla, Veracruz, and Tamaulipas 70
26. Frequencies of pelage traits of *Sciurus aureogaster* in Veracruz, Tabasco, and Chiapas 71
27. Frequencies of pelage traits of *Sciurus aureogaster* in the Isthmus of Tehuantepec 73
28. Color and pattern of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis* ..... following p. 74
29. Categories of gradation from gray to blackish phases in *Sciurus aureogaster* (Socialis Group) ..... following p. 74
30. Frequencies of pelage traits of *Sciurus aureogaster* in Chiapas and Tabasco 76
31. Cranial views of *Sciurus aureogaster, S. colliaei,* and *S. variegatoides* 80
32. Cranial views of *S. aureogaster* and *S. yucatanensis* 87
33. Geographic ranges of Aureogaster and Socialis segments of *Sciurus aureogaster* and intergrading areas 89
34. Geographic ranges of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis* and estimates of directions of gene flow 91

INTRODUCTION

Sciurus aureogaster is a diurnal tree squirrel of México and southwestern Guatemala. It is intermediate in size between the eastern gray squirrel (*S. carolinensis*) and the eastern fox squirrel (*S. niger*). Individual and geographic variation in pattern and color of pelage is striking. The grayish upper parts may be unpatterned or broken up by either nape and rump patches, a shoulder and costal patch, or various combinations of those patterns. The patches vary in size and color. The underparts vary from white through gradations of orange to deep chestnut. Melanism, varying in degree and frequency, occurs in populations from certain segments of the range.

The species occurs on the Gulf and Pacific coastal plains of México from Tamaulipas to Tabasco on the east and from Colima to Chiapas (Isthmus of Tehuantepec) on the west. It is also found in the mountains fringing the southern margins of the Mexican Plateau, and south and east through the highlands of México into the mountains of southwestern Guatemala. It inhabits a variety of forests ranging from tropical scrub and broadleaf formations of the hot lowlands to cold and wet temperate cloud forests of oak and conifer in the highlands. In these it occurs with the fox squirrels, *S. nayaritensis, S. oculatus,* and *S. alleni,* and the little brownish-red species, *S. deppei,* but apparently is narrowly or not at all sympatric with the other lowland gray squirrels, *S. colliaei, S. variegatoides,* and *S. yucatanensis.*

These gray squirrels of Middle America are among the most variable in color and pattern of Western Hemisphere tree squirrels. Commensurate with that variability they have been known by many scientific names. Highlights of their taxonomic history begin with F. Cuvier's (1829) description and illustration of *Sciurus aureogaster,* the earliest description of a gray squirrel from Middle America. Succeeding decades chronicled the descriptions of new forms and subsequent interpretations of their morphologic and distributional limits by J. A. Wagner (1837), J. E. Gray (1867), J. A. Allen (1877), E. R. Alston (1878), and others. These earlier contributions were summarized in 1899 by E. W. Nelson in his taxonomic revision of the squirrels of México and Central America—the most comprehensive study to that time. Nelson recognized 15 species: *aureogaster, poliopus, nelsoni, colliaei, sinaloensis, truei, socialis, griseoflavus, yucatanensis, thomasi, adolphei, boothiae, managuensis, goldmani,* and *variegatoides.* He grouped these in the subgenus *Echinosciurus.* In the following years,

collections of squirrels from Middle America increased greatly and a few new forms were described, but there was no review of any major segment until Harris (1937) studied samples of populations known as *thomasi, dorsalis, adolphei, boothiae, belti, variegatoides, managuensis,* and *goldmani.* He considered these populations to represent geographic races of one widely variable species, *variegatoides.* Included in *variegatoides* were populations known as *bangsi, underwoodi, atrirufus, austini,* and *helveolus,* all forms described and named after Nelson's study. As Harris understood it, *variegatoides* was primarily Central American in distribution (Guatemala to Panama), but also extended into México along the Pacific coastal plain and uplands of southeastern Chiapas.

Subsequent reports by Kelson (1952), Hall and Kelson (1959), Alvarez (1961), and others have contributed to knowledge of the group. Anderson (1962) studied squirrels from the Pacific coastal plain and uplands from southern Sonora south to Colima. Nelson had listed these as "species": *truei, sinaloensis,* and *colliaei.* The data indicated that these coastal populations vary clinally and are interbreeding segments of one species to which the name *colliaei* applies. These squirrels are not as vividly colored as the other Mexican and Central American gray squirrels.

My studies are focused on the populations which Nelson and subsequent authors have referred to under the names *aureogaster, poliopus, nelsoni, griseoflavus,* and *socialis.* I attempted to ascertain morphologic, distributional, and habitat relationships of those populations and their relationship to *colliaei, variegatoides,* and *yucatanensis.* Essentially, I asked this question: how many gene pools are represented by *aureogaster, poliopus, nelsoni, griseoflavus,* and *socialis,* and what are the morphologic and ecologic characteristics of those pools? I concluded from the accumulated data that *aureogaster, poliopus, nelsoni, griseoflavus,* and *socialis* represent interbreeding populations of one highly variable species, to which the name *aureogaster* applies.

ACKNOWLEDGMENTS

Many people have given freely of their time and effort towards the realization of this report. Emmet T. Hooper and William H. Burt deserve special mention. E. T. Hooper generously turned over to me all data and specimens he had earlier gathered towards an intended systematic revision of Middle American tree squirrels. He has carefully and most critically read the entire manuscript and has significantly contributed to its quality. W. H. Burt provided me with every facility at the Museum of Zoology, was instrumental in providing opportunity and funds for field work, read

the manuscript carefully, and offered criticisms and suggestions. Claude W. Hibbard and Morris Foster, both of the University of Michigan, have also read the manuscript; I appreciate their criticisms and suggestions.

My colleagues at the American Museum of Natural History, Department of Mammalogy—Sydney Anderson, Karl F. Koopman, Hobart M. Van Deusen, and Richard G. Van Gelder—have read the manuscript. Results of those readings and our discussions have enhanced the quality of this report.

Most of my field work in México has at different times been shared with Kraig Adler, James H. Brown, John P. Hubbard, and R. Jean Vandermeer. I am grateful to them for their companionship and their unselfish efforts in making my field seasons successful.

I also thank the custodians of those institutional collections (Appendix) who allowed me to study and borrow specimens under their care and who often made special efforts to obtain specimens for me.

Permits to collect specimens in México were kindly supplied by Sr. Rodolfo Hernández Corzo of the Secretaría de Agricultura y Ganadería de México.

Figures 3 and 4 were drawn by Rosalind Price. Robert E. Logan, staff photographer of the American Museum of Natural History, is responsible for the excellent color transparencies, from which Figures 21, 22, 28, and 29 were made, and the high-quality photographs of crania in Figures 31 and 32. Nylene Gilbert patiently translated my rough typewritten pages into finished manuscript.

Portions of my research at the University of Michigan were financially supported by an Edwin C. Hinsdale Scholarship, awarded by the Museum of Zoology, and a Graduate Student Dissertation Research Grant, administered by the Horace H. Rackham School of Graduate Studies.

Finally, I thank all those persons who served in various capacities as my Mexican hosts—*Campesinos, Indios,* and *Padrones* alike. Through their generous and honest *"mi casa es suyo"* they provided my companions and me with every hospitality. From my contact with them I gained an insight into their cultures, their daily spontaneity and philosophy, and their rich Pre-Columbian heritage.

MATERIALS AND METHODS

This study is based on 2178 specimens—conventional study skins with skulls—representing the following species (*sensu latu*): 1714 *Sciurus aureogaster,* 314 *S. colliaei,* 80 *S. variegatoides,* and 70 *S. yucatanensis.* These include most of the specimens of *aureogaster* and *colliaei* in institutional col-

lections. Most specimens of *yucatanensis* and *variegatoides* were examined, but only those pertinent to the problem and thus studied in greatest detail are listed here.

To facilitate the analysis of variation and obtain larger samples, I pooled most of the specimens to form 65 groups representing localities and regions as indicated below and in Figure 1. These groups served as geographic units for detailed analyses. Each was given a number and place name and those names and numbers are used throughout this report. Localities and numbers of specimens represented in each sample group are indicated in the Appendix.

SAMPLE GROUPS (SEE FIG. 1)

1. General Terán
2. Ciudad Victoria
3. Gómez Farías
4. Altamira
5. Eastern San Luis Potosí
6. Pinal de Amoles
7. Papantla
8. San Marcos
9. Central Veracruz Coastal Plain
10. Valle Nacional
11. Catemaco
12. Southeastern Veracruz
13. Sarabia
14. Minatitlán
15. Southern Tabasco
16. Tumbalá
17. Pueblo Nuevo
18. San Cristóbal
19. Chiapas-Guatemala Highlands
20. Soconusco
21. Tuxtla Gutiérrez
22. Oaxaca-Chiapas Coastal Plain
23. Chicapa
24. Tehuantepec
25. Puerto Angel
26. Ozolotepec
27. San Gabriel Mixtepec
28. Guerrero-Oaxaca Coastal Plain
29. Acapulco
30. Agua de Obispo
31. Omilteme
32. San Andrés de la Cruz
33. Southwestern Guerrero Coastal Plain
34. Zacatula
35. Southeastern Michoacán
36. Dos Aguas
37. Colima Coastal Plain
38. Pueblo Juárez
39. Platanar
40. Nevado de Colima
41. Ameca
42. Mazamitla
43. Patamban
44. Cerro de Tancítaro
45. La Salada
46. E Morelia
47. Lengua de Vaca
48. Volcán de Toluca
49. Distrito Federal
50. Volcán Popocatepetl
51. Northern Puebla Highlands
52. Hidalgo-Puebla Eastern Highlands
53. Las Vigas
54. Xico
55. Jalapa
56. Tlapancingo
57. W Oaxaca de Juárez
58. Sierra de Juárez
59. Jalisco-Colima Coastal Plain
60. San Blas
61. Southern Sinaloa
62. Sonora-Chihuahua
63. Chiapas-Guatemala Coastal Plain
64. Northern Chiapas-Guatemala
65. Eastern Tabasco

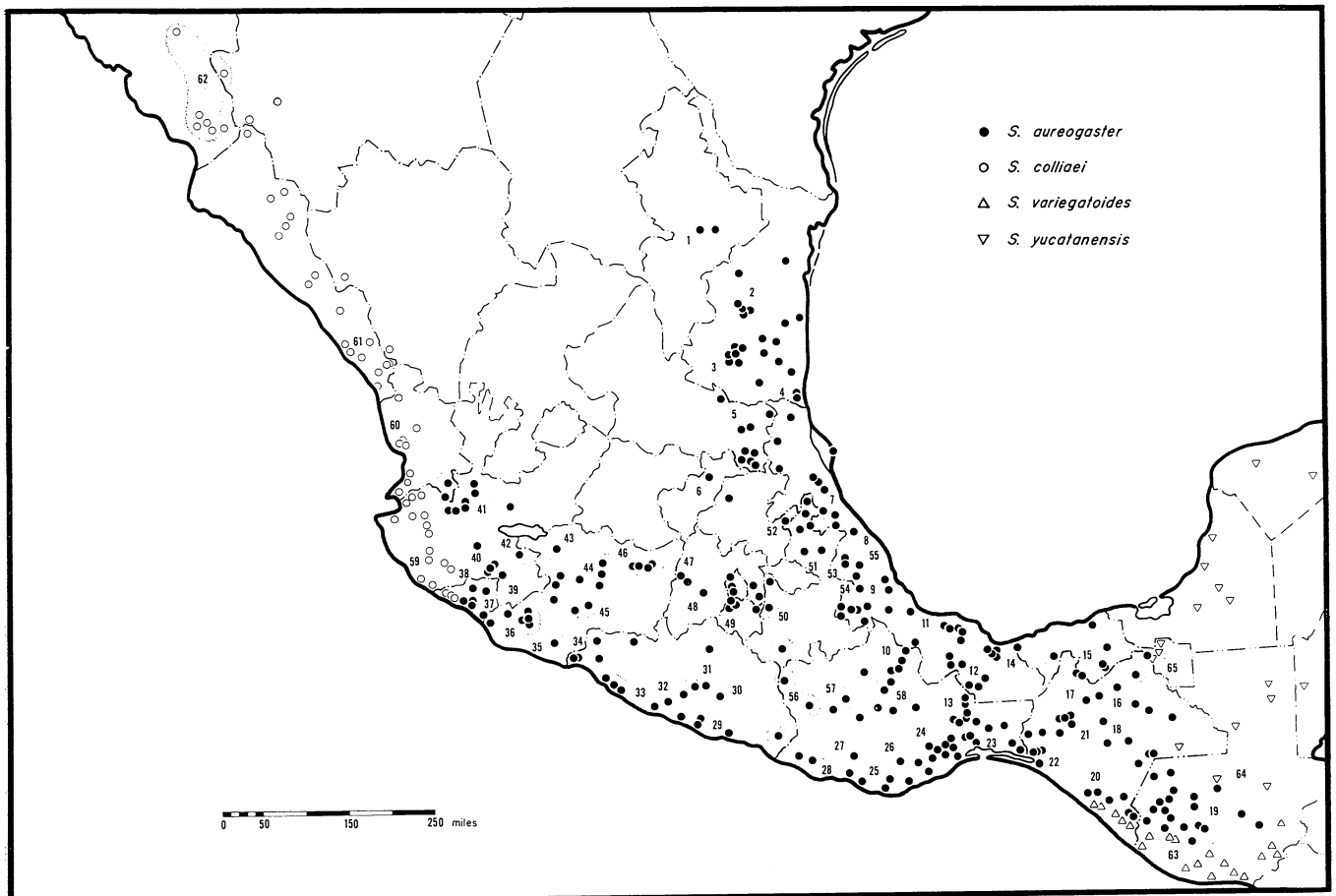


FIG. 1. Distribution of *Sciurus aureogaster, S. colliaei,* and segments of *S. variegatoides* and *S. yucatanensis,* as determined from specimens examined. Shaded areas indicate "sample groups" explained and listed in the text.

AGE, MOLT, AND SEX

In analyzing geographic variation I recognized two age groups, juveniles and adults. Juveniles include the age range from nestlings to individuals molting from juvenal into adult pelage and are additionally defined as follows: the skull is smaller than in adults (Fig. 2); the sutures of the cranium are incompletely closed (that between the basioccipital and basisphenoid, for example, is always open); various stages of tooth eruption

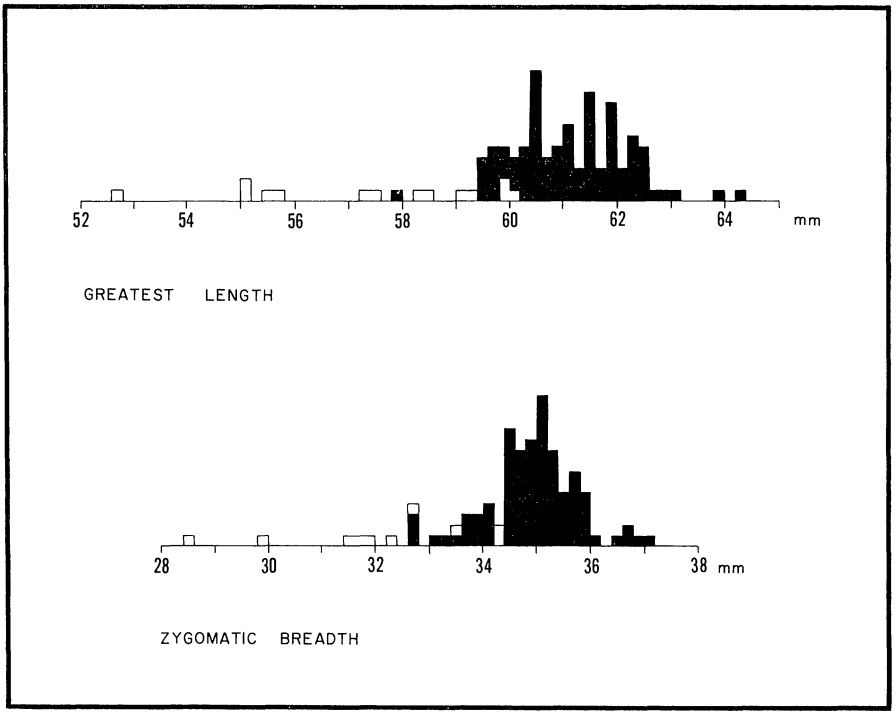


FIG. 2. Size differences between juveniles (unfilled squares) and adults (filled squares) in two cranial measurements as illustrated by specimens from the Nevado de Colima (sample 40). Each square represents one specimen.

are included, the oldest animals, for example, may still have their deciduous fourth premolars (although their permanent counterparts, including the peg-like upper third premolars, may have erupted above the alveoli, but usually not above the gum line); juvenal pelage is usual, though in older individuals the molt into adult pelage has started and may be more than half-way completed (juvenal pelage is softer, silkier, and shorter than adult pelage). In adults the skull is larger; the sutures are tightly closed, that

between the basioccipital and basisphenoid usually completely fused; permanent fourth premolars and upper third premolars (in *aureogaster* this tooth is absent from about 1 per cent of all adult specimens) have completely erupted and displaced the deciduous teeth; and the animals are in adult pelage.

The animals classed as juveniles are sexually immature, have not bred, and have undeveloped sexual features. Adults are usually sexually mature and the sexual features are well developed, resembling those in the eastern gray and eastern fox squirrels (Brown and Yeager, 1945).

I studied molt primarily to distinguish between juvenal and adult pelages and between fresh and worn pelages. The specimens indicate that juveniles molt directly into adult pelage without passing through a subadult stage. Further, the juvenal pattern is retained but the hues are brightened (color is brighter) in the adult pelage. Adults molt at least once a year. Because I did not have specimens from one area representing all months of the year, I am unsure whether a second molt occurs. Though the adult pattern apparently does not change from one pelage to another, fresh pelage is softer and the colors are brighter than in worn pelage. Typically, in pelages ready to be replaced the hairs are slightly shorter and frizzled, the white bands often changed to a dull, dirty whitish-yellow, and the black bands faded, becoming brown on melanistic specimens.

I could not corroborate Nelson's (1899) observations that winter and summer (and wet and dry season) pelages differ in color. The variation he described in size of the postauricular patches, color and amount of grizzling of the underparts, and degree of frosting on the back—to mention a few—was observed in squirrels in fresh pelage collected at the same time of year from one locality. Therefore, that variation apparently is not related to season. Thus, in the analysis I was able to increase sample sizes of adults by utilizing material collected at different times of the year.

Variation in cranial and external dimensions, color and patterning of the pelage, its length and density, and frequency and degree of melanism appears to be independent of sex. Thus, sexes were combined in samples and were not analyzed separately.

MEASUREMENTS AND OTHER CHARACTERS

EXTERNAL DIMENSIONS.—Measurements taken in the flesh—total length, tail (vertebrae) length, and lengths of hind foot and ear (height from notch)—are those of the collector and were obtained from specimen labels. Length of head and body was computed as total length minus tail length. Weights were available for few specimens. Of these several sets of data,

length of head and body and length of tail are the most reliable and complete; variation in those characters were mapped for adults (Fig. 5).

CRANIAL DIMENSIONS.—I tested several measurements of the cranium which appeared to vary geographically These are: greatest length of skull, zygomatic breadth, interorbital breadth, breadth of rostrum, length of nasals, anterior and posterior breadths of nasals, length of maxillary tooth row, diameter of orbit, and diameters and relative positions of various foramina. Two of these—greatest length of skull and frequency of occurrence and diameter of sphenopalatine vacuities (of adults)—are mapped (Figs. 6 and 7). The other dimensions correlate with length of skull or show no meaningful geographic variation.

Greatest length of skull is used as an index of size. The coefficient of variation in that dimension is less than in most external measurements (Tables 2 and 3).

Sphenopalatine vacuities are oblong perforations in each wall below the pterygoid fossa at the basisphenoid-palatine junctions (illustrated in Moore, 1959:165, and Guthrie, 1963:461). When the vacuities are absent the wall is solid, but often a tiny foramen is present in the basisphenoid next to the suture with the palatine. The vacuities are paired and usually symmetrical in shape. I measured the greatest diameter of the largest vacuity with an ocular micrometer in a dissecting microscope.

FEATURES OF PELAGE.—Most pelage traits were analyzed by indexing the gradations in color and size of a pattern; this facilitated analysis and description of the observed variation. The number of categories per trait that were recognized varied. For example, I recognized two categories (white and pigmented) for color of the eye ring and six categories in describing color of underparts and size of shoulder and costal pattern. The categories represent gradations observed in the samples; they are not preconceived categories into which I tried to fit the specimens.

Gradations in pelage characters were scored for adult specimens, then plotted on maps (Fig. 15, for example, illustrates geographic variation of size of shoulder and costal pattern). Each sample group (Fig. 1) on those maps is symbolized as a hexagon. At the angles of the hexagon are scores, indicated in the legends. The score increases clock-wise around the hexagon. A line radiating from a corner of that hexagon is proportional to the number of specimens receiving a particular score—one millimeter represents one specimen (each map has a 40-mm or specimen scale). The degree of shading inside the hexagon indicates the *mean* score per sample group. Thus, sample size, range of individual variation, mode, and an estimate of the mean of a character are indicated for each sample group; the symbol is

a graphic representation of the frequency distribution of gradations in a given trait. Only gradations in pelage features of non-melanistic phases were scored; the frequency of melanistic specimens in each sample group was analyzed and mapped separately. Any exception to this scheme is explained in the legends. Various gradations in pelage features (Figs. 3 and 4) are discussed below.

CROWN.—The overhair and underfur of the crown are about half the length of hairs covering the remainder of the dorsum. The frequencies of black hairs and those with reduced white or colored bands were estimated. The tonal range is from pale gray to black. Three categories were recognized: gray, gray contrasting, and black. In a gray crown (score 0) the hairs are colored like those of the back (Fig. 3, A), typically frosted gray suffused with varying amounts of buff to chestnut. The upper parts, thus, are uniformly colored if not broken up by a black area above the eye or by nape, rump or shoulder patches. The black patch above the eye is absent in some specimens and undelimited in animals with grizzled-black or black crowns. In a gray contrasting crown (score 1) the hairs are darker than those of the back, black hairs are more abundant than those tipped with white or orange, and the crown is grayish-black or black lightly suffused with white (Fig. 3, B). In a black crown (score 2) there may be a sprinkling of white-tipped hairs in the center (Fig. 4, D), but most of the hairs are black and often long, sometimes as long as those on the back.

EYE RING.—The narrow band (about 3 mm wide) of short bristle-like hairs that encircles each eye (Figs. 3 and 4) varies from white to orange-red. The two color extremes are conspicuous but the gradation between them is so complete that I recognized only two categories: white, including tinges of light buff (score 0), and colored, buff to orange-red (score 1).

POSTAURICULAR PATCHES.—Postauricular patches (Fig. 3, A–C) are tufts of long fine hairs—in diameter, comparable to those of the underfur—grayish basally, and usually white distally. In a few specimens the hairs are pigmented like the nape patch. The three categories recognized are based on size only: (0) patches absent (Fig. 3, A); (1) intermediate (Fig. 3, B); and (2) well developed, each patch a conspicuous explosion of white behind each ear and sharply contrasting with the nape region (Fig. 3, C).

NAPE AND RUMP PATTERN.—Nape (or nuchal) and rump patches are conspicuous components of the dorsal pattern in several populations of *S. aureogaster*. The size of each patch is defined by pigmentation of the subterminal bands of the hairs. When they are narrow and pale the patches are indistinct, hardly contrasting with the ground color of the back. When

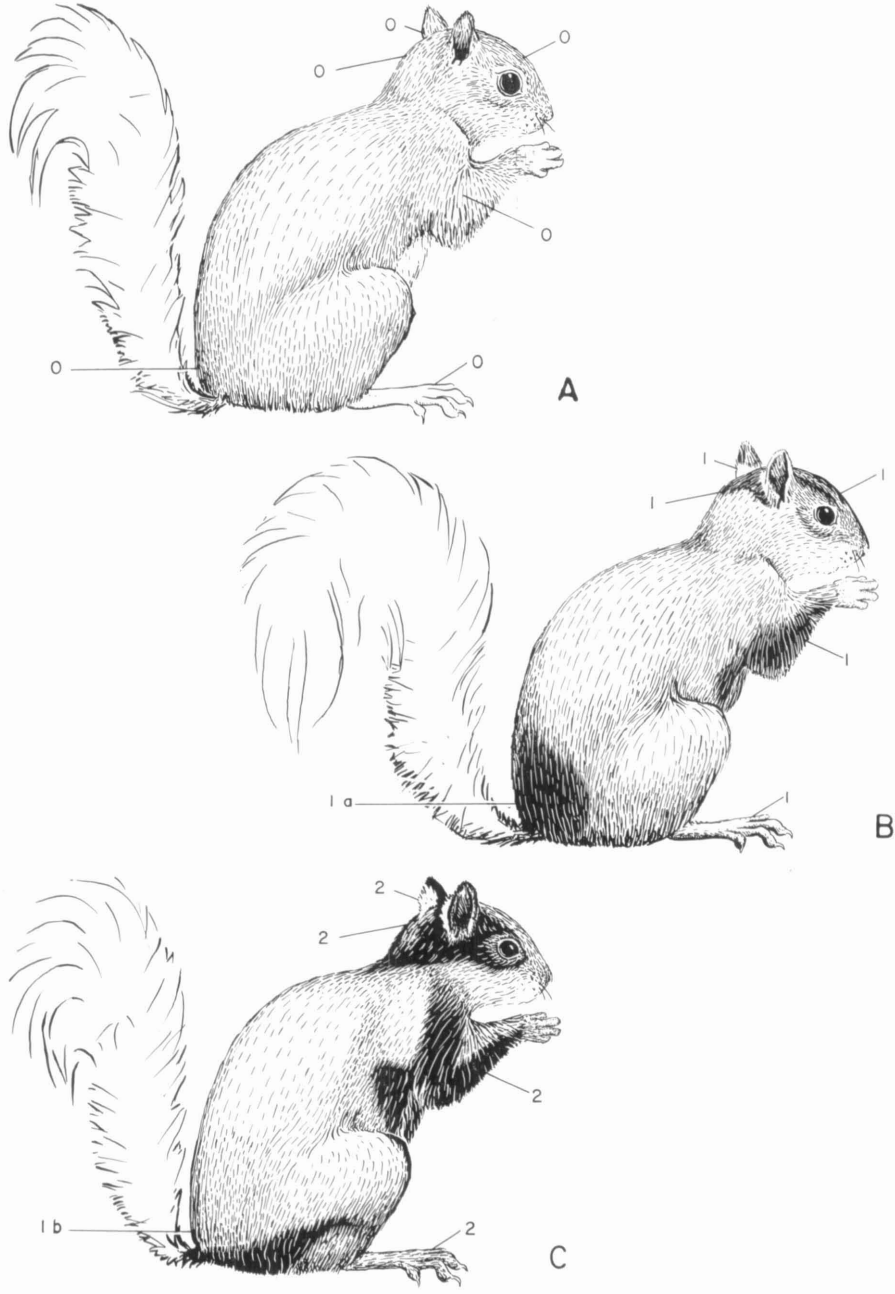


FIG. 3. Three of six sketches (see also Fig. 4) illustrating scored gradations, A–D, of the crown (0–2); A–C, of postauricular patches (0–2); A–D, of area of nape and rump patches (0–2); A–F, of extent of shoulder and costal pattern (0–5); and A–D, of the feet (0–3) in *Sciurus aureogaster*. Numbers indicate increasing values for each feature. See text for further explanation.

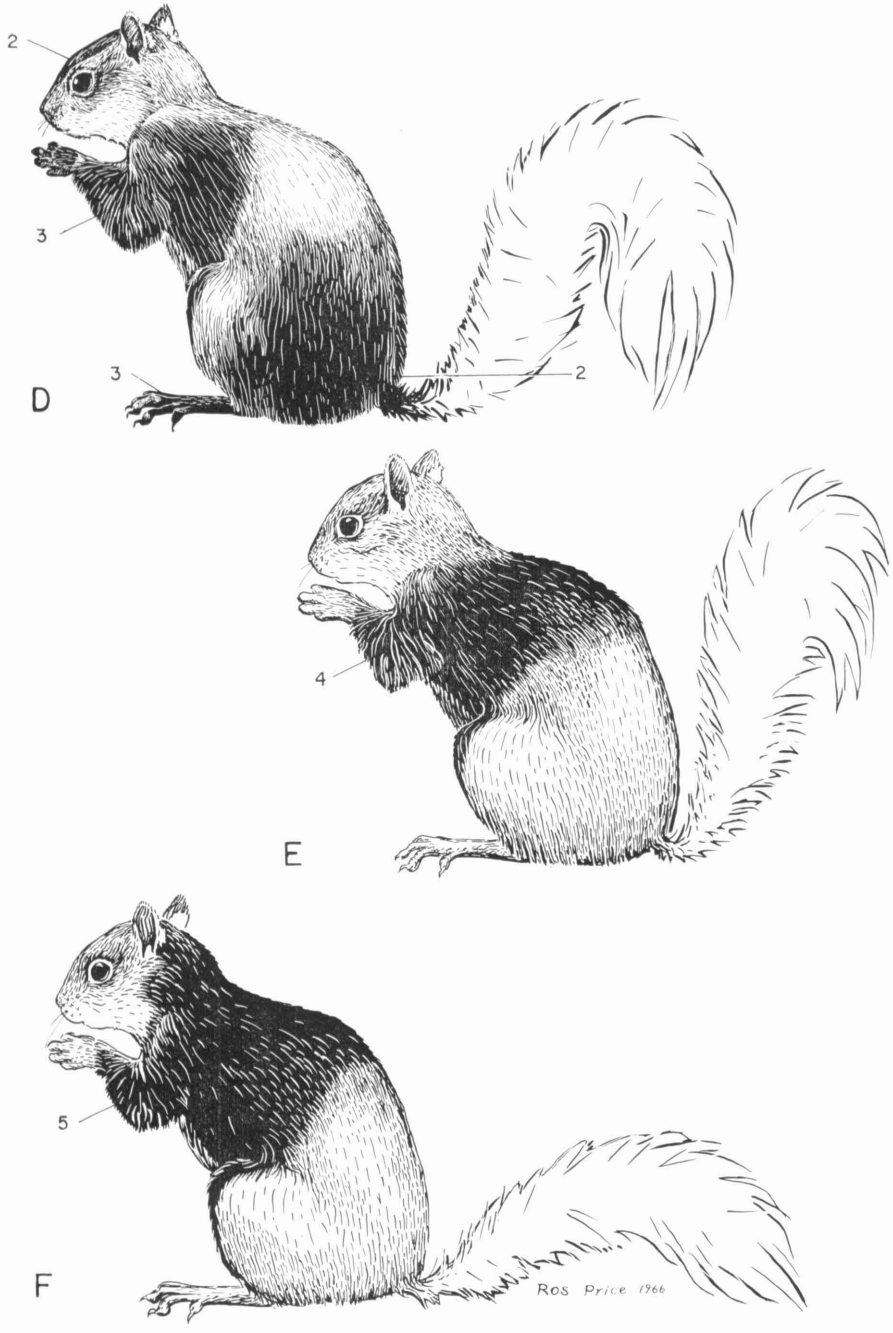


FIG. 4. Scored gradations of the characters enumerated in Figure 3.

they are wide and more intense (buffy-orange to chestnut, or black) the patches contrast sharply with the coloration of the back.

Grades in area of nape and rump patches are indicated in Figures 3 and 4. Size of nape and rump pattern varies from a slight suffusion of color behind the ears and on the rump near the base of the tail to a condition in which the two patches apparently have joined to cover the entire dorsum. I recognized four categories of nape patch (scored 0–3) and three of rump patch (scored 0–2). Gradations of nape patch are: (0) absent (Fig. 3, A); (1) intermediate, mainly concentrated in front and between the ears and about one-third down the neck (Fig. 3, B); (2) expansive (Fig. 3, C); and (3) a broad patch joined by a narrow isthmus of color to an expansive shoulder and costal patch, or broadly joined to that patch so the two appear as one unit (Fig. 4, F). Rump patch gradations are: (0) absent (Fig. 3, A); (1) intermediate with either a broad pattern (Fig. 3, B) or a chevron-shaped pattern in dorsal view (Fig. 3, C); and (2) expansive, covering almost all the dorsal posterior half of the body (Fig. 4, D). These gradations relate to *area* of patch, not to its color.

Color of the patches ranges from pale buff, where the areas scarcely are differentiated from the ground color of the upper parts, to a rich chestnut, boldly contrasted with the back. The five categories I recognized are: (0) color undifferentiated from back; (1) buff; (2) buff-orange; (3) orange-red; and (4) chestnut. Often long black hairs are intermingled with the buffy hairs; in some specimens all hairs of the nape and rump, but not the remainder of the animal, are black.

UNDERPARTS.—Hairs of the underparts of the body, which are shorter than those of the upper parts and tail, are light gray basally and either white or pigmented apically. A subapical black band interrupts the white or pigmented apical band in overhairs of some specimens, giving the underparts a speckled-black or grayish appearance.

I recognized the following six color categories (Fig. 21): (0) white; (1) whitish-orange; (2) buff; (3) orange; (4) orange-red; and (5) chestnut. Each score indicates a hue of a given index specimen and designates a category broad enough to encompass slightly lighter and darker tones of that hue. Underparts speckled with black were given negative values. Thus, white underparts suffused with black (appearing as a frosted gray or grayish-black) were scored –0 and pigmented specimens speckled with black were given negative scores corresponding to the solid counterparts. For example, a score of 4 indicates underparts of solid orange-red. Its speckled counterpart, which would be suffused or sprinkled with black and slightly darker, would be scored –4. Although both white and solidly pigmented underparts often have a few hairs with subapical black bands,

I considered such examples to be speckled only when the hairs with subapical banding were numerous enough to impart a peppered suffusion to the underparts.

SHOULDER AND COSTAL PATTERN.—The shoulder and costal pattern (shoulder patch, costal patch, or saddle) is formed by orange hues that extend from the venter for various distances dorsad over the forelegs, shoulder, and costal regions. The smallest orange area that was scored covers the outside of the forelegs and arcs shallowly behind the shoulder (Fig. 3, B). In the largest area the color of the belly extends over the anterior portion of the body from behind the pinnae to the middle of the back and gradually tapers down the sides onto the flanks (Fig. 4, F).

The six index categories and their scores are indicated in Figures 3 and 4. Categories 3–5 require comment. In specimens given a score of 3, the broad costal crescents are separated by a middorsal gap and are not connected with the nape patch, if one is present. Category 4 indicates a complete "saddle" and category 5 denotes maximum size of the pattern; it usually extends over the nape as illustrated, or connects with the nape patch by an orange or reddish isthmus. In a few specimens it covers the entire dorsum except for the head and margins of the rump.

A shoulder and costal patch is present only when the underparts are pigmented, but not all squirrels with pigmented underparts have a shoulder and costal pattern. The shoulder pattern is pigmented like the underparts and shows the same gradations in color; its extent varies independently.

COLOR OF FEET.—The fore and hind feet may be white, black, frosted-black (intermediate grades between those extremes), the same color as the upper parts, or occasionally suffused with buffy or orange hues of the underparts. Since amount of frosting of the feet is conspicuous and varies independently of venter coloration, I have analyzed it separately and ignored other colors of the feet which tend to be associated with those of the underparts.

Only intensity of frosting was indexed; the categories are as follows: (0) white, hairs white throughout (Fig. 3, A); (1) whitish, slightly speckled with black, hairs black basally and white apically (Fig. 3, B); (2) blackish-gray or frosted black, hairs mostly black or gray proximally and narrowly tipped with white (Fig. 3, C); and (3) melanistic, feet black or only slightly speckled with white (Fig. 4, D).

COLOR OF TAIL.—Long overhairs clothe the tail; underfur is absent. The hairs are pigmented with alternate black and gray to chestnut bands; the subapical band is always broad and black and subtends a white tip. The dorsal tail pattern is white with an underlying black suffusion and

appears frosted. The ventral pattern consists of a midventral solidly colored or variegated strip bordered by black, this margined by white—a result of the exposed proximal colored bands of the hairs. I indexed only the midventral strip: (0) grayish-white to grayish-buff, usually variegated as a result of the six to eight alternate black and whitish bands of each hair; (1) intermediate, variegated buff to orange; and (2) orange-red to chestnut, usually a solid color, but sometimes variegated with black.

Bands of the tail often resemble those of the body. For example, in many of the specimens from near Tehuantepec (sample 24), the tail hairs and overhairs of the upper parts have three bands: basal orange, subapical black, and apical white. Similarity of midventral tail strip and of underparts does not hold for all samples. Thus, though the tail is usually variegated grayish-white or grayish-buff in squirrels with whitish underparts, and orange-red or chestnut in specimens with deep orange underparts, in some samples deeply pigmented tails are associated with whitish venters, and grayish tails with richly pigmented underparts.

Length and Density of Pelage.—Variation in length of overhairs and density of underfur is difficult to analyze quantitatively. I have described this variation qualitatively but have not mapped it.

Melanism.—In *Sciurus aureogaster* melanism may affect the entire pelage or be restricted to parts—crown, nape, rump, feet, or tail, for example. In some samples, many degrees of melanism are present, ranging from normal gray and buff through a series of gradations to entirely black.

I have mapped the frequency of melanism in each sample group. That melanistic component includes both partial melanistic and black phases. From the melanistic segment of each sample, however, I excluded specimens that are melanistic only in one or several regions—on the crown, or only nape and rump, for example—and not over the entire body. In contrast to other features of the pelage where only adults are analyzed, both adults and juveniles are included in the analysis of melanism.

MORPHOLOGICAL VARIATION

MENSURAL CHARACTERS

External Dimensions.—There appears to be no geographic trend in length of head and body, but length of tail appears to vary geographically in some regions (Fig. 5; Table 1). For example, squirrels of the Pacific lowlands (samples 22–25, 29, 34–35, and 37) and those of the Gulf regions of northeastern México (samples 3–6, and 7) tend to have longer tails than do animals of the highlands, but there is gradation between the two.

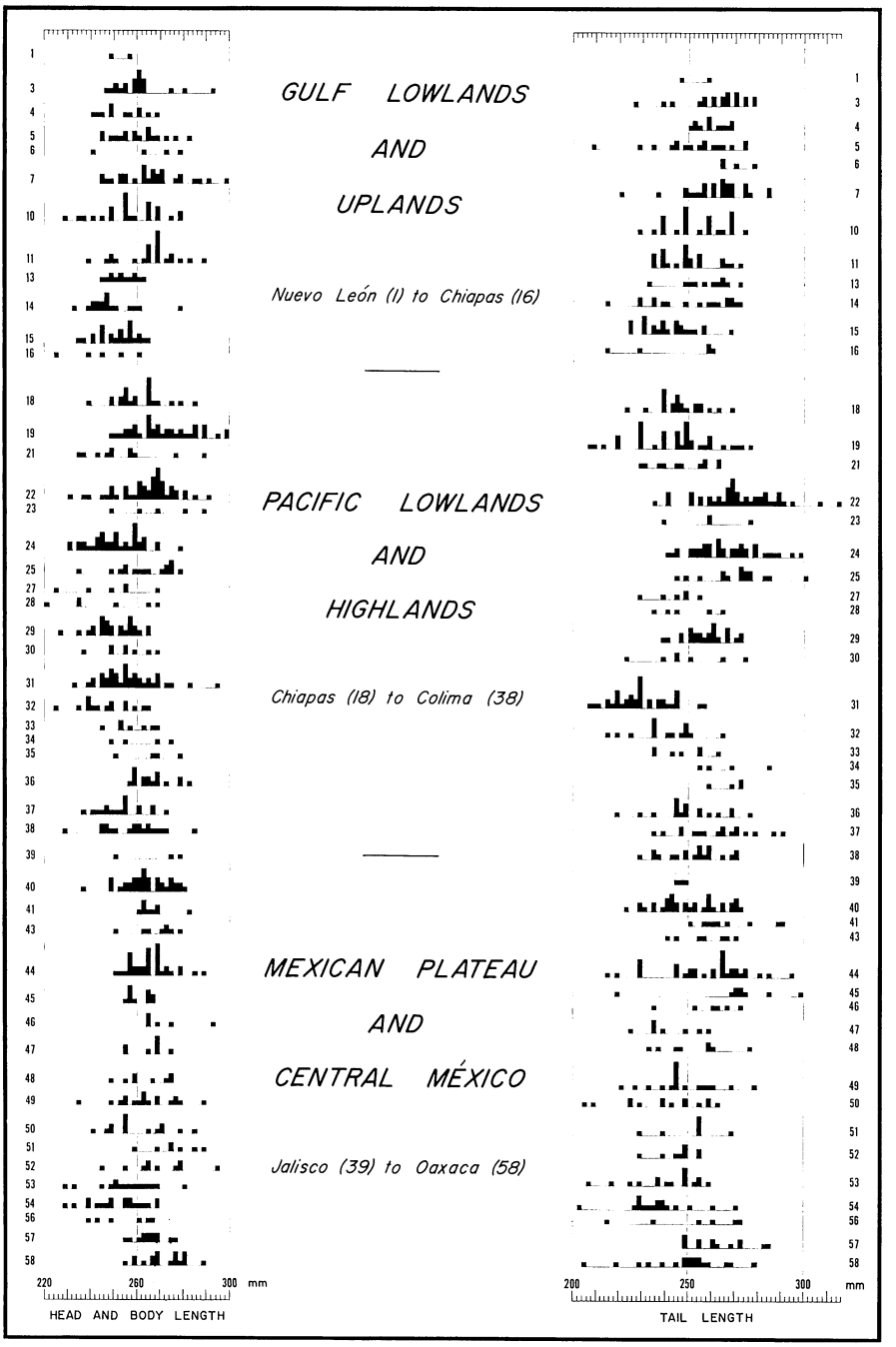


FIG. 5. Variation in length of head and body and length of tail in samples of *Sciurus aureogaster*. Numbers beside histograms correspond to numbered sample groups in Figure 1. Each square equals one specimen. See Table 1.

TABLE 1

HEAD AND BODY, AND TAIL LENGTHS (MM) IN SAMPLES OF *Sciurus aureogaster* (SEE FIG. 5)

Sample group	Head and body length					Tail length				
	n	M.±S.D.[a]	95% C.L.[b]	Extremes	C.V.[c]	n	M.±S.D.	95% C.L.	Extremes	C.V.
1	2	254.0± 5.7	203.2–304.8	250–258	2.2	2	253.5± 9.2	170.9–336.1	247–260	3.6
3	21	261.6±10.6	256.7–266.4	248–293	4.1	20	263.1±13.5	256.8–269.4	239–280	5.1
4	12	254.1± 9.2	248.2–259.9	241–270	3.6	12	260.5± 6.5	256.4–264.6	251–269	2.5
5	18	261.2±10.6	255.9–266.5	245–283	4.1	17	252.5±16.8	243.9–261.2	210–275	6.1
6	4	264.8±16.7	238.1–291.4	242–280	6.3	4	270.5± 7.1	259.1–281.9	265–280	2.6
7	29	266.9±13.7	261.7–272.1	245–300	5.1	29	262.8±13.3	257.8–267.9	237–286	5.1
10	26	257.4±13.1	252.1–262.7	230–280	5.1	26	254.5±12.6	240.4–257.5	230–275	7.1
11	24	266.0±12.1	260.9–271.2	240–290	4.5	24	250.7±11.1	245.9–255.5	235–273	4.4
13	10	252.2± 4.6	248.9–255.5	245–259	1.8	8	262.0± 7.5	255.7–268.3	251–273	2.9
14	17	249.4±10.8	243.8–254.9	233–280	4.3	17	254.4±15.7	246.3–262.5	230–274	6.2
15	26	252.0± 8.1	248.7–255.2	236–265	3.2	26	240.5±12.9	235.3–245.8	206–270	5.4
16	5	245.2±14.1	227.7–262.7	225–262	5.7	5	245.0±21.2	218.6–271.4	215–261	8.7
17*	8	248.9±20.9	231.4–266.3	220–285	8.4	8	248.0±24.2	227.8–268.2	218–295	9.8
18	24	263.3±13.4	257.6–268.9	240–305	5.1	23	246.9±10.1	242.5–251.2	223–270	4.1
19	40	273.1±14.7	268.4–277.8	249–310	5.4	40	243.7±17.3	238.1–249.2	208–277	7.1
21	11	254.9±16.5	243.8–266.0	235–290	6.5	11	248.1±12.2	239.9–256.3	230–264	4.9
22	49	264.5±12.3	260.9–268.0	232–291	4.5	48	273.6±23.3	266.8–276.3	235–315	8.1
23	5	270.8±15.8	251.1–290.5	250–290	5.9	4	259.3±15.5	234.6–283.9	240–278	6.0
24	41	251.6±11.1	248.1–255.1	231–280	4.4	40	266.8±14.1	262.3–271.3	242–299	5.3

Table 1 (Cont.)

Sample group	Head and body length					Tail length				
	n	M.±S.D.[a]	95% C.L.[b]	Extremes	C.V.[c]	n	M.±S.D.	95% C.L.	Extremes	C.V.
25	16	263.9±12.0	257.5–270.3	235–280	4.6	16	271.5±13.9	264.1–278.9	245–302	5.1
26*	3	261.3±13.3	228.3–294.4	246–270	5.1	2	271.0± 1.4	258.3–283.7	270–272	.5
27	6	249.2±15.3	233.1–265.2	225–270	6.1	6	245.0± 8.9	235.6–254.4	230–255	3.7
28	6	246.7±18.8	226.9–266.4	222–270	7.6	5	249.4±12.6	233.7–265.1	235–265	5.1
29	26	250.9± 9.3	247.1–254.6	227–265	3.7	25	258.2± 9.2	254.4–262.0	239–273	3.6
30	8	255.3±10.2	246.8–263.7	237–270	4.0	7	249.1±17.0	233.1–265.2	223–275	6.8
31	40	257.2±12.2	253.3–261.1	233–295	4.8	39	230.7±12.2	226.7–234.7	208–258	5.3
32	15	247.4±11.1	241.3–253.5	225–265	4.5	15	239.9±13.3	232.6–247.3	215–265	5.6
33	7	258.6± 8.7	250.6–266.6	245–270	3.3	7	247.9±11.1	237.6–258.1	234–264	4.5
34	4	262.5±11.9	243.6–281.4	250–275	4.5	4	267.5±13.2	246.5–288.6	255–285	4.9
35	4	267.2±11.6	248.8–285.7	252–280	4.3	4	269.0± 6.2	259.2–278.8	260–273	2.3
36	17	267.5± 7.7	263.6–271.5	258–283	2.9	18	250.7±14.4	243.5–257.9	220–277	5.8
37	18	253.9± 9.7	249.1–258.7	237–273	3.8	17	263.0±15.8	254.9–271.1	235–291	6.0
38	20	259.0±12.6	253.1–264.9	230–285	4.9	20	253.0±12.4	247.1–258.8	229–272	4.9
39	3	269.0±14.9	231.9–306.1	252–280	5.6	3	247.7± 2.5	241.4–253.9	245–250	1.0
40	37	264.4±10.2	261.0–267.8	238–281	3.9	35	251.1±13.8	246.4–255.9	224–273	5.5
41	9	267.2± 6.6	262.2–272.3	261–283	2.5	9	268.8±14.1	257.9–279.6	252–292	5.3
42*	4	272.0±16.8	245.3–298.7	255–294	6.2	3	286.7± 3.5	277.9–295.4	283–290	1.2
43	8	269.3± 8.9	261.8–276.7	252–280	3.3	7	258.3±11.6	247.6–269.0	242–272	4.5

Table 1 (Cont.)

Sample group	Head and body length					Tail length				
	n	M.±S.D.[a]	95% C.L.[b]	Extremes	C.V.[c]	n	M.±S.D.	95% C.L.	Extremes	C.V.
44	35	266.5± 8.7	263.5–269.4	252–289	3.2	34	258.3±18.8	251.5–265.1	215–295	7.3
45	11	261.8± 4.8	258.6–265.0	255–268	1.8	9	271.2±21.4	254.8–287.7	220–300	7.9
46	6	272.5±10.9	261.1–283.9	265–293	4.0	6	259.3±13.2	245.5–273.2	236–274	5.1
47	8	266.3± 7.4	260.0–272.5	255–275	2.8	8	241.9±11.9	231.9–251.9	225–260	4.9
48	8	262.0± 9.3	254.2–269.8	249–275	3.6	8	252.9±14.2	241.0–264.8	234–277	5.6
49	18	264.8±12.7	258.5–271.1	236–290	4.8	18	248.4±14.3	241.3–255.5	221–280	5.8
50	14	260.9±13.2	253.3–268.5	241–280	5.0	14	239.8±18.4	229.2–250.4	206–263	7.7
51	7	276.4± 9.9	267.3–285.6	260–290	3.6	7	251.4±12.8	239.6–263.3	230–270	5.1
52	10	269.5±14.2	259.3–279.7	245–295	5.3	9	246.8± 7.9	240.8–252.9	230–255	3.2
53	16	256.1±13.0	249.2–263.0	230–282	5.1	16	241.7±14.6	233.9–249.5	208–260	6.0
54	19	252.5±11.7	246.9–258.1	230–270	4.6	17	238.1±14.6	230.6–245.6	203–272	6.1
55	4	251.0± 3.4	245.6–256.4	247–255	1.3	3	246.7± 7.6	227.7–265.6	240–255	3.1
56	6	254.7±11.9	242.1–267.2	240–268	4.7	6	252.0±22.8	228.0–276.0	215–273	9.1
57	13	265.9± 6.4	262.0–269.8	255–278	2.4	13	263.8±12.3	256.3–271.2	249–285	4.7
58	18	272.5± 9.1	268.0–277.0	255–290	3.3	19	248.9±17.6	240.4–257.5	205–280	7.1

a. Mean ± Standard Deviation (n–1 formula).
b. 95% Confidence Limits of Mean (see Simpson, *et al.* 1960:160).
c. Coefficient of Variation.
*. Not represented in Figure 5.

Squirrels from the Sierra Madre del Sur of Guerrero (sample 31) have tails that are short relative to lengths of head and body, while those from the coastal plain near Acapulco (sample 29) have head and body similar to those in the nearby mountains, but have appreciably longer tails. Samples from intermediate elevations—near San Andrés de la Cruz and Agua de Obispo (samples 32 and 30, respectively)—are intermediate in tail length between the highland and lowland populations, but are closely similar to them in length of head and body.

LENGTH OF SKULL.—Geographic variation in cranial length (Fig. 6, Table 2) is irregular. Skulls average short in squirrels from Nuevo León and Tamaulipas, the Gulf lowlands of Tabasco and Chiapas, and from

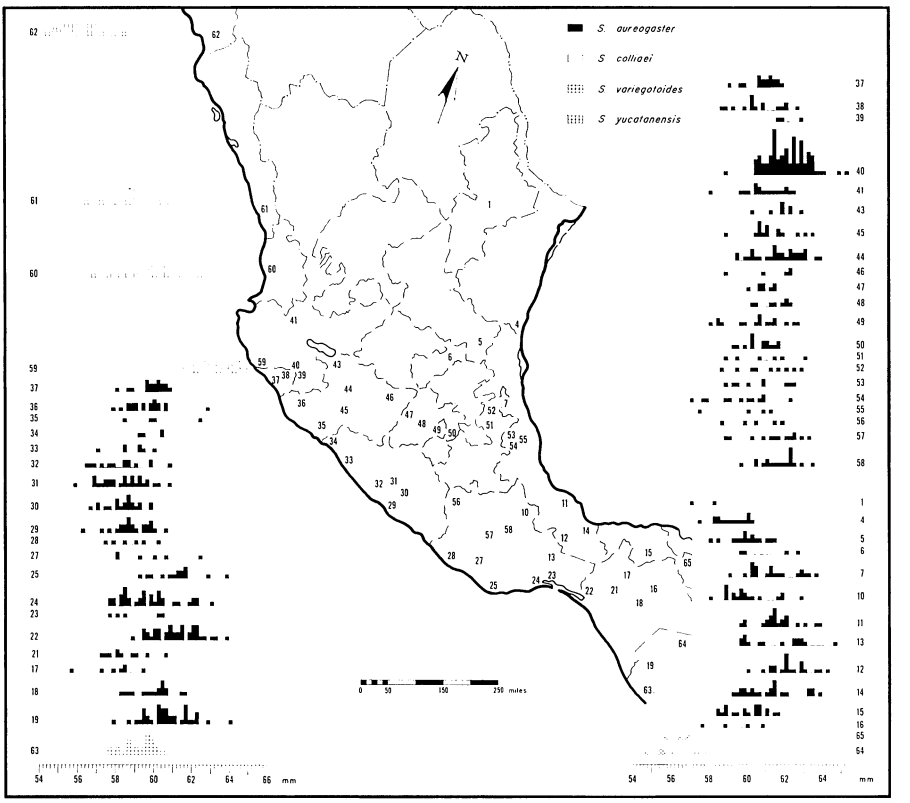


FIG. 6. Variation in cranial length in samples of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis.* For continuity, the histogram for sample 37 is repeated on the right side of the map. Numbers beside histograms correspond to numbered sample groups on the adjacent map and those in Figure 1. Each square equals one specimen. See Table 2.

TABLE 2

CRANIAL LENGTHS (MM) OF SAMPLES OF *Sciurus aureogaster, S. colliaei, S. variegatoides* and *S. yucatanensis* (SEE FIG. 6)

Species	Sample group	n	M.±S.D	95% C.L.	Extremes	C.V.
aureogaster	1	2	56.70± .85	49.08–64.32	56.1–57.3	1.50
	4	16	58.23± .83	57.78–58.67	56.6–59.3	1.42
	5	16	59.08± .94	58.57–59.58	57.1–60.6	1.60
	6	4	60.15±1.52	57.74–62.56	58.8–61.7	2.52
	7	22	60.49±1.21	59.95–61.02	58.2–62.8	2.00
	10	28	59.10±1.30	58.59–59.60	57.0–61.9	2.20
	11	24	60.68±1.04	60.25–61.11	58.7–63.0	1.71
	12	21	61.33±1.01	60.87–61.79	59.2–63.3	1.65
	13	17	60.61±1.56	59.81–61.41	58.7–63.7	2.58
	14	25	60.30±1.40	59.73–60.88	58.3–63.0	2.33
	15	21	59.10± .96	58.66–59.54	57.5–60.7	1.62
	16	4	58.43±1.44	56.14–60.71	57.9–60.0	2.46
	17	7	57.99±1.19	56.89–59.09	55.7–59.5	2.05
	18	18	60.10± .94	58.12–62.08	58.4–61.7	1.56
	19	41	61.80±1.23	60.41–61.18	57.9–64.2	2.03
	21	10	58.60±1.07	57.83–59.37	57.3–60.8	1.83
	22	42	61.24±1.17	60.87–61.61	58.9–63.9	1.91
	23	5	59.08±1.23	57.50–60.66	57.8–60.5	2.16
	24	39	59.76±1.41	59.80–61.11	57.8–63.2	2.39
	25	15	61.28±1.18	60.63–61.99	59.3–63.9	1.92
	27	6	59.85±1.73	58.03–61.67	58.1–62.6	2.90
	28	6	58.85±1.04	57.75–59.95	57.5–60.3	1.77
	29	24	58.96± .99	58.55–59.38	56.4–60.7	1.68
	30	22	58.50± .87	58.10–58.90	56.7–60.0	1.45
	31	30	58.51±1.18	58.07–58.95	55.9–61.0	2.02
	32	14	58.34±1.23	57.63–59.05	56.6–60.9	2.11
	33	7	58.96± .98	58.05–59.86	57.2–60.2	1.66
	34	4	59.98± .61	59.01–60.94	59.4–60.5	1.01
	35	4	60.30±1.70	57.60–63.00	58.5–62.6	2.82
	36	20	59.99±2.02	59.04–60.94	58.0–62.9	3.37
	37	18	59.99± .74	59.62–60.36	58.2–60.9	1.23
	38	16	59.72±1.18	59.09–60.35	57.8–61.7	1.98
	39	3	61.20± .62	59.65–62.75	60.7–61.9	1.02
	40	19	60.01±1.13	59.48–60.53	57.2–61.6	1.82
	41	88	61.14±1.13	60.90–61.38	58.0–63.9	1.85
	43	8	60.88± .78	60.22–61.53	59.3–61.9	1.28
	44	34	60.76±1.20	60.13–61.39	58.5–62.9	1.97
	45	16	60.38±1.10	59.79–60.96	59.6–62.5	1.83
	46	4	60.93± .69	59.82–62.03	59.9–61.4	1.14
	47	8	59.98± .50	59.55–60.40	59.1–60.6	.84
	48	8	60.58± .76	59.94–61.21	59.4–61.3	1.26
	49	17	59.58±1.43	58.84–60.32	57.1–61.8	2.43

TABLE 2 (Cont.)

Species	Sample group	n	M.±S.D	95% C.L.	Extremes	C.V.
	50	15	59.71± .77	59.28–60.14	58.3–60.8	1.30
	51	6	60.02±1.58	58.36–61.68	58.0–62.2	2.63
	52	9	60.10±1.44	58.99–61.21	57.7–61.9	2.40
	53	9	59.80±1.36	58.76–60.84	58.0–61.5	2.27
	54	12	58.69±1.55	57.71–59.67	56.2–61.3	2.63
	55	4	59.03±1.76	56.23–61.82	56.5–60.4	2.97
	56	5	59.54±1.23	58.01–61.07	57.8–60.9	2.07
	57	13	60.55±1.38	59.71–61.38	57.9–62.4	2.28
	58	16	60.77± .95	60.31–61.22	58.7–62.5	1.56
colliaei	59	34	62.88±1.09	62.50–63.26	61.3–64.9	1.73
	60	22	59.87±1.21	59.34–60.41	57.0–62.6	2.02
	61	19	59.27±1.22	58.68–59.86	56.5–61.3	2.06
	62	29	56.05± .91	55.71–56.40	54.4–58.6	1.62
variegatoides	63	33	59.38± .81	59.10–59.65	57.8–60.8	1.37
yucatanensis	64	8	55.34±1.13	54.39–56.29	53.7–56.9	2.05
	65	3	55.40± .56	54.02–56.78	54.8–55.9	1.01

the Pacific lowlands and Sierra Madre del Sur of Guerrero, and there is a gradient between these and adjacent samples to the north or to the south.

SPHENOPALATINE VACUITIES.—Frequency of occurrence and size of sphenopalatine vacuities vary geographically (Fig. 7). They occur infrequently in samples from northwestern México and are absent in most specimens from southern Nayarit, Jalisco, Colima, and western Michoacán; when present they are small, averaging about 0.5 mm, as in *S. colliaei* of the same region. Southward and eastward from northwestern México there is a gradual increase in frequency of occurrence and in size (mean diameters eventually exceed 2.0 mm). Variation in frequency and size of the vacuities throughout the range of *aureogaster* beyond Michoacán is irregular, but vacuities are usually present and large in populations near the eastern limits of the range and smaller and less frequent in adjacent populations of *S. yucatanensis* and *S. variegatoides*.

PELAGE CHARACTERS

CROWN.—Amount of pigmentation of the crown varies geographically (Fig. 8). The highest incidence of animals with frosted-black and black crowns is in northwestern México: black on many examples from Ameca

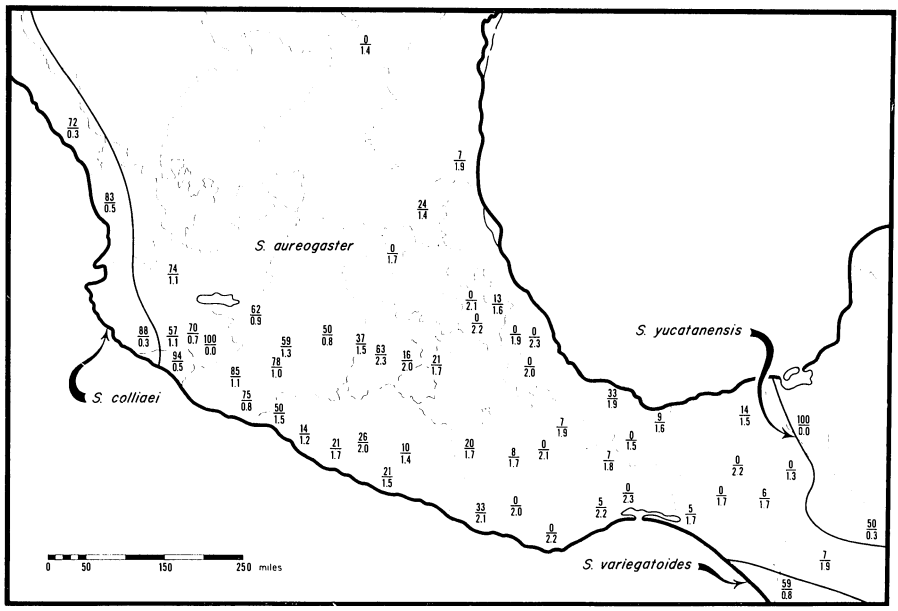


FIG. 7. Frequencies of occurrence and diameters of sphenopalatine vacuities in samples of *Sciurus aureogaster, S. colliaei, S. yucatanensis,* and *S. variegatoides.* Upper number of each symbol is the per cent of the sample with vacuities absent; lower number is mean diameter (mm) of those vacuities present in each sample.

(sample 41), on the majority of specimens from the Nevado de Colima (sample 40), and on many from areas near Mazamitla and Patamban (samples 42 and 43, respectively). The shading of the crown is gradually diluted to the northeast, east, and southeast until in Tamaulipas, San Luis Potosí, Querétaro, and through the Isthmus of Tehuantepec into the highlands of Guatemala, crowns typically are grayish suffused with orange, and blackish crowns are infrequent.

Partially melanistic squirrels from southern Veracruz and Tabasco have black crowns, but the incidence of gray phases is low.

EYE RING.—Eye rings are pigmented in the majority of samples (Fig. 9). They tend to be most highly colored (usually orange or orange-red) in squirrels of the Gulf lowlands and uplands from Tamaulipas to Tabasco. Elsewhere, color varies: usually buffy in the highlands of Chiapas, grizzled orange in the highlands of Guatemala; variously white to orange in the Pacific lowlands and highlands of Chiapas, Oaxaca, and Guerrero; and white to pale orange in samples from the Pacific coastal plain and the highlands of southwestern Guerrero north to Colima. White eye rings predominate in fewer samples, but are characteristic of squirrels from high-

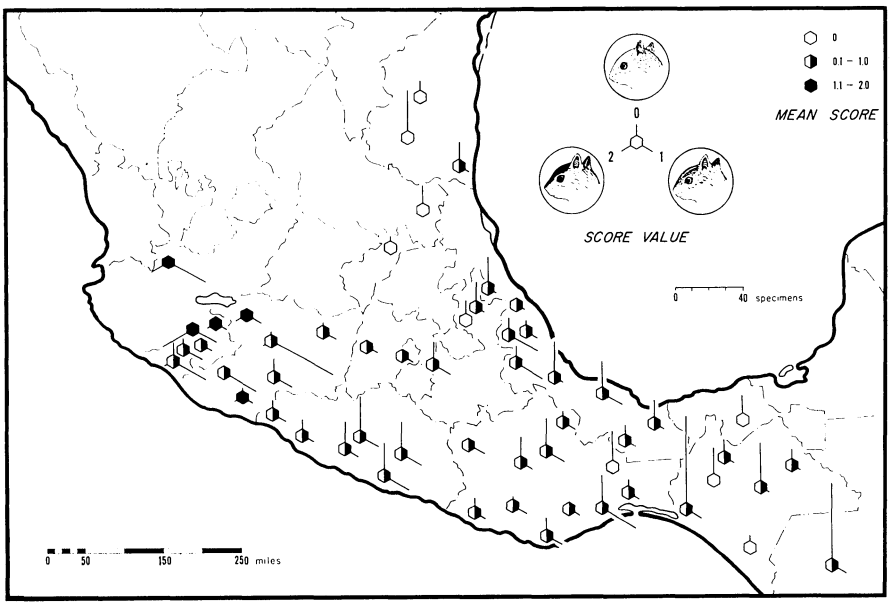


FIG. 8. Amount of pigmentation of the crown in samples of non-melanistic *Sciurus aureogaster*.

lands and middle elevations of Nayarit, Jalisco, central Michoacán, and western and northern Oaxaca.

POSTAURICULAR PATCHES.—Postauricular patches are usual in *S. aureogaster* (Fig. 10). Small ear patches (score 1) characterize samples from the Gulf lowlands and highlands from Tamaulipas southward to Tabasco, Chiapas, and Guatemala. In the altitudinal range from sea level to more than 11,000 feet, there is no obvious correlation between size of postauricular patches and habitat or environmental factors related to altitude. Large white ear patches (score 2) are characteristic of highland populations of the southern and western margins of the Mexican Plateau, central Michoacán, Guerrero, and western and northern Oaxaca. The remaining samples, i.e., those from southern Nayarit and from the Pacific lowlands (Colima to Oaxaca), are variable with moderate and large postauricular patches occurring in nearly equal frequencies in many samples.

NAPE AND RUMP PATTERN.—Frequencies of occurrence, size, and color of nape and rump patches are geographically variable (Fig. 11). Large nape and rump patches are characteristic of squirrels of the Cordillera Volcánica from Jalisco and Nayarit eastward to central Veracruz and Hidalgo, and of animals of the lowlands and highlands of Michoacán,

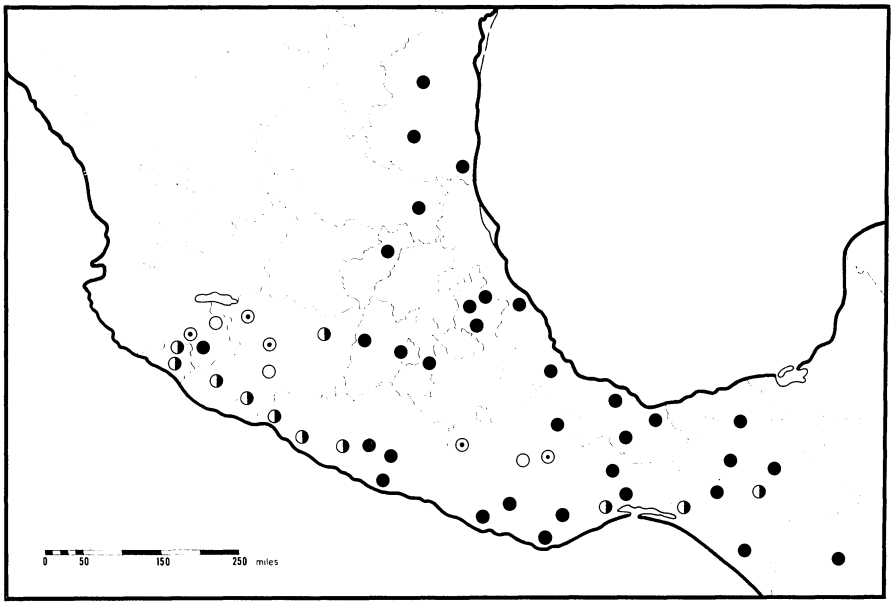


FIG. 9. Color of eye ring in samples of non-melanistic *Sciurus aureogaster*. Empty circles, eye ring white in all examples; filled circles, eye ring pigmented (pale buff to orange-red) in all specimens; dots enclosed by circles, eye ring white in over 50 per cent of specimens; and half-filled circles, eye ring pigmented (usually buff to pale orange) in over 50 per cent of specimens.

Guerrero, and western Oaxaca. Few examples from those regions have neither nape nor rump patch. In eastern México near the Isthmus of Tehuantepec, the nape patch is large and conspicuous and may join the shoulder and costal areas (Gulf regions of the Isthmus); the rump patch is usually absent, small at the most. Farther east in Chiapas, Tabasco, and Guatemala, nape and rump patches may be inconspicuous or absent.

Geographic variation in area of nape and rump patches is seen in two geographical transects: one extending from the western edge of the Mexican Plateau in Nayarit and Jalisco eastward across the Cordillera Volcánica to central Veracruz, thence northward through the lowlands of northern Veracruz and southern Tamaulipas; the other traversing the Pacific lowlands and uplands from Colima southward to the Isthmus of Tehuantepec, thence into the uplands of eastern Chiapas and Guatemala. Squirrels from the Cordillera Volcánica (Nayarit and Jalisco to Veracruz) typically have large nape and rump patches (Fig. 12). In this segment of the transect there is a low incidence of individuals with no nape patch and a slightly higher incidence of those without rump patches. Prominent nape and rump patches

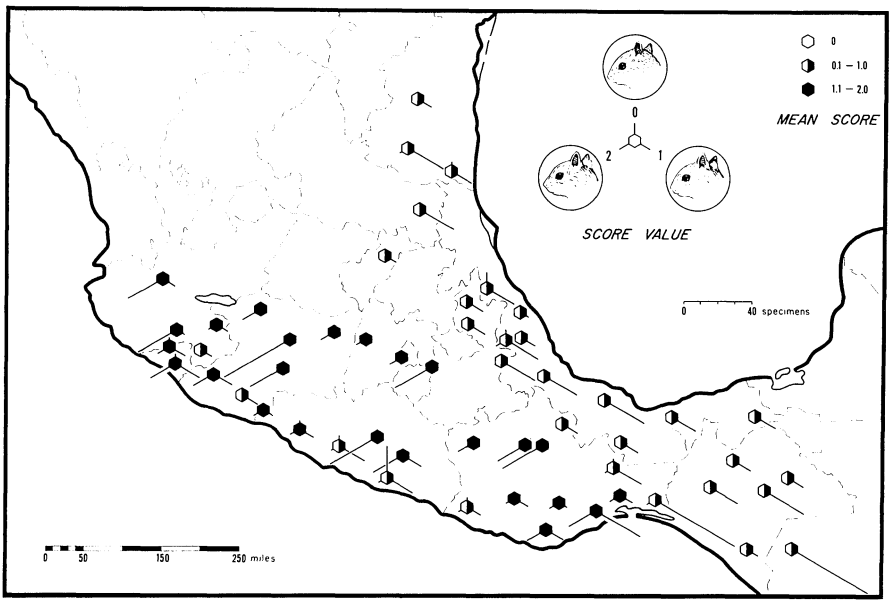


FIG. 10. Size of postauricular patches in samples of non-melanistic *Sciurus aureogaster*.

are characteristic also of the animals from middle elevations near Xico and Jalapa. In lowlands to the north, rump patches may be slight or absent and the nape patch large (Papantla region of Veracruz) or nape patch small or absent and the rump patch infrequent (samples north of Papantla).

As is characteristic of samples from the Cordillera Volcánica, large nape and rump patches are seen in squirrels from the Pacific lowlands and adjoining highlands from Colima to western Oaxaca (Fig. 13); some expression of a nape patch is present in all samples. In the region from southern and eastern Oaxaca to southwestern and northwestern Chiapas the nape patch is also present, but its area is more variable and the incidence of the rump patch decreases rather abruptly—typically, animals from those regions do not have rump patches, but when present they are small. In the highlands of Chiapas and Guatemala the rump patch occurs infrequently and the incidence of the nape patch, often diffuse and inconspicuous, decreases.

Nape and rump patches are deeply pigmented (orange-red or chestnut) on squirrels from the Pacific lowlands and highlands, the middle elevations of northern Puebla, the highlands of central Veracruz, and throughout the Isthmus of Tehuantepec. In these the areas stand bold and conspicuous against grayish or whitish backs; elsewhere they are more subdued buff or

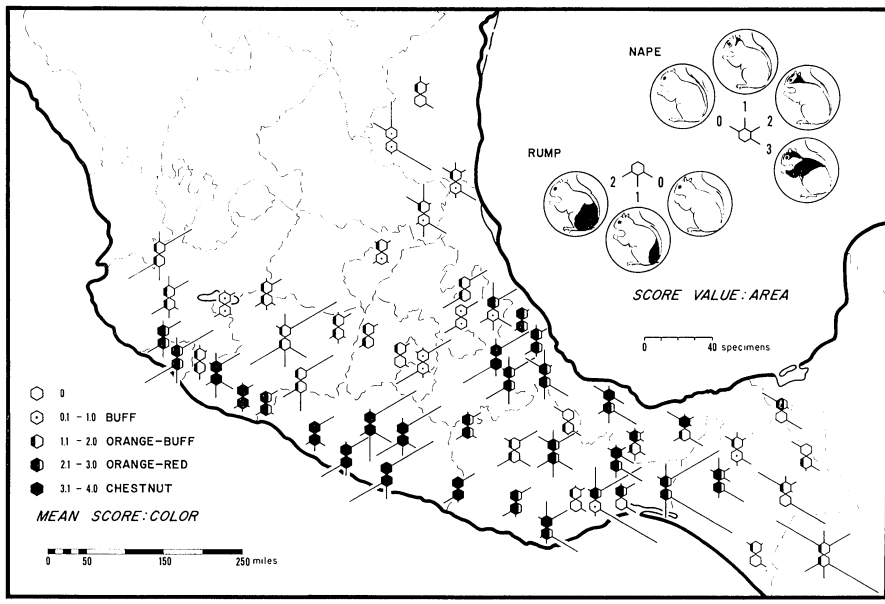


FIG. 11. Size and average color of nape and rump patches in samples of non-melanistic *Sciurus aureogaster*. Upper hexagon of each pair symbolizes nape patch, lower hexagon refers to rump patch. Lines radiating from the top and bottom sectors of each hexagon indicate frequencies of patch-size. Shading inside the hexagons designates mean color score for each patch (i.e., the mean of only those specimens with patches). For example, refer to the sample from Nayarit and Jalisco (first pair of hexagons in upper left-hand corner). Radiating lines at the top and bottom of that symbol indicate that all specimens have nape and rump patches and that those patches are broad (score 2) in most specimens. Shading inside the hexagons shows the average color of nape and rump to be orange-buff.

light orange in hue, contrasting less with the color of the back. The patches are partially melanistic or black in some examples from the Nevado de Colima (sample 40), and melanistic in a few from southeastern Veracruz.

COLOR OF UNDERPARTS.—Color of underparts grades from white to orange-red and chestnut (Fig. 14). Orange-red and chestnut characterize squirrels of southern Tamaulipas, southeastern San Luis Potosí, Veracruz, Tabasco, northern Chiapas, eastern Oaxaca, and central Guerrero. White underparts are typical of those from southern Nayarit, Jalisco, Colima, and southern Michoacán. Samples from other areas range from white to chestnut and frosted grayish-black. White grades to orange over a wide geographic area. Whitish-orange appears at a low frequency in central Michoacán and darker hues predominate in samples from eastern Michoacán and western

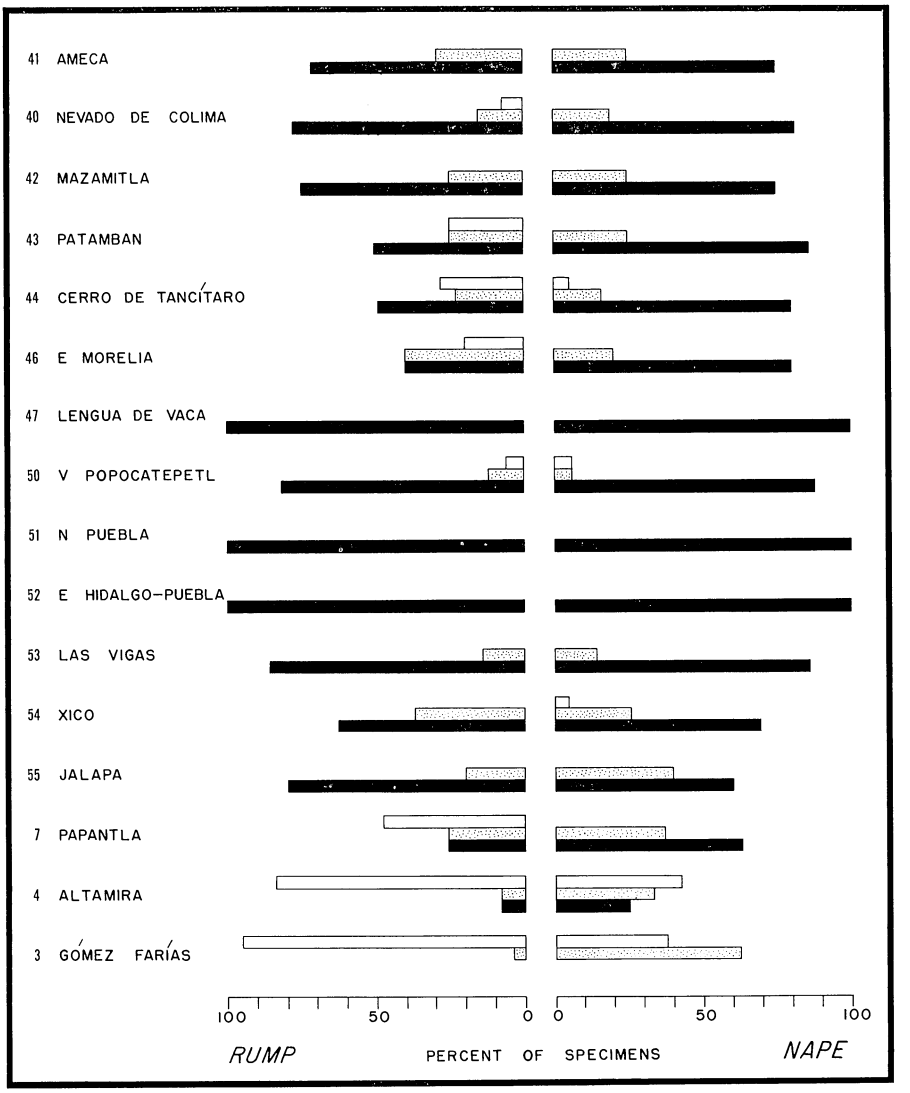


FIG. 12. Geographic variation in area of nape and rump patches in samples of *Sciurus aureogaster* as explained in text. Patches are indicated as absent (score 0) by unfilled bars, intermediate in area (score 1) by stippled bars, and expansive (score 2) by solid bars. Color is not indicated. Numbers at left correspond to those in Figure 1 which designate sample groups. Number of specimens per sample group is indicated in Figure 11.

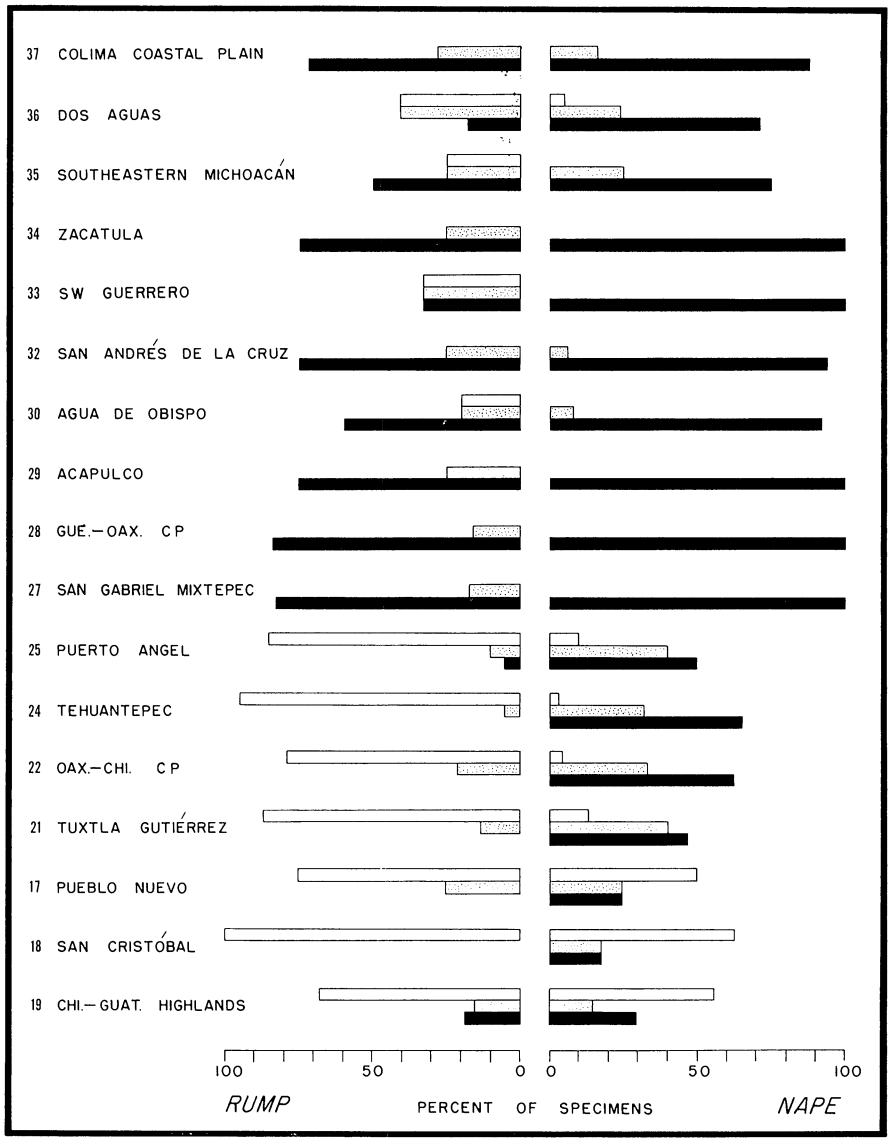


FIG. 13. Geographic variation in area of nape and rump patches in samples of *Sciurus aureogaster*. See legend of Figure 12 for explanation.

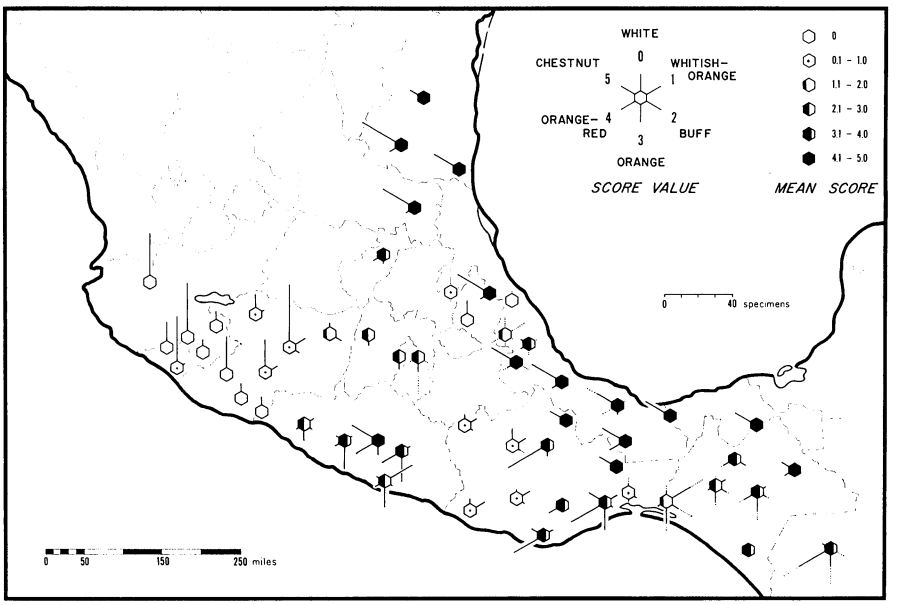


FIG. 14. Color of underparts in samples of nonmelanistic *Sciurus aureogaster*. Solid radiating lines indicate number of specimens with solidly pigmented underparts. Dotted lines indicate specimens with black-flecked underparts. For example, the sample from Chiapas and Guatemala (extreme lower right-hand corner) contains specimens with both solid and black-flecked color. The mode is orange-red (score 4); of the 27 specimens receiving that score, 17 are solid orange-red and ten are flecked with black.

Estado de México; farther eastward, between western Estado de México and northern Puebla, orange is seen in all specimens and apparently is fixed in the populations. South of the Mexican Plateau in southern Puebla, eastern Guerrero, and western Oaxaca, white or buff occurs in various frequencies; farther westward and eastward some shade of orange occurs in all samples.

There is black on the underparts in most samples from areas east of Estado de México. For example, in many specimens from the Pacific end of the Isthmus of Tehuantepec and from areas to the east in Chiapas and Guatemala the underparts are whitish-orange to orange-red speckled with black and in some (e.g., those from near Cintalapa and Tonalá) they are frosted gray. Speckled underparts also occur in samples from the northern end of the Isthmus near Lago de Catemaco, and they increase in frequency to the northwest until they are black-flecked in most squirrels from central Veracruz and northern Puebla. Black flecking is characteristic of squirrels from the slopes of Volcán Popocatepetl but is not a conspicuous feature in samples from south and west of that Volcán.

SHOULDER AND COSTAL PATTERN.—Occurrence and size of the shoulder and costal pattern vary (Fig. 15). This pattern is absent in squirrels from Nayarit, Jalisco, Colima, Michoacán, Estado de México, Distrito Federal, northern Puebla, and southeastern Hidalgo, and usually from Guerrero and western Oaxaca; a small part of the total pattern (score 1) occurs in a few examples. The pattern is best developed (scores 4 and 5) in those from the lowlands of Tabasco, eastern Veracruz, and northeastern Oaxaca. In most of these squirrels the orange of the pattern either extends broadly over the front appendages, shoulders, sides of the chest, and across the back in the shape of a saddle, or covers the entire dorsum from the nape and sides of the neck to the rump and flanks. One example (KU 67589, from northern Oaxaca), the extreme of all the specimens, is reddish everywhere except on the rostrum, cheeks, throat, margin of rump, and dorsal surface of tail. Smaller shoulder and costal patches are typical of samples from Tamaulipas, northern Veracruz, and southern San Luis Potosí. Pattern 3 is most frequent in those; I have seen no examples that approach pattern 5. Squirrels from Querétaro, central Veracruz, southern and central Oaxaca, Chiapas, and Guatemala are variable in occurrence and size of the pattern. Gradations from no pattern to pattern 5 are found in samples from Jalapa (sample 55), above Xico (sample 54), and from near Laguna Catemaco (sam-

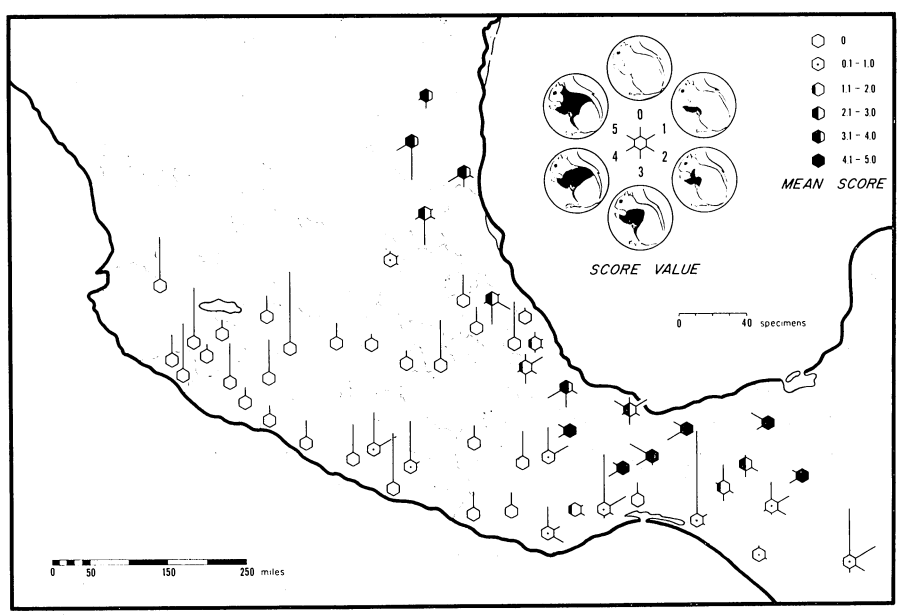


FIG. 15. Size of shoulder and costal pattern in samples of non-melanistic *Sciurus aureogaster*.

ple 11). Similar gradations characterize the samples from eastern Oaxaca, through the Pacific end of the Isthmus of Tehuantepec, and across central Chiapas into the highlands of Guatemala.

COLOR OF FEET.—In most samples the fore and hind feet are speckled with black (Fig. 16). White feet, some lightly flecked with black (scores 0 and 1), are seen in the samples from the southeastern margin of the Mexican Plateau in Michoacán and Jalisco, the Pacific lowlands from Michoacán to western Oaxaca, and in the highlands of Guerrero and Oaxaca. White feet are most frequent in samples from central Michoacán, from the mountains west and southwest of Chilpancingo in Guerrero, and from the highlands west of Oaxaca de Juárez and north of there in the Sierra de Juárez. Elsewhere, in the northern Gulf lowlands and highlands of Chiapas and Guatemala, for example, most squirrels have dark feet, between white flecked with black and frosted-black (scores 1 and 2). Melanistic feet (score 4) are most frequent along the central Gulf lowlands and the highlands of central Veracruz and northern Puebla.

COLOR OF TAIL.—Color of the underside of the tail varies geographically (Fig. 17). Grayish tails are characteristic of the white-bellied squirrels of Nayarit, Colima, eastern Michoacán, and extreme southwestern Guerrero;

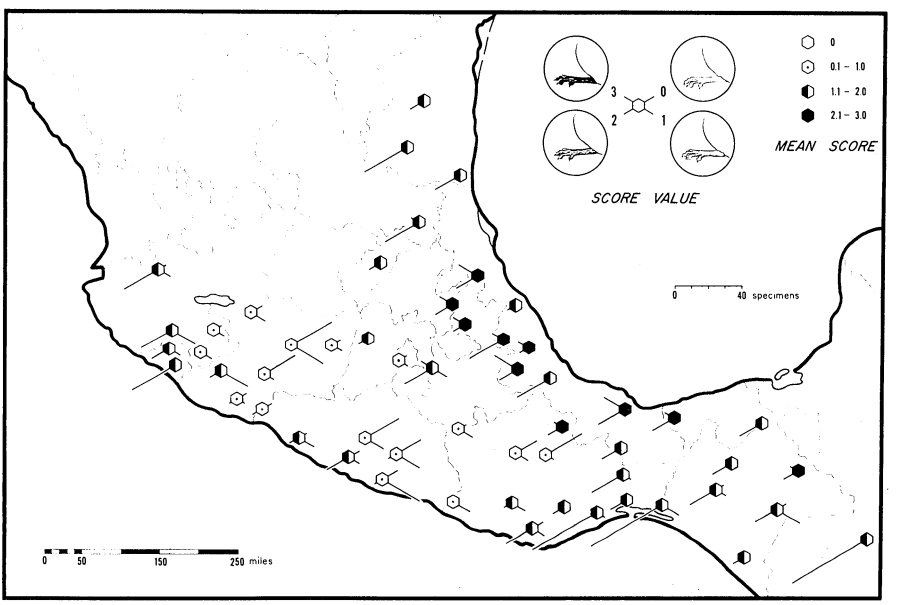


FIG. 16. Amount of pigmentation of the feet in samples of non-melanistic *Sciurus aureogaster*.

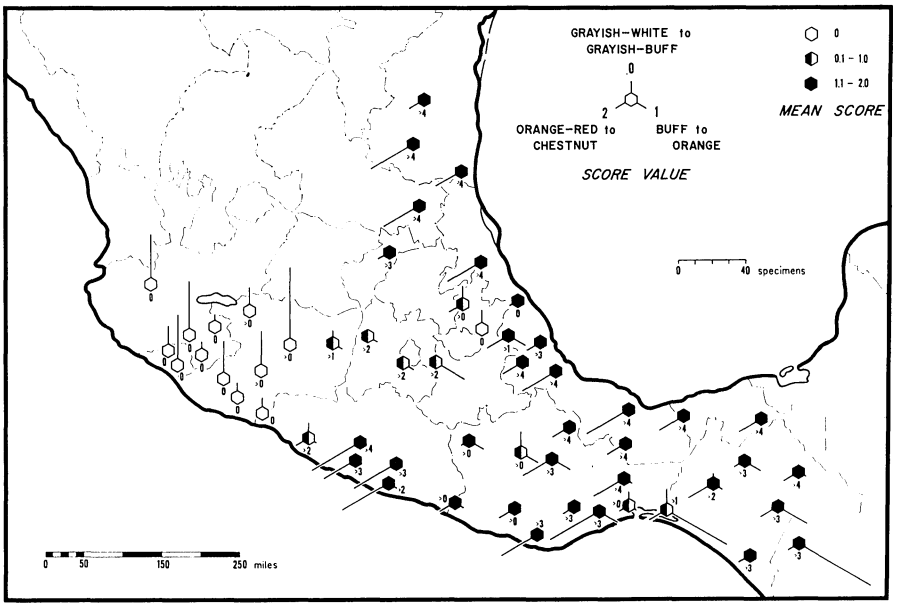


FIG. 17. Color of underside of tail in samples of non-melanistic *Sciurus aureogaster*. Numbers beside each symbol indicate mean color scores for underparts as follows: 0, white or frosted grayish-black; > 0, white to whitish-orange; > 1, whiitsh-orange to buff; > 2, buff to orange; > 3, orange to orange-red; > 4, orange-red to chestnut; see Figure 14.

though lightly pigmented underparts occur in the samples from central Michoacán, tails are still grayish. Orange-red to chestnut is dominant in the red-bellied squirrels of the Gulf lowlands and middle elevations from Tamaulipas to Tabasco. Animals of most of Guerrero, Oaxaca, and parts of Chiapas also have orange-red or chestnut tails, but in several regions there is no correlation between color of tail and that of underparts.

Squirrels with grayish to deep orange or chestnut tails occur from eastern Michoacán across the Cordillera Volcánica, in southern Michoacán, the Pacific lowlands of southwestern Guerrero, and the highlands of western Oaxaca. In these regions the frequency of orange underparts increases over that of white. Samples from Chiapas and the highlands of Guatemala are mostly intermediate in tail coloration between the extremes of grayish-white and chestnut; in some of these samples there are low frequencies of these extremes.

LENGTH AND DENSITY OF PELAGE.—Variation in length and thickness of pelage is distributed independently of other pelage features and appears to be correlated with environmental factors—presumably temperature and

humidity are important. Squirrels living in the lowlands and foothills are clothed with short thin pelage; the overhairs are short (10–15 mm long on the back) and the underfur is sparse. This type of pelage is seen in squirrels from the Gulf coastal plain from Neuvo León and Tamaulipas south and east to eastern Tabasco and Chiapas, the Pacific coastal plain and foothills from Colima to the Isthmus of Tehuantepec in southwestern Chiapas, the low foothills of western Chiapas, and the Balsas-Tepalcatepec area. Animals living in highland habitats, usually above 3000 feet, have longer and thicker pelage. The overhairs are longer (20–25 mm on the back) and the underfur is thicker. The pelage of the head and body is often luxuriant and soft and the tails are much bushier than those of squirrels from the lowlands. This condition is typical of squirrels from the edge of the Mexican Plateau and elsewhere throughout the highlands of México and Guatemala.

Wherever adequate samples are available from regions of transition between lowland, warm habitats that are either tropical or semi-arid and highland environments that are cold and wet, the pelage varies gradually from short and sparse to long and dense, respectively. This also obtains in highland environments; length and density vary with local conditions.

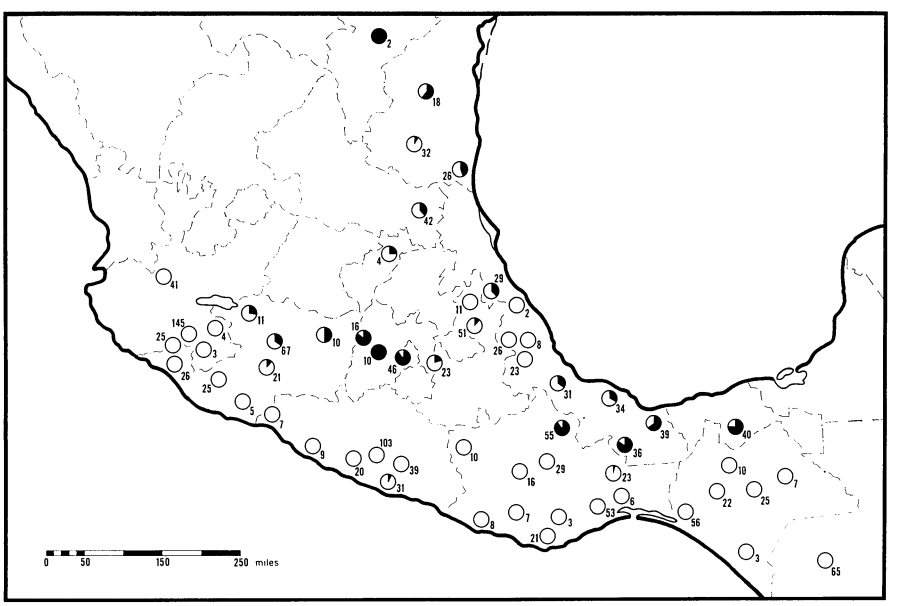


FIG. 18. Frequency of melanism in samples of *Sciurus aureogaster*. Area of shaded sector of each circle is proportional to frequency (per cent) of melanistic specimens per sample. Numbers indicate sample sizes.

Squirrels from highland, dry pine-oak forests (Ameca, sample 41, for example)—though their pelage is longer and denser than that in animals from the lowlands—do not have the luxuriant, denser pelage that is typical of squirrels living in colder and wetter forests, for example those of the Cordillera Volcánica. I cannot detect such differences between pelages from dry and humid forests of the lowlands.

MELANISM.—Melanistic phases occur in varying frequencies in populations of *Sciurus aureogaster* along the Cordillera Volcánica and throughout the Gulf coastal plain and uplands of eastern México, and are absent or rare elsewhere in the range of the species (Fig. 18). Samples from the following areas are primarily bimodal in frequency distribution of gray and black phases: central Michoacán, northeastern México (Nuevo León, Tamaulipas, San Luis Potosí, Querétaro, and northern Veracruz), and eastern Tabasco. In others partially melanistic specimens may comprise most of the sample (as in series from the Cordillera Volcánica in Estado de

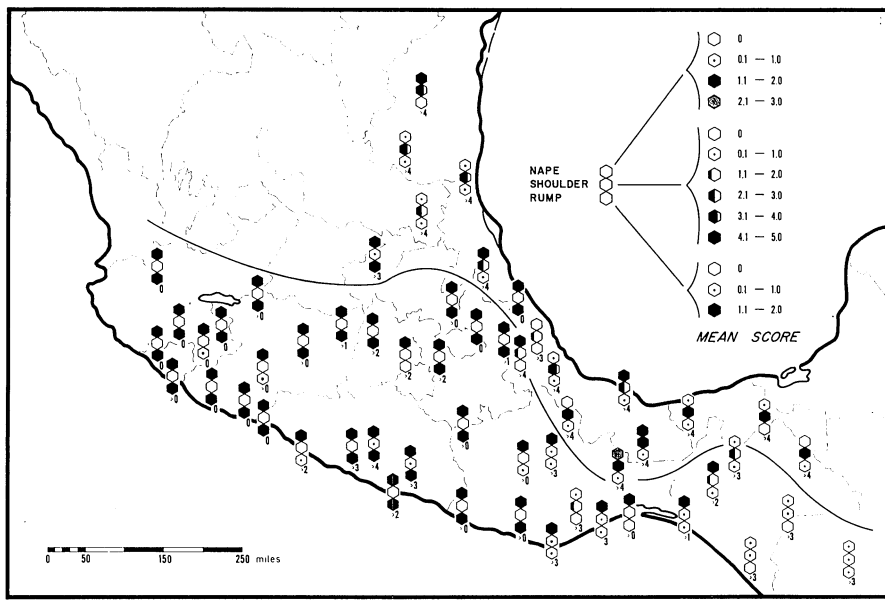


FIG. 19. Distribution of principal pelage features in samples of non-melanistic adult *Sciurus aureogaster*. Average size of nape, rump, and shoulder patches, and color of underparts are indicated for each sample group. Curved lines roughly separate samples of the Aureogaster (eastern México) and Socialis (western México, Guatemala) segments. Numbers indicate mean color scores for underparts as follows: 0, white or grayish-white; > 0, white to whitish-orange; > 1, whitish-orange to buff; > 2, buff to orange; > 3, orange to orange-red; > 4, orange-red to chestnut; see Figure 14.

México, Distrito Federal, and Morelos) or they may form a smaller part of it (as in those from eastern Veracruz, northeastern Oaxaca, and western Tabasco).

PATTERN SUMMARY.—Clearly, each trait is individually and geographically variable. Variation in many characters is distributed in discordant geographic patterns. Nevertheless, on the basis of a combination of features the samples fall into two groups that appear to be natural assemblages. Each of these groups is morphologically defined using principally the nape and rump patches, shoulder and costal patches, and coloration of underparts. The geographic distribution of these "principal" pelage patterns is illustrated in Figure 19. Portrayed there is the average expression, per sample, of those pelage traits. Although that figure is useful in illustrating geographic distribution of average patterns, it does not convey the actual pattern composition of each sample. Therefore, I segregated the variation in size of nape and rump patches, shoulder and costal patches, color of underparts, and frequency of melanism into eleven "patterns." These are described in Tables 3 and 4 and illustrated in Figure 20.

TABLE 3
DESCRIPTION OF PATTERNS IN *Sciurus aureogaster*

Pattern	Upper parts	Underparts
1	small or expansive (scores 1 or 2) *nape and rump patches*	
2	small or expansive (scores 1 or 2) *nape patch,* no rump patch	white or frosted-gray (scores 0 or –0)
3	no nape or rump patches, dorsum essentially unpatterned	
4	small or expansive (scores 1 or 2) *nape and rump patches*	
5	small or expansive (scores 1 or 2) *nape patch,* no rump patch	
6	no nape or rump patches, dorsum without pattern	
7	both *nape and rump patches* (scores 1 or 2) with *shoulder and costal patch* (scores 1 to 5)	pigmented: whitish-orange to chestnut (scores 1 to 5), including black speckling
8	*shoulder and costal patch* (scores 1 to 5), *nape patch* (scores 1 or 2), no rump patch	
9	*shoulder and costal patch* (scores 1 to 5), *rump patch* (scores 1 or 2), no nape patch	
10	*shoulder and costal patch* (scores 1 to 5), no nape or rump patches	
11	partial to complete melanism, usually obscuring any basic pattern	partially to completely melanistic

TABLE 4

FREQUENCY OF PATTERNS (SEE FIG. 20)

Sample group	Patterns											
	1	2	3	4	5	6	7	8	9	10	11	n
1											2	2
2								5			10	15
3							1	14		9	2	26
4							2	5		5	12	24
5							7	5	1	7	11	31
6						1	2				1	4
7							10	9			10	29
8	1											1
9							3	6	3	6	4	22
10									1	5	47	53
11				2		1	3	10	2	4	11	33
12							3	2	1	1	29	36
13							3	12		2	2	19
14								4	3	5	24	36
15								1		9	26	36
16									1	5		6
17					1		2	1		4		8
18					2	7		6		8		23
19				7	1	19	6	5	1	8		47
20					1	1				1		3
21		1			5	2	2	5				15
22		3		10	35			3		1		52
23		4			2							6
24					26	1	1	12				40
25				2	8	1		8		1		20
26								1		2		3
27	1			5								6
28	2			5								7
29				28							2	30
30				17	5		2					24
31				11		6	7	4				28
32				16								16
33				6	3							9
34	3	1										4
35	3	1										4
36	10	7										17
37	24			1								25
38	10											10
39	3											3
40	25	2										27
41	24											24

TABLE 4 (Cont.)

Sample group	Patterns											
	1	2	3	4	5	6	7	8	9	10	11	n
42	3	1										4
43	5	2		1							3	11
44	23	8	1	6	1	1					15	55
45	8	7		2	1						3	21
46	1	1		3							5	10
47				2							13	15
48											8	8
49					3						47	50
50				16	1						3	20
51	7											7
52	9			2								11
53	5			16								21
54				3			16					19
55				2			3					5
56	2			4								6
57	4		2	3	4	1						14
58				4	3	6	9					22

The results of my analysis of morphological variation lead me to conclude that all samples, drawn from populations that have been considered as five species—*aureogaster, poliopus, socialis, griseoflavus,* and *nelsoni*—represent one species (*S. aureogaster*) comprised of two major "groups" with geographic variants in each. One group, long referred to under the name *Sciurus aureogaster,* I here refer to as the Aureogaster Group (samples 1–16). The other group—known by the names *socialis, poliopus, griseoflavus, nelsoni,* and *frumentor*—are termed the Socialis Group (samples 17–58). Morphological differences between the geographic variants within each group are usually average and each is morphologically connected through gradual character changes. The pattern of intergradation between the two major groups, however, suggests a secondary contact of once geographically and ecologically isolated populations. Aspects of this geographic variation and intergradation are subjects of the following sections.

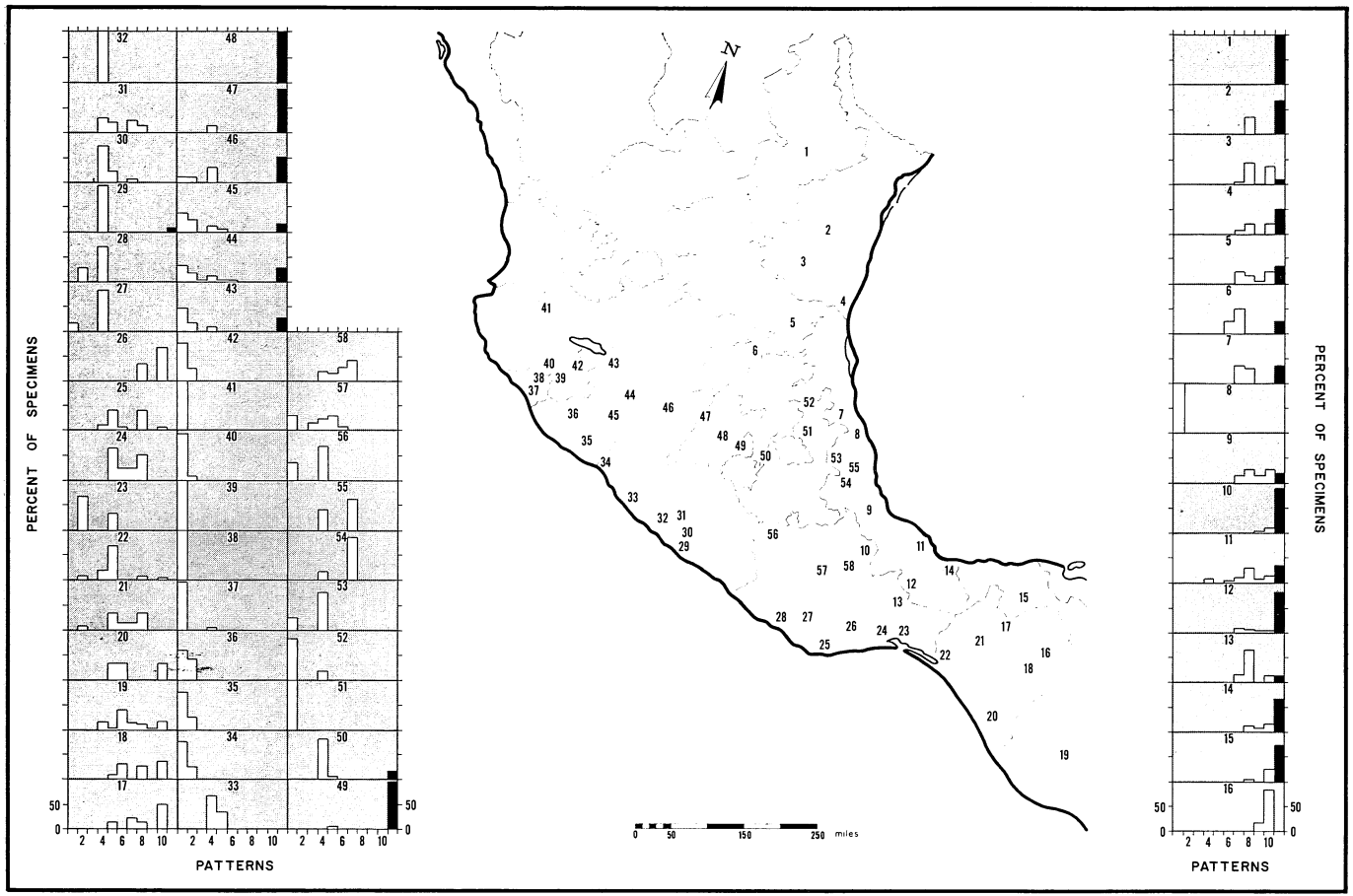


FIG. 20. Percentage of 11 "patterns" in 58 samples of adult *Sciurus aureogaster*. Based on data from Table 4. In each rectangle the empty bars are non-melanistic patterns, solid bars represent melanistic phases (Table 3), and the number at the top refers to the geographic origin plotted on the adjacent map.

GEOGRAPHIC VARIATION AND INTERGRADATION

This section focuses on characteristics of the Aureogaster and Socialis groups, and on intergradation between and within those groups.

AUREOGASTER GROUP

DISTRIBUTION.—(Fig. 33 and localities listed in Appendix) the Eastern Gulf lowlands and uplands from the vicinity of General Terán in Nuevo León and San Fernando in northeastern Tamaulipas southward and eastward through Tamaulipas, eastern San Luis Potosí, northeastern Querétaro, (probably the tropical lowlands of eastern Hidalgo), Veracruz, northeastern Puebla, and northern Oaxaca to Monte Cristo in eastern Tabasco and Laguna Ocotal in the Selva Lacandona of northeastern Chiapas. Primarily lowland in distribution; altitudinal range usually below 5000 feet. An exception is the population from Pinal de Amoles, about 8000 feet, in the mountains of northeastern Querétaro.

HABITAT.—Primarily arid or humid tropical broadleaf forests (semideciduous, semi-evergreen, and evergreen), but also dry oak-pine woodland and deciduous riparian associations in northeastern México. Apparently absent from virgin cloud forests. Specimens have been collected in the following situations: tropical deciduous and tropical evergreen forests throughout eastern México in Tamaulipas, Veracruz, northeastern Puebla, and Oaxaca; in regions where those forests are extensive, or where they dendrify as tall gallery forests along streams and rivers through wet lowland savannas, thorn forests or thorn scrub (particularly along the coastal plain in Tamaulipas and northern Veracruz), or ramify as riparian forests in canyons along the flanks of the Sierra Madre Oriental, Mexican Plateau, and eastern escarpments to the south; tropical rain forest in eastern Veracruz, Chiapas, and Tabasco, but primarily where the original forest has been cut and second growth predominates; second-growth tropical forest either adjoining or interrupted by milpas (south of Catemaco, for example), cacao plantations (near Monte Cristo, Tabasco), or nut-palm forests (Tabasco); pine forest near Pinal de Amoles in northeastern Querétaro and dry pine and oak woodland at higher elevations of the Sierra de Tamaulipas (near Acuña and Santa María); oak and other hardwood riparian bottom lands in canyons that dissect the flanks of the Sierra Madre Oriental (near General Terán in Nuevo León); and the Sierra San Carlos (Marmolejo, Tamaulipas).

GENERAL DESCRIPTION.—Medium-sized squirrels (Tables 1 and 2) in which patterns 8, 10, and 11 (Table 3) are usual. Chin, throat, and cheeks usually whitish-gray; eye rings orange or orange-red; an orange wash from behind eyes to bases and anterior edges of the pinnae in some; crown frosted-gray (same color as back), sometimes suffused

with black; whitish postauricular patches small and usually inconspicuous; nape patches in many samples, but usually an indistinct suffusion of color rather than sharply defined; rump patches usually absent, when present, an inconspicuous buffy or orange wash; shoulder and costal pattern usually expansive, orange through chestnut; feet frosted-black or black, often washed with color of underparts which are usually orange-red or chestnut; tail white dorsally with black suffusion; midventral strip of tail usually chestnut, often melanistic; back varies from whitish-gray to frosted bluish-gray, sometimes suffused with orange. Melanistic phases are common.

GEOGRAPHIC VARIATION AND INTERGRADATION.—Characters showing geographic variation are external and cranial dimensions, size of shoulder and costal patch, frequencies and sizes of nape and rump patches, frequency and degree of melanism, and tone (light or dark) of the pelage. Other features of the pelage that were analyzed, such as size of postauricular patches, color of eye rings, color of underparts and tail, and length and density of pelage, show little or no geographic variation.

Some variations in external and cranial dimensions are distributed in geographic patterns. Squirrels from the northern (Nuevo León and Tamaulipas) and eastern (eastern Tabasco) segments of the range average smaller in most external and cranial lengths than animals from intervening regions (Tables 1 and 2; Figs. 5 and 6). Variation in other proportions and features (including frequency of occurrence and diameter of sphenopalatine vacuities) of the skull, as Kelson (1952:246) noted, apparently are not correlated with geography.

The main pelage features of the Aureogaster Group are best developed and least variable in populations of the northern (Tamaulipas and eastern San Luis Potosí) and southeastern (northeastern Oaxaca, eastern Veracruz, Tabasco, and northeastern Chiapas) segments of its range. Non-melanistic squirrels of Tamaulipas and eastern San Luis Potosí have whitish-gray backs with little or no buff or orange suffusion. The whitish tone results from the long white tips of the overhair. Upper parts are broken by reddish shoulder and costal patches that form high crescents along the sides of the body but rarely coalesce dorsally (score 3 is the mode in most samples, score 4 occurs less frequently; Fig. 15), and are never united with the nape patch when that element is present. Nape patches are usually small (score 1 is typical), an indistinct buffy to orange wash on many specimens. Rump patches are infrequent; when present they are usually light buffy inconspicuous washes along edges of the rumps.

A melanistic phase is common in the northern populations. The two specimens (sample 1) from Nuevo León are melanistic (the melanistic skin from 20 kilometers north of Galeana in Nuevo León that Hooper [1947:44] reported as *aureogaster* is an example of *Citellus variegatus*). About 40 per

FIGURES 21 AND 22

FIG. 21. Gradations in color of underparts in samples of *Sciurus aureogaster*. From left to right: (0) *white* (UMMZ 109367 ♂, Dos Aguas, Michoacán); (1) *whitish-orange* (USNM 68205 ♂, W Oaxaca de Juárez, Oaxaca); (2) *buff* (UMMZ 114623 ♀, Lagos Montebello, Chiapas); (3) *orange* (UMMZ 109392 ♂, S San Fernando, Chiapas); (4) *orange-red* (UMMZ 114604 ♂, S Papantla, Veracruz); and (5) *chestnut* (UMMZ 114029 ♂, SW Xilitla, San Luis Potosí).

FIG. 22. Variation in pelage color and pattern and gradation from gray to black phases in a sample of *Sciurus aureogaster* (Aureogaster Group) from the Isthmus of Tehuantepec south of Catemaco, Veracruz (part of sample 11). Underparts and tails are orange-red or chestnut in the gray phases, reddish-black in the melanistic ones. The example at extreme right is black everywhere. All are UMMZ specimens as follows (from left to right): 114617 ♂, 114615 ♂, 114616 ♂, 114619 ♂, 114605 ♂, 114606 ♂, 114620 ♀, and 114614 ♂.

cent of the specimens from Tamaulipas and eastern San Luis Potosí (computed from the combined samples, 2–5) are black or nearly so. Along the back of the latter the hairs may be dirty buff to orange basally, however, those hues typically are hidden and the animals appear black overall. Phases representing other intermediate grades between gray and black phases are rare.

Squirrels of the eastern foothills of the Sierra Madre de Oaxaca, the Gulf lowlands of the Isthmus of Tehuantepec, southeastern Veracruz, Tabasco, and northern Chiapas are darker and have a larger shoulder and costal patch than do those of Tamaulipas and San Luis Potosí. The back varies from frosted bluish-gray with no orange suffusion to frosted dark gray heavily suffused with chestnut, rather than whitish-gray. The short white tips of the overhairs are not long enough to mask the grayish-black or chestnut suffusion. In almost all specimens the shoulder and costal pattern forms a broad chestnut saddle which is often joined to a nape patch either by a narrow strip or so broadly that the two appear as one pattern (scores 4 and 5 are common, score 3 is rare). Nape patches, often large and conspicuous, occur in the samples at about the same frequency as in samples from Tamaulipas and San Luis Potosí, but are usually chestnut rather than orange. Rump patches are rare. The gray phase resembles sketches E and F in Figure 4 and in Weber's (1945:195, Plate III) renditions.

Frequency of the melanistic phase is about 50 per cent (mean of samples 10–16), slightly higher than in samples from Tamaulipas and eastern San Luis Potosí. The melanistic component from the Isthmus of Tehuantepec in eastern Veracruz and western Tabasco (samples 11–12, and 14) represents almost the entire gamut between gray and black (Fig. 22), while most of the melanistic specimens from Tabasco (sample 15), northeastern Oaxaca (sample 10), and central Veracruz (sample 9) are black; partially melanistic phases are uncommon.

Northern populations gradually intergrade with the southeastern populations through central Veracruz. Squirrels of the Gulf lowlands southeast of the Jalapa region (sample 9) average darker than those from northern areas and in overall tone of pelage grade towards the darker southeastern populations. Size of shoulder and costal patch falls between the northern and southeastern populations (categories 3 and 4 occur in about equal frequencies, category 2 is uncommon); small nape and rump patches occur in less than half the sample. Squirrels from Querétaro, northern Veracruz, northeastern Puebla, and eastern Veracruz in the Isthmus of Tehuantepec are more variable in pattern of pelage than are those from areas farther north in Tamaulipas, west in San Luis Potosí, and east in Tabasco and

northern Chiapas. Some of this variation probably results from gene exchange between populations of Aureogaster in the lowlands and Socialis in the adjoining highlands (see below).

SOCIALIS GROUP

DISTRIBUTION.—(see Fig. 33 and localities listed in Appendix) Cordillera Volcánica from Nayarit and Jalisco eastward to eastern margins of the Mexican Plateau in eastern Hidalgo, northern Puebla, and central Veracruz; the Pacific coastal plain and adjoining highlands from Colima southeastward to the Isthmus of Tehuantepec in Oaxaca and Chiapas, thence eastward through lowlands and highlands of Chiapas into mountains of western Guatemala. Peripheral localities are in the vicinities of the Río Grande de Santiago in Nayarit and Jalisco, Zimapán in Hidalgo, Cofre de Perote and Pico de Orizaba in Veracruz, and San Lorenzo near Volcán de Jumay in mountainous western Guatemala. Known altitudinal range extends from near tree line throughout the highlands (e.g., above 13,000 feet on Volcán Popocatepetl, Estado de México) down to the Pacific coastal plain near sea level (e.g., Laguna Mantialtepec, west of Puerto Escondido, Oaxaca).

HABITAT.—Occurs in most available forests ranging from thorn or scrub formations through tropical deciduous and broadleaf gallery forest to dry, scrubby, oak-pine woodland and cold, wet, oak and conifer forests. Apparently absent from virgin cloud forest (sub-tropical cloud forest like that along Gulf slopes of Oaxaca, usually below 6000 feet—not the higher altitude temperate cloud forests of oak and conifer) and possibly from virgin rain forest (e.g., along the Sierra Madre de Chiapas). Specimens are from the following habitats: virgin or second-growth oak, pine, and fir forests (Mexican Plateau and highlands of Guerrero, Oaxaca, Chiapas, and Guatemala); oil-palm forests intermixed with figs and other broadleaf tropical trees (Paso del Río, Colima) in Pacific lowlands; riparian oak forest intermixed with tropical deciduous forest or thorn forest on Pacific slopes (Michoacán and near the Isthmus of Tehuantepec in Oaxaca); thinned tropical deciduous forest (Guerrero); nut palms intermixed with tropical broadleaf trees and mangrove formations (Laguna Mantialtepec, Oaxaca); gallery forest through thorn forest or tropical scrub (Chiapas).

GENERAL DESCRIPTION.—Similar in size to squirrels in the Aureogaster Group but strikingly different in pelage pattern. Dorsum grayish, either broken by nape and rump patches of various sizes and hues or uniformly suffused with orange, with no nape or rump patches; shoulder and costal patches rare, usually indistinct except in intergrades between Aureogaster and Socialis forms; chin, throat, and cheeks usually white or whitish-gray; eye rings white to orange; crown grayish (similar to the back) to black; postauricular

patches usually large and conspicuous, small in some populations; feet white to grayish-black, often washed with color of underparts (white to chestnut); tails grayish to chestnut; backs vary from frosted blue-gray through whitish-gray to grizzled-buff. Pelage of animals that live in cold, wet environments is long and dense, shorter and sparser on squirrels from drier and warmer lowland habitats. Melanism is frequent.

GEOGRAPHIC VARIATION AND INTERGRADATION.—To facilitate description of geographic variation and intergradation in this group I have separated the following discussion into three overlapping sections: Mexican Plateau and central México, Pacific Coast, and highlands of Chiapas and Guatemala.

Mexican Plateau and Central Mexico: White underparts associated with nape and rump patches are prevalent in samples from the Mexican Plateau in northwestern México (Nayarit, Jalisco, and central and southern Michoacán). To the east there are increasing frequencies of nape and rump patterns associated with pigmented underparts, and at some localities gray phases are gradually or abruptly replaced by melanistic phases.

Pattern 1 is typical of squirrels of the Mexican Plateau in southern Nayarit and northern Jalisco (sample 41): back coloration frosted gray to frosted blue-gray, slightly to moderately suffused with buff or pale orange; nape and rump patches buffy or orange, usually broad but not contrasting sharply with grayish backs, their limits usually indistinct; crowns conspicuous, frosted black or black; eye rings usually white, may be buffy; postauricular patches white and prominent; feet usually frosted black, white in few specimens; underparts white, slightly speckled with black in some; tails variegated gray; pelage moderately full and long—typical of squirrels living in upland, dry, oak-pine forests. I have seen no melanistic examples.

Pattern 1 is also usual in samples from foothills and upper slopes of the Nevado de Colima in southern Jalisco (sample 40). Though similar to the squirrels of sample 41 in head and body length, squirrels from Nevado de Colima have longer tails, larger skulls (Fig. 5 and 6), darker pelage, and more conspicuous and richer nape and rump patches (often suffused with black); backs are frosted steel-gray rather than whitish-gray (only a few specimens show any buff) and black crowns are more frequent. Approximately 35 per cent of the Nevado sample is melanistic, the melanism confined to crown, nape and rump, and tail. Thus, those specimens have frosted blue-gray upper parts broken up by a black crown and black nape and rump (often melanistic crown and nape patch continuous) with white underparts and grizzled-black tail. All partially melanistic examples are from the higher slopes of the Nevado where they were taken in cold wet forests of oak, pine, and occasionally of fir. Squirrels from the base of the Nevado, below about 6000 feet, are brighter; except for their blackish-gray

crowns, none are melanistic. The pelage of squirrels from the high wet and cold forests of the Nevado is dense and long.

The range of morphological variation in the Nevado de Colima series overlaps that of samples from the Pacific lowlands of Colima (samples 37 and 38). The lowland Colima squirrels have longer tails than those from the Nevado, but average smaller in head and body and cranial lengths (Figs. 5 and 6). Their backs are paler (usually frosted grayish-white suffused with orange), crowns paler (usually frosted-black), nape and rump patches brighter and more conspicuous, and pelage shorter and thinner. None of the Colima specimens are melanistic.

Thus, the Nevado and Colima populations intergrade through individual variation; some individuals from each are practically indistinguishable. Unfortunately, there are only six specimens from intervening elevations: three from Platanar and one each from Tuxpan, Tonila, and the Plains of Colima. The first three localities are in Jalisco at above 4000 feet elevation, the last is in Colima near 1800 feet. I have no specific habitat data for these localities; all are in or slightly below the pine-oak belt. Those from Platanar, on foothills of the Nevado (sample 39), may have come from tropical broadleaf forest (riparian gallery or tropical deciduous forest) since they were collected in a deep canyon and found feeding on figs (Nelson, 1899:52). Certainly the elevation of 1800 feet on the Plains of Colima is well below the oak and pine forests. The specimens from Platanar resemble series from higher elevations on the Nevado, but are slightly paler, with slightly brighter nape and rump patches, in which respect they overlap the lowland sample from Colima.

The specimen from Tonila also is brighter than those from higher elevations on the Nevado, and in other pelage and cranial features it is a duplicate of many specimens from the Sierra de Coalcomán (sample 36) in Michoacán. The example from Tuxpan, with slightly paler and less conspicuous nape and rump patches than the one from Tonila, is more like the darker squirrels from higher elevations on the Nevado, but the difference is slight and it, too, could fit in the series from the Sierra de Coalcomán. Indeed, most specimens from the lower slopes of the Nevado closely resemble those of the Sierra de Coalcomán. Thus, the magnitude of differences in pelage between samples from the base of the Nevado (about 4000 feet) and those from the lowlands of Colima is comparable to that between the latter and sample 36 from slopes of the Sierra de Coalcomán. The specimen from the Plains of Colima, a juvenile in worn pelage, matches juveniles from both highland and lowland populations.

There are no apparent physiographic or habitat barriers between

the lowland population in Colima and those of slopes of the Nevado de Colima. Where not disturbed by man's agricultural activities, forests are continuous from lowlands to the highlands. Tropical broadleaf forests (riparian gallery or deciduous) and thorn or shrub forest in cutover or arid areas give way to oak woodland and to oak and pine formations (Schaldach, 1963).

There is morphological overlap between samples from the Nevado, eastern Jalisco (sample 42), and western Michoacán (samples 43 and 44). Some specimens from western Michoacán (sample 44) average paler than those from higher slopes of the Nevado, and in this respect are more similar to, though slightly darker than, samples from northern Jalisco and southern Nayarit (sample 41). Sample 44 also differs from the others in pattern (Fig. 20), reflecting greater variability in occurrence of the rump patch (absent from more individuals than in the Jalisco and Nayarit samples), in whitish-orange underparts (though tails are still grayish), and more frequent melanism (36 per cent). Also, their backs are more strongly suffused with deeper orange, and their feet are either white or lightly speckled with black instead of frosted-black. Most of the melanistic examples are blackish with lightly grizzled sides and rump, smoky gray underparts, and grizzled tails. A completely black phase is uncommon as are intermediate phases between gray and blackish.

Most morphological traits of the highland squirrels in western Michoacán also characterize squirrels of the dissected flanks of the Plateau in the Balsas-Tepalcatepec Basin (sample 45). Specimens from La Salada and La Huacana, north of the Balsas and Tepalcatepec rivers at approximately 2000 feet elevation, and examples from the vicinity of Apatzingán at about 1000 feet, are lowland counterparts of squirrels that occur in oak and conifer forests near Cerro de Tancítaro and Pátzcuaro. Those lowland animals are similar to the highland squirrels in external dimensions, cranial dimensions and configuration (Figs. 5 and 6), and there are no great differences between the two in pelage features. The lowland squirrels average slightly paler, their nape and rump patches are slightly less distinct (and about half of the sample lack rump patches, instead of about thirty per cent as in the highland sample), their pelage is much shorter and thinner, and melanistic morphs are less frequent (Fig. 18).

The population represented by series from La Salada and La Huacana also morphologically connects with populations in western Guerrero through small samples from El Zopilote and El Naranjo, and with the squirrels of Sierra de Coalcomán through the specimens from Apatzingán. Not only are squirrels in the last series short-pelaged counterparts of those from higher

elevations at Tancítaro (including gray and melanistic phases), but the gray phase also matches many examples from the Sierra de Coalcomán, differing primarily in shorter and thinner pelage.

To the east, on highlands of Estado de México, Distrito Federal, Morelos, and slopes of Volcán Popocatepetl, squirrels are like those from Pátzcuaro and Cerro de Tancítaro in external and cranial dimensions (Figs. 5 and 6) though their tails average slightly shorter. There is a marked change in pelage, however. Eastward across the Cordillera Volcánica the frequency of pigmented underparts, heavily orange-suffused backs, and melanistic phases gradually increases until orange underparts (and tails) are apparently fixed in the populations, orange-suffused dorsums are common, and melanistic phases nearly or completely replace the gray phase. Judging from available samples, that pattern transition occurs along the edge of the Mexican Plateau in northeastern Michoacán (sample 46). Specimens are available from four localities in that area: two specimens from 15 and 30 miles east of Morelia (7300 and 8500 feet, respectively) resemble those from Pátzcuaro except both have orange tails. Underparts are buff in the example from the first locality, white in the other specimen. Of five examples from farther east at Puerto Morillos (9500 feet), about 37 miles east of Morelia, two are non-melanistic. Underparts of one are orange; the other, buff. Both have orange tails and heavily orange-suffused backs. They resemble the bright orange-bellied gray phase (score 0, Fig. 29) that occurs farther east near Lengua de Vaca in Estado de México (sample 47). Other specimens from the sample are partially melanistic. Two are dark gray (score 1, Fig. 29) and one is blackish (score 5) and indistinguishable from comparable melanistic specimens from Lengua de Vaca and Volcán de Toluca (sample 48). The only example from Puerto Garnica (9400 feet), east of Puerto Morillos, is also blackish. One of two adults from west of Ciudad Hidalgo (9150 feet), the easternmost locality in sample 46, resembles the dark gray examples from Puerto Morillos; the other resembles the gray phase from Lengua de Vaca, except that it has a greater suffusion of orange between nape and rump patches—those elements are almost indistinguishable from the back.

East of Ciudad Hidalgo, from the vicinity of Lengua de Vaca through the Volcán de Toluca region, to mountains west and south of the Valley of México (samples 47, 48, and 49, respectively), melanistic phases, ranging from tawny to blackish as shown in Figure 29, are common and the bright gray phase is rare. Most specimens from samples 47 to 49 resemble one of those illustrated melanistic grades, but some from Lengua de Vaca and Distrito Federal are intermediate; they range from dark gray (score 1) to blackish (score 5). Their frequencies are shown in Figure 23. Grizzled-black

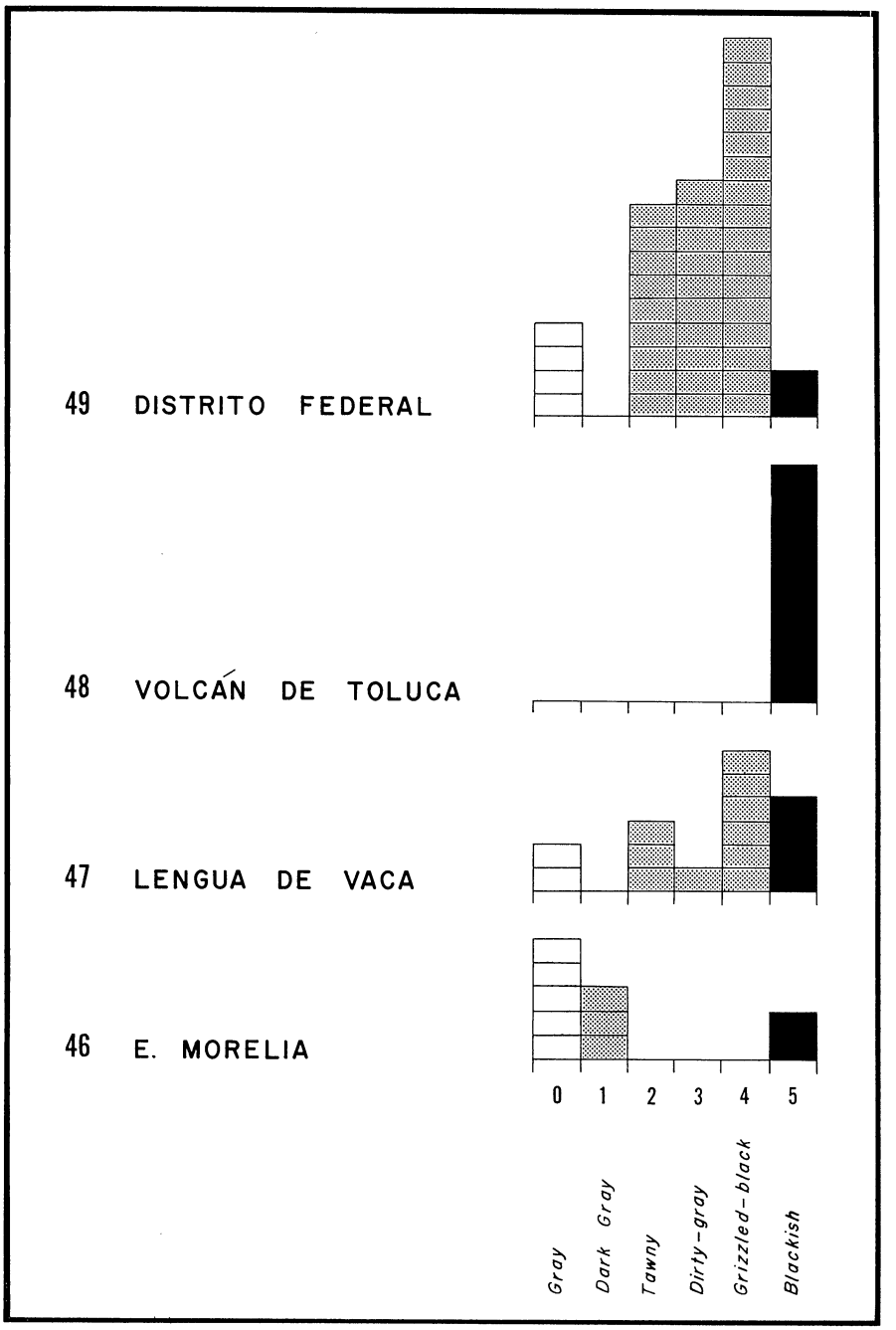


FIG. 23. Frequencies of gray and melanistic phases in samples of the Socialis Group from the Cordillera Volcánica. Each rectangle equals one specimen. See Figures 1, 29, and text for further explanation.

is most common in the vicinity of Lengua de Vaca, while all specimens from Volcán de Toluca are blackish (including USNM 55930, which Nelson [1899:90] misidentified as the only melanistic *S. oculatus* from Volcán de Toluca), and both dirty-gray and grizzled-black are the usual phases in samples from Distrito Federal. Both bright gray and melanistic variants are handsome squirrels clothed in long, luxuriously dense pelage.

East of Ciudad Hidalgo the gray phase is represented by two examples from Lengua de Vaca (sample 47), already mentioned, four specimens in sample 49 from northwestern Morelos (Huitzilac region and Cerro Cuatepetl), and two from pine forest above Cuernavaca. The four from northwestern Morelos have no rump patches but are like those from Lengua de Vaca in all other features. The two specimens from above Cuernavaca also resemble the Lengua de Vaca examples, but their backs are frosted bluish-gray like squirrels from Volcán Popocatepetl, and rump patches are absent. Also, except for their grizzled feet and pigmented eye rings, they closely resemble squirrels from the western segment of the Sierra Madre del Sur of Oaxaca.

The tone of the pelage is dark on squirrels from the slopes of Volcán Popocatepetl (sample 50) but melanism is not as common as in populations to the west (Fig. 18). Pattern 4 characterizes the gray phase, in which the crown is usually similar in tone to the back; eye rings are orange or grizzled; postauricular patches are white and conspicuous; the back is frosted blue-gray with little orange suffusion; and nape and rump patches are broad and buffy but do not contrast sharply with the back. In many specimens the overhairs along sides of the body and over the nape and rump are tipped with buff and the white-tipped hairs are restricted to the middle of the back; thus, nape and rump patches are connected along the sides of the body. Feet are frosted black, often washed with color of the underparts which varies from buff to orange-red (orange is the mode), and are usually speckled with black. Tails are grayish-buff or orange. Pelage is long and dense. The few intensely melanistic specimens resemble the grizzled-black squirrels of highlands to the west except they always retain a small frosted steel-gray area on the back.

The population of Volcán Popocatepetl morphologically ties in with squirrels from northeastern Hidalgo and central Veracruz through populations in the highlands of northern Puebla. Squirrels from high oak and conifer forests in northern Puebla (9000–10,000 feet) near Cruz Alta (sample 51) closely resemble those from Volcán Popocatepetl. They differ only in having frosted grayish-black instead of orange underparts, slightly paler crowns, smaller postauricular tufts, slightly darker feet, and grayish-buff instead of orange tails. One specimen is partially melanistic and, except

for its frosted belly, is indistinguishable from comparable melanistic specimens in the series from Volcán Popocatepetl.

The lot from Cruz Alta morphologically and ecologically connects with squirrels from the eastern edge of the Mexican Plateau near Las Vigas and the Cofre de Perote (Central Veracruz) through samples from eastern Hidalgo and northeastern Puebla, particularly those from Zacapoaxtla and nearby Apulco (sample 52). Most of the latter are brighter versions of the series from Cruz Alta: upper parts frosted gray moderately suffused with orange; nape and rump patches broad and brighter (orange and orange-red rather than buff) than on squirrels from Cruz Alta; postauricular patches inconspicuous; eye rings grizzled or pigmented; feet frosted-black; underparts of most frosted-gray, some lightly suffused with orange; tails either grayish-buff, orange-red, or chestnut; and pelage slightly shorter and thinner than in those from Cruz Alta. None are melanistic. A specimen from northeast of Metepec (eastern Hidalgo) fits with the series from Zacapoaxtla as does an orange-bellied individual from Scapa (Puebla) and a juvenile from north of Zimapán (northwestern Hidalgo).

The range of variation in pelage features in sample 53 from near Las Vigas (collections from 4600 to 8500 feet from pine-oak forest) overlaps that in the Zacapoaxtla series to the extent that several individuals are indistinguishable. Pigmented underparts (that vary from frosted gray to orange-red speckled with black; mode is whitish-orange suffused with grayish-black) are more common, therefore pattern 4, instead of 1, is usual. Nape and rump patches are brighter (orange-red or chestnut) and contrast sharply with a frosted blue-gray back that is lightly suffused with orange. The crown is darker, usually frosted black. Melanism is confined to feet, crown, and tail.

Samples from southeast of Las Vigas, from the east slope of the Cofre de Perote above Xico (sample 54) and from near Jalapa (sample 55) apparently represent intergrades between Socialis and Aureogaster groups (see below).

Before describing the geographic variation in populations south of the Mexican Plateau I wish to emphasize that the previous discussion has focused on variation in *pelage features* of populations on the Plateau. In external dimensions (Fig. 5), cranial dimensions (Fig. 6), and most cranial configurations, samples from the Plateau are closely similar to each other; differences between any of them are slight.

Morphologically and ecologically, squirrels of the oak-conifer forests on the Cordillera Volcánica in Michoacán and other areas along the mountainous southern margins of the Mexican Plateau resemble squirrels of the Sierra Madre del Sur in Guerrero and Oaxaca, those of other highlands in

western and northern Oaxaca, and squirrels of southern Puebla. Ranges of variation in external dimensions and cranial dimensions and configuration in samples from southern Puebla and northwestern Oaxaca (sample 56), mountains west of the Valley of Oaxaca (sample 57), Cerro San Felipe and the Sierra de Juárez in northern Oaxaca (sample 58), and Sierra de Miahuatlán in southern Oaxaca (sample 27) are almost encompassed by the sample from Cerro de Tancítaro and Pátzcuaro in Michoacán (sample 63).

In features of the pelage, series from highlands west of the Valley of Oaxaca closely resemble those from near Cerro de Tancítaro, Pátzcuaro, and eastern Michoacán; differences between them are slight. Upper parts of the Oaxacan series average slightly paler and have a slightly greater suffusion of pale orange than those from Michoacán. The buff-orange nape and rump patches are indistinct and rump patches are less frequent than in the Michoacán squirrels (absent from 50 rather than 30 per cent of the sample). None are melanistic. Otherwise, overlap in pelage variation between the Michoacán and Oaxacan samples is so broad that over half the specimens in each sample are inseparable. Except for their long, lush pelage, squirrels from west of the Valley of Oaxaca also closely resemble those from near La Salada and La Huacana (sample 45) in color and pattern as well as in external and cranial dimensions.

Squirrels from northern and southern Oaxaca (samples 56, 58, and 27) are like those from the mountains west of the Valley of Oaxaca. Specimens from Cerro San Felipe resemble those from west of the Valley of Oaxaca, except that they have orange or orange-red underparts and orange-red or chestnut tails. Farther north in the Sierra de Juárez, backs are frosted blue-gray and heavily suffused with orange, distinct nape and rump patches are usually orange-red or chestnut, eye rings are white, pelage is long and thick, and melanistic phases are absent. In a few specimens the belly coloration extends slightly onto sides of the body in a low inconspicuous orange wash (score 1). Specimens from southern Puebla, Tlapancingo and northwestern Oaxaca (sample 56) differ from those west of the Valley of Oaxaca in having slightly shorter and thinner pelage, more distinct and brighter (orange or orange-red rather than buff or orange) nape and rump patches, slightly darker backs suffused with slightly darker tones of orange, and more deeply pigmented tails (orange to chestnut rather than grayish-buff to orange); the samples overlap broadly. The two from Piaxtla, except for their whitish underparts, resemble those from Reyes in northern Oaxaca. In their darker backs, distinct and bright nape and rump patches, deeply pigmented tails, white postauricular tufts, and whitish feet, sample 56 overlaps series from mountains west of Chilpancingo, Guerrero (sample 31), and from southern Oaxaca near San Gabriel Mixtepec (sample 27).

Sample 27, from the Sierra de Miahuatlán, southern Oaxaca, combines features of the highland squirrels (sample 56) with those of the Pacific lowlands (sample 28). As in samples 56 and 28, patterns 1 and 4 typify the Mixtepec squirrels, which resemble those from San Andrés Chicahuastla (sample 56) except for slightly shorter and thinner pelage, chestnut tails, brighter (orange-red instead of orange or buff) nape and rump patches, and less distinct postauricular patches. Compared with squirrels from the Pacific coastal plain and uplands, those from Mixtepec have slightly longer and thicker pelage, darker backs more heavily suffused with orange, and slightly paler nape and rump patches (but within the same color category), but are otherwise closely similar; the differences are of the same magnitude as those between samples from the Pacific coastal plain and from adjacent highlands at around 3000 feet (between samples 29 and 32, for example) in Guerrero. The Mixtepec squirrels also resemble those from San Andrés de la Cruz (sample 32) in Guerrero, but have whitish instead of reddish underparts and whitish instead of frosted-black feet.

Squirrels from above 7000 feet in the Sierra Madre del Sur of Guerrero (sample 31) combine pelage features and external dimensions of animals from the Sierra de Juárez in Oaxaca with some cranial features of those from the Pacific coastal plain near Acapulco. Pattern 4 predominates (Fig. 20). Upper parts are frosted blue-gray suffused with chestnut, usually broken up by bright orange-red or chestnut nape and rump patches (the latter often absent); eye rings range from whitish-orange to chestnut; postauricular patches are large; feet are usually white, but may be lightly peppered; underparts range from orange to chestnut (the mode); tails are chestnut; a chestnut shoulder wash (score 1) occurs in several specimens; pelage is long and thick; there are no melanistic phases. Color and pattern closely resemble those in squirrels from the Sierra de Juárez in Oaxaca (part of sample 58); the latter have slightly paler nape and rump patches, underparts, and eye rings, and longer bodies, tails, feet, and skulls (Tables 1 and 2). Except for grayer crowns, greater frequency of white feet, and deeply pigmented underparts and tail, squirrels from Guerrero also resemble those from the Sierra de Coalcomán, Michoacán.

The highland Guerrero populations grade into those of the Pacific coastal plain (samples 29 and 33). The latter have shorter bodies, longer tails (Fig. 5), whitish-gray rather than frosted blue-gray upper parts, bold orange-red or chestnut nape and rump patches, whitish-orange or orange rather than chestnut underparts, and short, thin rather than long and dense pelage. Intergradation between the highland and lowland populations is seen in samples from about 3000 feet at Agua de Obispo and Acahuizotla (sample 30), and from San Andrés de la Cruz and San

Vicente de Jesús (sample 32). Patterns in samples from Agua de Obispo and Acahuizotla are similar to those in sample 31 (Fig. 20), though backs average slightly paler, rump patches are more frequent and distinct, underparts are lighter (mode is orange rather than chestnut), and pelage is thinner and shorter. Tails are intermediate in mean length between lowland and highland samples (Fig. 5).

Examples from near San Andrés de la Cruz share features of Pacific lowland samples and the Agua de Obispo series, though those from San Andrés have some expression of a nape and rump patch, have no shoulder wash, and their underparts usually are orange rather than orange and orange-red. In these traits they resemble the lowland squirrels. The squirrels from San Andrés de la Cruz are like those from near Agua de Obispo in external and cranial dimensions, and in variation of pelage they also overlap the lowland samples in the same way as do the Agua de Obispo series.

There are apparently no physiographic or habitat barriers to gene flow between highland and lowland populations of the Sierra Madre of Guerrero. Where undisturbed by man, forest is more or less continuous. Oak and pine (with cloud forest at higher elevations) of the Sierra extend down to about 3000 feet, depending on slope exposures, where they integrate with deciduous or semi-evergreen tropical broadleaf forests. On the coastal plain these merge with arid thorn forest or scrub, or extend as gallery forest along rivers (Davis and Dixon, 1959; Goldman, 1951). Take the sample from Agua de Obispo and Acahuizotla, for example. Agua de Obispo (3000 feet) is in relatively dry, open pine-oak forest. Acahuizotla, at 2800 feet, is in moist tropical deciduous forest that extends up ravines and canyons into the pine-oak belt at higher elevations. Squirrels from both localities are part of the same interbreeding population; morphologically they are inseparable. I have collected them from near leaf nests in large oaks and pines growing at the edge of steep canyons in which the vegetation was predominantly of tropical deciduous elements; nests were there also, and squirrels regularly moved from one area to the other.

The forest transition is similar near San Andrés de la Cruz (3000 feet), but the original forest there has been altered. Thinned, humid, tropical deciduous forest shades coffee groves and mango trees, and oak and pine are intermingled with tropical broadleaf elements only in canyons where the original forest remains relatively intact. At higher elevations, beginning near San Vicente de Jesús for example, pine and oak predominate and eventually merge with cold and wet temperate cloud forest.

Pacific Coast: Described below are samples from the Pacific coastal plain and adjoining highlands from Colima through Michoacán, Guerrero,

Oaxaca, and western Chiapas. Squirrels of the coastal plain are essentially long-tailed, sparsely haired, bright and boldly patterned counterparts of animals living in adjoining highlands.

Pattern 1 is common to populations of the coastal plain from sea level at least to 1800 feet elevation in Colima (samples 37 and 38). All examples from there have conspicuous, usually bright orange to orange-red nape and rump patches (score 2, mode of size; score 3, mode of color) that contrast sharply with backs which vary from grayish-white to frosted blue-gray, lightly to moderately suffused with buff or orange. The crown is usually frosted black; eye rings vary from white to orange (pigmented rings predominant); either prominent or inconspicuous postauricular patches occur in about equal frequencies; feet are frosted black; underparts are white, rarely pigmented (1 of 35 specimens); and tails are grayish.

The lowland Colima population (sample 37) grades into those of the Nevado de Colima (sample 40), as discussed elsewhere, and into those from the coastal plain and adjoining highlands in Michoacán (samples 35, 36). Samples from slopes above 6000 feet in the Sierra de Coalcomán, Michoacán, are highland counterparts of the lowland Colima series, but in Coalcomán tails average shorter, bodies are longer (Fig. 5), pelage is slightly longer and denser, backs are darker (closer to a frosted blue-gray with little or no buff or orange suffusion), rump patches are more variable (absent from 50 per cent of the sample), rump and nape patches average darker (either orange-red or chestnut), and feet are slightly paler. The overlap in range of variation between the two samples is broad. Two specimens from Coalcomán (3500 feet) and one from the Río Coahuayana on the coastal plain are similar in color and pattern to many from higher elevations on the Sierra Coalcomán, but the pelage is slightly shorter.

Squirrels from the Pacific lowlands in southeastern Michoacán (sample 35) resemble those from the Sierra de Coalcomán, but they have longer tails (Fig. 5), shorter and thinner pelage, and brighter grayish-white backs with a greater orange suffusion. Variability in the series also overlaps that in samples from both Colima and southwestern Guerrero (sample 34). Samples from lowlands of western Guerrero to southwestern Oaxaca (samples 34, 33, 29, and 28) are morphologically close to those from Colima and southeastern Michoacán. They differ primarily in having grayer, less blackish crowns (tend to be same tone as back), greater variation in backs, and increased frequency of pigmented underparts and tails. Patterns 1 and 2 and 4 and 5 are usual. Eye rings vary from white to orange in specimens from western Guerrero but most examples from farther east are pigmented; postauricular patches are moderate (mode is score 1), absent or deeply tinged with color of the nape in specimens from near Acapulco (sample 29); backs

tend to be whitish-gray, vary from frosted blue-gray to creamy white heavily suffused with orange; nape and rump patches, though orange in samples from western Oaxaca, are bright chestnut elsewhere along the coast; these patches are broad and conspicuous, contrasting with whitish-gray backs; feet are usually lightly suffused with black, sometimes whitish; underparts are white in squirrels from western Guerrero, whitish-orange or orange is usual farther east (range extends from whitish-orange to chestnut).

Pigmented underparts are rare in populations along the coast to the northwest, appear in coastal populations in southwestern Guerrero (sample 33) where they range from whitish-orange to orange-red; the mode is orange. Orange is not yet fixed in the tails since they are grayish in about half of the sample, orange-red or chestnut in the other half. Farther east, orange-red or chestnut tails are apparently fixed in the populations regardless of color of underparts.

In the largest sample from the Pacific Coast, from Acapulco, pelage varies greatly, almost encompassing that seen in the samples from western Guerrero to eastern Oaxaca. The Acapulco series also contains examples that are overall whitish, reddish, or melanistic (Nelson, 1899:65); the latter are the only melanistic phases that I have seen from the Pacific Coast (Fig. 18). Through foothills and highlands of the Sierra Madre del Sur in Guerrero these populations intergrade morphologically and ecologically with those in the highlands.

Farther eastward, from central Oaxaca to the Isthmus of Tehuantepec, squirrels resemble those of southwestern Oaxaca and the Acapulco region in most characters; they differ mainly in frequencies of three conspicuous pelage features: (1) rump patches are usually absent; (2) a shoulder and costal patch is frequent; and (3) underparts average deeper orange. Thus, in samples from Puerto Angel (sample 25) patterns 5 and 8 are most frequent (Fig. 20). Most pelage features of these squirrels are like examples from Acapulco and eastern Oaxaca, except they have a diffuse orange shoulder and costal wash, usually no rump patch (when present it is an indistinct wash over the posterior margin of the rump), orange-red or chestnut rather than orange underparts, and darker feet. External and cranial dimensions of the Puerto Angel series average larger than in samples from the northwest near Acapulco or from the southeast near Tehuantepec (Figs. 5 and 6).

Of two examples from Colotepec (sample 25), one (USNM 71261, collected at 300 feet elevation according to information on the specimen label) resembles the series from Puerto Angel, but has a broad orange rump patch; the other (USNM 71260, 5000 feet is the elevation written on the specimen label) is like those from near Puerto Escondido (west of Puerto

Angel) with nape and rump patches and whitish-orange underparts. A specimen from Santa Cruz Bay, southeast of Puerto Angel, resembles squirrels of the latter area, but has whitish-orange rather than orange-red or chestnut underparts. A single specimen from north of Puerto Angel at Pluma Hidalgo (about 3000 feet) falls within the range of variation of the Puerto Angel series.

In samples from the coastal plain and adjacent highlands (to about 5000 feet elevation), east of Puerto Angel near Tehuantepec (sample 24), patterns 5 and 8 are most common, other patterns occur infrequently (Fig. 20). These animals resemble those occurring farther west along the Pacific coastal plain and adjoining uplands and morphologically link them with populations of the Isthmus and western Chiapas. The Tehuantepec squirrels usually have orange or orange-red underparts. A low orange shoulder wash (mode is score 1) occurs in about 30 per cent of the sample. Rump patches are usually absent, but orange nape patches tend to be expansive (score 2). The frequency of indistinct nape patches (score 1) is higher than in samples from farther up the coast. The back varies from frosted blue-gray with little orange suffusion to whitish-gray strongly suffused with buff or orange. Most, however, are frosted-gray. In them, the white tips of the overhair almost mask the underlying orange. The wide orange subbasal bands of the overhair and similarly pigmented tips of the shorter underfur produce that underlying orange suffusion. Tails are orange-red or chestnut in about two-thirds of the sample, variegated buff to orange in the remainder.

There is apparently uninterrupted gene flow between populations of the lowlands and foothills near Tehuantepec and those of higher elevations, to at least 5000 feet, in the adjoining spurs of the Sierra de Miahuatlán (sample 24). Also, apparently gene exchange exists between the population represented by sample 24 and those of higher elevations to the west; samples of the latter include but one adult from Chontecomatlán, approximately 6500 feet, and three adults from the mountains near Santa María Ozolotepec, about 10,000 feet (sample 26). These localities are in the southeastern limits of the Sierra de Miahuatlán. The Chontecomatlán specimen, which matches several specimens in sample 24, has a large pale nape patch and an orange shoulder and costal wash (score 2). Three examples from Ozolotepec, though in worn pelage and molting, resemble the Chontecomatlán specimen and those in sample 24. They differ in being darker (dorsally all are frosted blue-gray with a slight orange suffusion), with longer and thicker pelage. Nape patches are absent or inconspicuous in two specimens, broad in one. All have small shoulder and costal washes.

Squirrels of the coastal plain east of Tehuantepec, from the vicinity of Chicapa (sample 23) through southwestern Chiapas near Arriaga and

Tonalá (sample 22), to Mapastepec, are similar in most features to those from Tehuantepec but differ in pattern frequencies (Fig. 20) and other pelage traits in which they are more like squirrels of eastern Chiapas and western Guatemala.

Compared with Tehuantepec squirrels, those from southeastern Oaxaca and southwestern Chiapas have pale crowns and smaller postauricular patches. Nape patches are slightly less frequent, rump patches, orange and indistinct (score 1), slightly more common. Shoulder and costal patches, a low pale orange wash, occur infrequently. Back coloration is variable, a frosted, somewhat grizzled, buff or orange in most specimens. The overall visual impression is a variegated orange, white, and black—an effect resulting from short white bands and wide orange bands of the overhair and wide orange tips of the underfur. Because the white tips of the overhair are short the proximal wide orange bands and shorter black bands are not masked by the overlay of white tips. At one extreme of the range of variation are specimens like those in the Tehuantepec series; with long white tips that almost mask the underlying orange so the back appears frosted grayish-white. At the other end are specimens with dark frosted blue-gray backs only moderately suffused with buff or orange as in squirrels of the Sierra Madre de Chiapas and Guatemala. Underparts average between whitish-orange and buff (rather than orange or orange-red) and are often speckled with black. Tails are usually buff to orange rather than orange-red to chestnut as in the Tehuantepec sample.

There is apparently no significant interruption of gene flow between the populations of the Pacific Coast in southwestern Chiapas (sample 22) and those of higher elevations on the Mesa Central of northern Chiapas (sample 18) and of southeastern Chiapas and Guatemala (samples 19 and 20). These samples from northern Chiapas and Guatemala (samples 17–19) are similar in cranial and external dimensions and resemble squirrels of the Cordillera Volcánica, the highlands of Oaxaca, and the Isthmus of Tehuantepec but they tend to have shorter tails than the latter series (Figs. 5 and 6).

Chiapas and Guatemala: Though pattern and color of the Chiapan and Guatemalan squirrels vary, patterns 6, 8, and 10 are usual (Fig. 20). Samples from the southern highlands adjoining the Pacific coastal plain in Guatemala represent one extreme pattern, those from northern Chiapas represent the other extreme, and the two intergrade. Squirrels from the highlands of southern Guatemala, east of the Sierra Madre de Guatemala (Chichicastenango, San Lucas, Antigua, for example), have variegated, peppered buffy (or yellow-orange) upper parts and no nape, rump, or shoulder patches. The variegated effect results from alternate black and buffy banding of the overhairs; either the tips or subterminal bands are buff and they

overlay the buffy and black bands underneath. Eye rings are orange flecked with black; postauricular patches are usually inconspicuous; underparts vary from buff to chestnut (often black-speckled), but orange or orange-red is usual; tails vary from buff to orange; and pelage is long and thick. Some specimens are partially melanistic, but never to a degree that obscures the basic pattern; they are usually dark grayish-orange.

Variegated buffy upper parts are replaced by frosted buff to the west and north from the southern highlands of Guatemala. This effect results from a gradual increase of white-tipped (rather than buff-tipped) hairs. The white overlays, but does not mask, the proximal buff or orange bands. The frosting first appears on the middle of the back and gradually becomes more expansive until the entire dorsum resembles those of squirrels from northeastern Chiapas—frosted buff or orange. In the intermediate stages between variegated orange and frosted orange, the frosting covers only the back so that the buff or orange-tipped hairs are confined to nape and rump, where they form broad (but indistinct) patches, or along the sides of the body. Also, in some specimens the frosting may extend along the back over the rump and flanks, leaving the variegated buff as a wash extending from the belly onto the shoulder, costal, and nape regions. Some samples from the southern highlands of Guatemala (Tecpan, for example) contain the complete gradation from variegated-buff to frosted-buff upper parts.

Samples from the Sierra Madre de Guatemala (Volcán Tajumulco) and from throughout the northwestern highlands of Guatemala (Momostenango, Chancol, Totonicapan, and Calel, for example) are a mixed lot. They contain all gradations between the unpatterned variegated-buff and the frosted-buff upper parts, but the frosted types are most common. Finally, in the northern Guatemalan highlands near La Primavera, Nebaj, and Sacapulas, and the Sierra de los Cuchumatanes near San Juan Ixcoy and San Mateo, frosted-orange upper parts are prevalent and are broken either by nape and rump patches, a shoulder wash, or combinations of those elements.

Samples from farther to the northwest, in the Mesa Central of Chiapas (sample 18), resemble those from the Sierra de los Cuchumatanes, except the underparts are slightly paler (mode is orange rather than orange-red) and less peppered, and feet are paler, sometimes white. Upper parts vary from grayish-white (almost masking an orange suffusion) through frosted orange (the average) to frosted blue-gray lightly suffused with orange; no rump patches; nape patches are absent from over half the sample, otherwise they are usually broad and pale orange; about one-third of sample has pale orange shoulder washes (usually small, score 1); eye rings are usually pigmented; postauricular patches are inconspicuous; and tails tend to be buff

or orange (several are orange-red or chestnut); no melanistic specimens in the sample.

Series from still farther northwest in the Mesa Central, near Pueblo Nuevo (5000 feet, sample 17), resemble those from northeastern Chiapas (sample 18) except that pattern 10 is usual, upper parts average darker, and underparts are orange-red instead of orange; the sample is variable in pattern (Fig. 20), probably a result of gene exchange between Aureogaster and Socialis groups, as discussed elsewhere. Thus, squirrels of the highlands of northern Chiapas grade morphologically into those of adjacent highlands in Guatemala and through squirrels of intermediate elevations in the Tuxtla Gutiérrez and San Bartolomé regions (sample 21) into those of the coastal plain of southwestern Chiapas. Through gradual changes in external dimensions and pelage characteristics, series from these intervening regions morphologically completely connect samples from the Pacific lowlands with series from the Mesa Central in northern Chiapas. Also, the pelage variation in samples from northern Chiapas, especially in the series from Lagos Montebello (part of sample 18), is similar to that seen in series from Volcán Tacaná and Cerro Mozotal (part of sample 19) in southeastern Chiapas. Though the Tacaná and Mozotal series average slightly darker (less orange suffusion of the upper parts) with a greater frequency of nape (more of a buff or orange suffusion) and rump patches, morphological overlap between the two samples is broad and many specimens in each series are indistinguishable.

The Mozotal and Tacaná series are highland counterparts of squirrels of the lowlands and foothills of southeastern Oaxaca and southwestern Chiapas (sample 22), except that those highland samples have longer bodies, much shorter tails (Figs. 5 and 6), longer and denser pelage, average darker color, and less distinct nape patches. The magnitude of morphological difference between the two series is comparable to that between other highland and lowland sets of samples from regions farther to the northwest along the Pacific lowlands and adjacent highlands from Colima to Oaxaca.

INTERGRADATION BETWEEN AUREOGASTER AND SOCIALIS GROUPS

Judging from morphological and ecological aspects of samples, gene exchange between the Aureogaster and Socialis groups occurs in Puebla and Veracruz, possibly in the mountains of northeastern Querétaro, across the Isthmus of Tehuantepec, and in Chiapas. In at least one region—northeastern Oaxaca—the highland population of Socialis is geographically and apparently ecologically separated from the adjoining lowland population of Aureogaster and the two forms may not interbreed there.

NORTHEASTERN OAXACA.—In northeastern Oaxaca, the Socialis Group occupies highlands covered by oak and conifer in the Sierra Madre de Oaxaca. Aureogaster types occur in the adjoining tropical lowlands, and each is apparently absent from the steep intervening slopes covered by subtropical cloud forest. A transect through the area follows a road leading from Oaxaca de Juárez over the Sierra de Juárez to Tuxtepec near the Oaxaca-Veracruz border (Fig. 24). I worked in the forests near the Cerro San Felipe and in the Sierra de Juárez in the summer of 1963, and in 1964 James H. Brown and I spent two weeks of July collecting specimens and gathering habitat information on the northern flank of the Sierra de Juárez and in adjoining lowlands.

The uplands of the Sierra Madre from Cerro San Felipe to the northeastern flanks of the Sierra de Juárez once were covered by oak and conifer forest. Much of that forest between San Felipe and Ixtlán de Juárez has been cleared and the land placed under cultivation, but cutover forest still remains on higher ridges and slopes. Goldman (1951) and Sibley (1950)

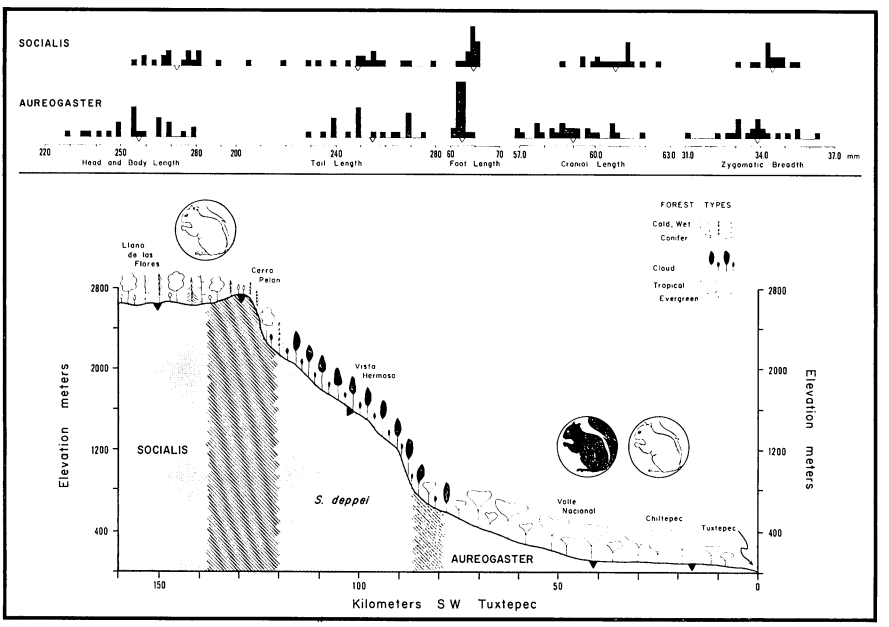


FIG. 24. Schematic profile of a segment of northeastern Oaxaca indicating morphological and ecological relationships between the Aureogaster (sample 10) and Socialis (sample 58) forms of *Sciurus aureogaster,* and *S. deppei.* Gray in the figures represents orange-red or chestnut dorsal patterns; black indicates melanistic phases. Each square of a histogram equals one specimen; inverted triangles indicate means. See Table 5 and text.

provide more detailed descriptions of the region. Northward along the crest of the Sierra de Juárez near Llano de las Flores (north of Ixtlán de Juárez) at an elevation of about 2870 meters, wet and cold forests of oak, pine, and fir clothe the slopes; Hooper (1961) described the forest there. To the southeast at the edge of the Sierra on slopes of Cerro Pelon (elevations, 2700–2800 meters), cold wet forests composed predominantly of oak with some pine (Musser, 1964) cover the rugged steep Gulf slopes of the Sierra down to at least 2000 meters and probably extend lower in the cool steep canyons. Near 2000 meters, where the trees are smaller than at higher elevations, the oak-pine forest grades into a wet, cool, cloud forest that covers the slopes down to 700 or 800 meters (Bogert and Duellman, 1963, describe the region near Campamento Vista Hermosa which is in the cloud forest belt). At approximately 760 meters, the cloud forest grades into tropical evergreen forest, the dominant forest type in the lowlands toward Tuxtepec. Transitions between forest types along the flanks vary according to slope exposure. Above 2000 meters the forest has been thinned by logging operations. The cloud forest is relatively undisturbed and forms a lush blanket of green that clothes the precipitous slopes. At lower elevations, the tropical evergreen forest has been more disrupted. Areas have been cleared and planted to various agricultural crops, and around 100 meters much of the forest has been thinned and only the taller trees that now shade an understory of coffee remain. Elsewhere, second growth is choked with vine-entangled understory.

Populations of the Socialis group occupy the oak and conifer forests of the Oaxacan uplands from Cerro San Felipe to the edge of the Sierra de Juárez (e.g., Llano de las Flores, south slopes of Cerro Pelon) and on Gulf slopes down to at least 2240 meters where we saw one and heard it scold, but were unable to obtain specimens. At that locality and on the slopes of Cerro Pelon, Socialis types are sympatric with *Sciurus deppei,* a small brown squirrel about one-third the size of the larger gray squirrel. *S. deppei* reaches its local upper distributional limits somewhere south of Cerro Pelon, for it is absent from the forests around Llano de las Flores and other Oaxacan highlands where the gray squirrel is the only *Sciurus.*

The tropical lowlands are occupied by populations of the Aureogaster group. Specimens are from near Tuxtepec, five miles west of Chiltepec, near Valle Nacional, and about 11 road miles southwest of Valle Nacional at 760 meters where the gray squirrel is apparently sympatric with *deppei.*

Morphology of Socialis populations from northern areas of the Sierra Madre de Oaxaca (sample 58) is described elsewhere. Aureogaster types of the lowlands (sample 10) are primarily melanistic; the gray phase occurs infrequently. The two samples differ appreciably in most external and

TABLE 5

EXTERNAL AND CRANIAL MEASUREMENTS (MM) OF SAMPLES OF THE SOCIALIS AND AUREOGASTER GROUPS OF *Sciurus aureogaster* IN NORTHEASTERN OAXACA

Sample T_{05} and P	M.±S.D., 95% C.L., (Extremes), and N Lengths				Breadths
	Head and Body	Tail	Hind Foot	Cranium	Zygomatic
Socialis					
(Sample 58)	272.5± 9.1	248.9±17.6	69.1±2.1	60.77± .95	34.52± .60
	268.0–277.0	240.4–257.5	68.1–70.2	60.31–61.22	34.20–34.84
	(255–290)	(205–280)	(64–72)	(58.7–62.5)	(33.2–35.5)
	18	19	18	19	16
Aureogaster					
(Sample 10)	257.4±13.1	254.5±12.6	64.5±1.7	59.10±1.30	33.86±1.15
	252.1–262.7	240.4–257.5	63.8–65.1	58.59–59.60	33.36–34.36
	(230–280)	(230–275)	(62–70)	(57.0–61.9)	(31.2–36.4)
	26	26	26	28	23
T_{05}	4.139	1.242	8.126	4.810	–2.053
P	.001	.3–.2	.001	.001	.05–.02

cranial dimensions (Table 5; Fig. 24). Contrasting features of the pelage are listed below.

Character	Aureogaster Group	Socialis Group
Eye ring	orange	white
Postauricular patches	dull white, indistinct	white, conspicuous
Nape patch	absent	moderate to broad (scores 1, 2), orange-red or chestnut, sometimes absent
Rump patch	occurs rarely and always indistinct	moderate to expansive (scores 1, 2), orange-red or chestnut, sometimes absent
Shoulder patch	expansive (scores 4, 5), orange-red or chestnut	usually absent, an indistinct wash (score 1) otherwise
Feet	frosted black or black	white
Underparts	chestnut	orange to orange-red
Pelage	relatively short, thin, little underfur	luxuriant, long and dense, abundant underfur
Melanism	common, 89 per cent of sample are blackish	no melanistic phase

Apparently neither the Socialis nor the Aureogaster types penetrate the subtropical cloud forest and *Sciurus deppei* is the only squirrel occupying that habitat—at least in the first half of July when Jim Brown and I spent one week in the cloud forest attempting to discern the altitudinal limits of the highland and lowland gray squirrels. The flanks of the Sierra are deeply dissected. Hunting was difficult; in some areas we used Indian trails that descended from the high ridges through the cloud forest to the river valley below, but otherwise our hunting was confined to the sides of the ridges. Both *deppei* and the gray squirrel were collected on the slopes of Cerro Pelon. There both species spend much time on the ground where they feed on fungi, acorns, and berries growing in the entangled understory. More specimens of *deppei* were collected from the entangled undergrowth and on the ground than in tall trees. Gray squirrels were also seen high in the tops of oaks and pines. They strip the pine cones of nuts and eat the new tender needles growing at the ends of branches. *S. deppei* was vociferous and called throughout the day. In contrast, gray squirrels were usually quiet and chattered only when surprised or chased by us. The calls of each species are distinctive and diagnostic. That of the gray squirrel is a resonant, harsh, trilling chatter. The call of *deppei* is higher pitched, sometimes a bird-like trill, but more often it is a series of high pitched notes

emitted close together. *S. deppei* were often found in small aggregations (up to six or seven in a grove of trees) calling to each other. According to our records, *deppei* occurs with gray squirrels down the Gulf slopes to at least 2240 meters where we collected specimens of it and saw and heard one gray squirrel that had been feeding in a large pine. Between that locality and approximately 700 meters, we found no evidence of either Socialis or Aureogaster squirrels, but *deppei* was common throughout; we obtained specimens from 2000, 1620, and 1200 meters in the cloud forest. I asked several Indians who live in areas adjacent to the road, or down in the valleys (and commute by the steep trails to the road) about squirrels and showed them our specimens of *deppei*. All emphatically stated that the little brown squirrel was the only kind in the forests on the ridges, but that a larger black squirrel lived in the river bottoms where it is primarily tropical evergreen forest. Some individuals familiar with the area around Cerro Pelon did not realize that *deppei* occurred there, but they were familiar with the large red-bellied gray squirrel, and said that it did not live on the lower slopes.

At 760 meters, where the cloud forest merges with tropical evergreen forest, we heard and saw two *deppei,* but were unable to obtain specimens. A native hunter gave us a melanistic Aureogaster that he had just killed nearby. He claimed that black squirrels were uncommon at that elevation, but were abundant in the lowlands. We saw leaf nests at the 760-meter level (which we hadn't seen higher in the cloud forest belt) but did not see any Aureogaster. At lower elevations near Valle Nacional we saw five melanistic Aureogaster in thinned forest that was shading coffee groves and in dense entanglements in nearby second-growth forest, and collected three. We found leaf nests in the taller trees shading the coffee. We encountered no *deppei*.

Though we did not collect in the lowlands northeast of Valle Nacional, I have recent samples from there. For example, the large series (43 specimens) from near Chiltepec was obtained in August, 1962. No *deppei* have been taken from that region but the species probably occurs in the lowlands where stands of deep relatively undisturbed forest remain, for it occurs in such habitats elsewhere in the Gulf lowlands. Whether squirrels of either the Aureogaster or Socialis Group migrate into the cloud forest at other times of the year is unknown. If they do, and interbreeding occurs between the populations, there is no apparent morphological indication of that interbreeding in the samples. Certainly a year-round study of the biology of both highland and lowland gray squirrels, along with *deppei,* in the region is needed.

The distribution of vegetation and squirrels in the Oaxacan region

may represent the original situation along eastern México where cloud forest occurred between lowland tropical broadleaf forest and highland oak and conifer forest along the eastern escarpments of the highlands (see vegetation map in Leopold, 1959). If so, then intergradation between populations of the Aureogaster and Socialis groups in areas to the north and east may have been facilitated by man's destruction or modification of the cloud forest. But there have probably been areas where tropical lowland forest is not separated from highland oak and conifer forest by cloud forest and these areas may be natural regions of intergradation.

QUERÉTARO.—Four adults, all molting and in worn pelage, from Pinal de Amoles (sample 6), collected in pine forest at approximately 8000 feet elevation (Goldman, 1951:239, described the habitat of that locality), may represent a population of intergrades between the Aureogaster and Socialis groups. Features of skin and skull of three specimens are within the range of variation in the series from Papantla (Veracruz, sample 7): one example (USNM 81457, misidentified by Nelson, 1899:89, as a melanistic *Sciurus oculatus)* is melanistic and two (USNM 81450 and 81458) have orange-red underparts and tail, expansive (score 2) orange or buffy nape patches, broad (score 2), though indistinct, buffy rump patches, and low (scores 1, 2) shoulder and costal patterns—duplicates of some specimens in the series from Papantla. The fourth specimen (USNM 81454) has orange underparts and tail, grayish upper parts, and no nape and rump or shoulder and costal patches.

Nelson (1899) suggested that the occurrence of these squirrels at Pinal de Amoles resulted from migration from the Gulf lowlands in search of food. This is a reasonable hypothesis, especially in view of the morphological similarity between those specimens and examples from the lowlands of northern Veracruz and northeastern Puebla (especially sample 7) that have attributes probably resulting from intergradation between the Aureogaster and Socialis groups. The nearest geographic sample, from northwestern Hidalgo in the mountains north of Zimapán, is a juvenile (UMMZ 91895) collected in dry oak and pine forest at an elevation of 7000 feet. It has orange underparts and tail, expansive orange nape and rump patches, but no shoulder and costal patch. Except for the pigmented underparts, it fits with the series from Zacapoaxtla to the southeast. If the specimen is characteristic of squirrels from northwestern Hidalgo, then that population is more like the Socialis than the Aureogaster types. I have hunted the region several times attempting to acquire additional specimens but was always unsuccessful. Nelson (1899:42) lists specimens of *S. aureogaster* from Sierra Encarnación, a locality north of Zimapán in Hidalgo, but there are no specimens from there. That record is based on Goldman's

collecting notes ("Mammal Notes from Encarnacion, Hidalgo, Mex. . . ." in manuscript and in the files of the U. S. Fish and Wildlife Services, Washington, D. C.), namely: "I saw a hunter's skin of this species [*S. aureogaster*] but failed to get any specimens. They are said to be very scarce here. Black squirrels with chestnut on lower parts are described by the native hunters and may belong to this species." Thus, the nature of the interaction between the Socialis and Aureogaster groups in the Querétaro-Hidalgo region cannot be resolved with the available specimens. Series are needed from highlands and from lower elevations down to the coastal plain.

NORTHERN PUEBLA-VERACRUZ.—Populations from the high mountains of northern Puebla near Cruz Alta (elevations, 9000–10,000 feet; sample 51) and those represented by sample 52 from lower slopes to the east near Zacapoaxtla (about 5000 feet) and Apulco (4500 feet), and to the northeast near Huauchinango (Scapa, between 4000 and 4500 feet) and northeastern Hidalgo (6600 feet) are Socialis forms with frosted gray or pigmented underparts, expansive nape and rump patches, no shoulder and costal patch, inconspicuous postauricular patches, and black-speckled feet. Melanistic phases are rare. Squirrels from near Cruz Alta are from extensive oak and conifer forest. Samples from Zacapoaxtla, Apulco, Hidalgo, and Scapa are from the lower limits of those forests where they meet with tropical broadleaf formations.

Squirrels from the adjoining lowlands of Puebla and Veracruz (samples 7 and 8), at elevations below 2500 feet, are Aureogaster types in which patterns 1, 7, 8, and 11 occur (Fig. 20). These are like the squirrels of Tamaulipas and San Luis Potosí except that the shoulder and costal patch is slightly smaller (scores 2 and 3), broad orange nape patches occur on all nonmelanistic specimens, and about half of the specimens have either expansive or smaller buffy rump patches. Thirty-four per cent of the sample is melanistic. A few specimens, for example those from San Marcos (Kelson, 1952:247), are patterned like those from Zacapoaxtla; they have broad orange-red nape and rump patches that break up a gray dorsum, frosted gray underparts, and no shoulder and costal patch.

Throughout the lowlands in this region, either the original forest or secondary growth (as near Papantla, Veracruz) is broken up by milpas, other agricultural crops, and pasture land. Tropical evergreen forest was extensive near Metlaltoyuca, Puebla, (Goldman, 1955:233).

The genetic influence of Socialis types apparently gradually diminishes to the north until in Tamaulipas squirrels are essentially of the Aureogaster type, only an indistinct nape patch recalling the Socialis Group (Fig. 25).

I lack specimens from intervening areas on the eastern slopes of the Mexican Plateau between 4000 and 2000 feet where populations of the

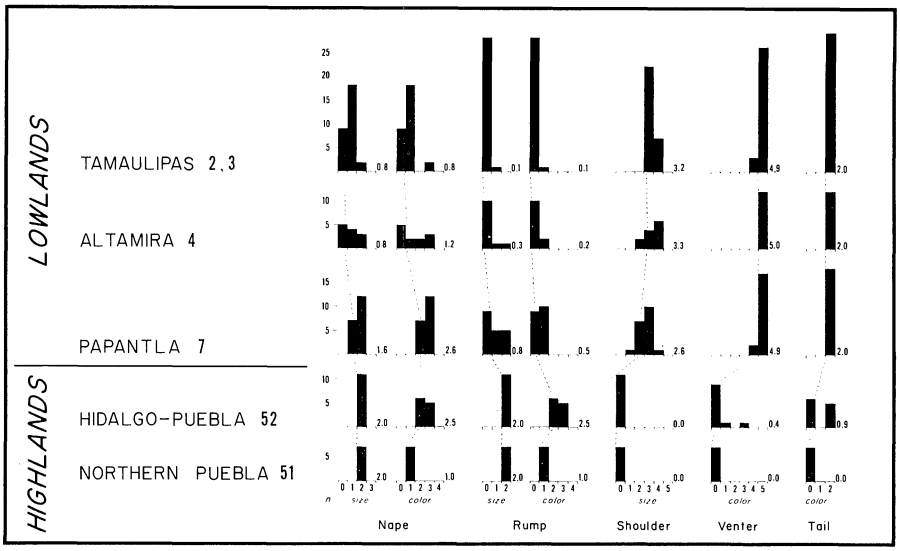


FIG. 25. Frequencies of some pelage features in the highland Socialis Group (samples 51 and 52) and lowland Aurcogaster Group (samples 2–4 and 7) of *Sciurus aureogaster* in northeastern Puebla, northern Veracruz, and Tamaulipas. Mean score for each trait is indicated beside each histogram, dashed lines connect those means. Distances between base lines of histograms are not proportional to geographic distances.

two groups may actually come together. The specimen from Scapa is the highland sample geographically closest to those of the lowlands. It is a Socialis type with expansive orange nape and rump patches, orange underparts and tail, and no shoulder and costal patch. Samples from the lowlands geographically nearest the Plateau are from 18 airline miles east of Scapa, elevation 1200 feet, and from the vicinity of Apapantilla, 1000–2200 feet. The five specimens from these localities fit within the range of morphological variation of specimens from lower elevations toward the coast—near Papantla, Veracruz, for example. Three examples are melanistic, two have orange-red or chestnut underparts and tails, orange nape patches, buffy rump patches, and a shoulder and costal patch extending well onto the sides of the body.

Gene exchange between highland populations of Socialis and lowland populations of Aureogaster in the northeastern Puebla-Veracruz region was probably facilitated, at least in part, by human modification of the original forests. Pine and oak forests, now extensively thinned and in many places cut out and replaced by milpas, extend to the edge of the Mexican Plateau near Huauchinango and gradually thin out downslope (Hooper, 1957:2), giving way to tropical and subtropical forests. Lower slopes of the plateau,

from 4000 to 2500 feet, were probably originally covered by cloud forest—as mapped by Leopold (1959)—similar to the cloud forests along the Sierra Madre de Oaxaca. Patches of this forest, usually thinned or replaced by second growth, occur in the vicinity of Villa Juárez (about 3600 feet), but it is also disrupted by milpas, coffee groves, and other clearings converted to agricultural crops. I have hunted the forests around Villa Juárez and seen only *Sciurus deppei*. Emmet T. Hooper, who earlier collected in the same area, obtained specimens of *deppei* and noted in his field notes that the local residents said two other kinds of squirrels occurred in the forest with *deppei*. One was black, the other dark gray with a red belly, with red patches on shoulders and sides. Members of Hooper's party saw both phases, but obtained no examples.

Central Veracruz.—Gene exchange between populations of highland Socialis and lowland Aureogaster apparently occurs on the slopes of the Cofre de Perote and Pico de Orizaba. The transition from Socialis to Aureogaster patterns in samples from the highlands of Puebla, Hidalgo, and Las Vigas, through Xico and Jalapa to the lowlands of central Veracruz, Tabasco, and Chiapas is documented in Figure 26. Squirrels of oak-pine forests near Las Vigas and below Las Minas (sample 53) on the edge

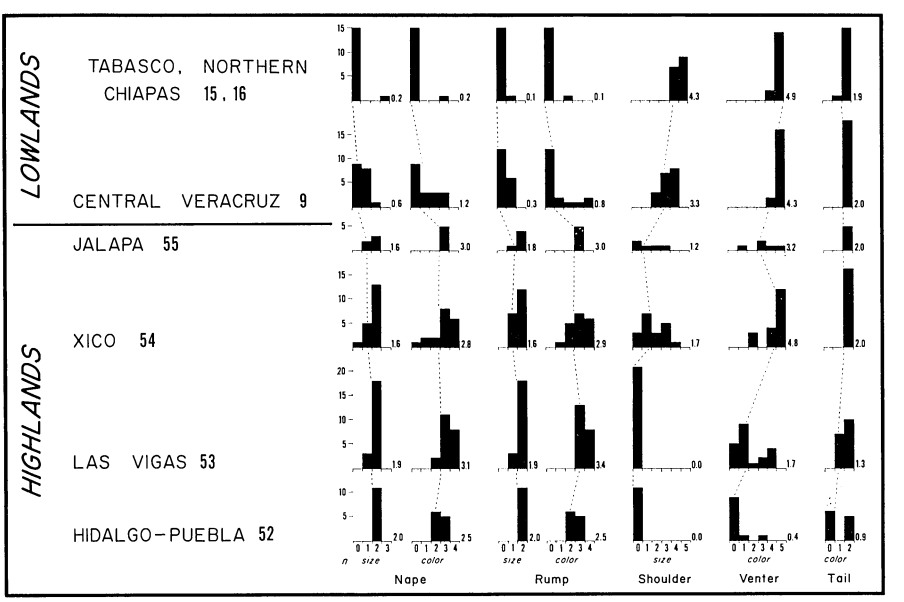


Fig. 26. Frequencies of various pelage traits in the highland Socialis Group (samples 52–55) and lowland Aureogaster Group (samples 9 and 15–16). Samples from Hidalgo, Puebla, Veracruz, Tabasco, and Chiapas. See legend of Figure 25 for explanation.

of the Plateau resemble those from Zacapoaxtla (sample 52), but average darker and are more deeply pigmented; they are clearly Socialis types that morphologically intergrade with the Zacapoaxtla series and occupy a similar habitat (p. 53).

Forests on Gulf slopes of the Cofre de Perote, from Jalapa (4500 feet) to the higher slopes above Xico (between 5000 and 6500 feet), are occupied by squirrels like those from Las Vigas in all morphological features but two: the majority of specimens have orange-red or chestnut underparts and a shoulder patch that varies from a low crescent (score 1) to a distinct chestnut saddle (score 4). They are dark, red-bellied squirrels with frosted blue-gray upper parts broken by broad orange-red or chestnut nape and rump patches and a chestnut shoulder and costal patch; thus pattern 7 (Fig. 20) is typical, a pattern that is probably the result of gene exchange between populations of Aureogaster and Socialis. Not all of the sample is composed of intergrades, however, for several specimens from the series above Xico lack a shoulder and costal patch and are indistinguishable from the orange-bellied squirrels of Las Vigas. Melanism is confined to the crown, feet, and tail of the Cofre de Perote specimens, as it is in the Las Vigas squirrels. Specimens from higher elevations on the Cofre (10,500 feet on the north slope) and those from farther south on the higher slopes of the Pico de Orizaba (vicinity of Malacara, at 9600 feet on the south slope) appear to be part of the same population of intergrades; they closely resemble examples from Jalapa and those from above Xico.

The series from the east slopes of the Cofre de Perote above Xico were collected by Nelson and Goldman in 1893. Most specimens were obtained at elevations above 5000 feet. Goldman (1951:273) described the region and indicated that above approximately 5500 feet the slopes were covered by a mixed forest in which oak predominated. Oak and conifer forests occurred at higher elevations. The original forest had been cleared from the lower slopes. I worked in the region west of Xico in 1963 and 1964 and my observations on the habitat accord with Goldman's. Jalapa and Xico are within the cafetal zone. Most of the original forest has been cleared and the region converted to agricultural products—coffee, corn, and orange and banana groves, for example—and about two miles west of Xico the lower slopes of the Cofre have been converted to pasture and milpas. Judging from the patches of forest left in steep canyons just west of Xico, the original cover was probably cloud forest that gave way to humid oak and conifer forest at higher elevations on the east slopes of the Cofre. The disruption of the original habitat may have been an important factor in facilitating contact and then gene exchange between populations of Socialis and Aureogaster in this area.

Squirrels of the lowlands of central Veracruz to the south (sample 9) are Aureogaster types but an indistinct nape patch persists in about half the sample and about one-third of the sample has an indistinct rump patch. Squirrels of regions farther to the east in Tabasco and northern Chiapas (samples 15 and 16) are Aureogaster types, with almost no Socialis features.

ISTHMUS OF TEHUANTEPEC.—Apparently gene exchange occurs between Aureogaster of the Gulf regions of the Isthmus and Socialis of the Pacific side (Fig. 27). Squirrels of the Pacific coastal plain and highlands near Tehuantepec to southwestern Chiapas (samples 22–24) are Socialis forms; they have broad orange nape patches but usually no rump patches. Seventeen per cent of the combined samples have an orange shoulder and costal pattern that is usually small (score 1), rarely expansive (three specimens were scored 2, one received a score of 3). The frequency of this patch is higher in the Tehuantepec series than in samples from areas to the east or west along the Pacific lowlands. Other aspects of their pelage were discussed elsewhere (p. 59).

Series from Gulf areas of the Isthmus of Tehuantepec (samples 11–13), though as a group are basically the dark southeastern Aureogaster types, are variable in composition of patterns. For example, in sample 11 from the

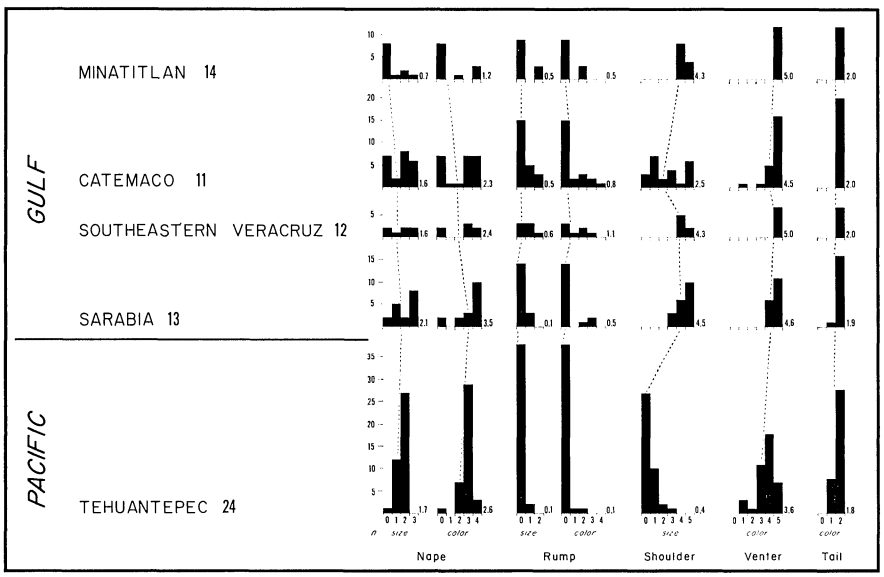


FIG. 27. Frequencies of some pelage features in the Pacific Socialis Group (sample 24) and Gulf Aureogaster Group (samples 11–14) of the Isthmus of Tehuantepec. See legend of Figure 25 for explanation.

Catemaco region about one-third of the specimens fall under pattern 8, the remainder under patterns 4, 6, 7, and 9–11; the range is greater than in samples from areas north and east of Catemaco (Fig. 20). A sample from one locality, part of 21 specimens collected south of Catemaco in two days, is illustrated in Figure 22. Most of the specimens were collected in the vicinity of a large fig tree in second-growth tropical broadleaf forest that was probably originally tropical evergreen. Ten examples are melanistic and range from the black to partial melanistic phases; the transition from melanistic to gray phases is gradual and complete in the sample. The gray phases include specimens with Socialis patterns, those with Aureogaster patterns, and examples that combine features of both.

Socialis features occur less frequently in samples of Aureogaster from farther east, near Minatitlán, and are absent or rare in series from Tabasco and northern Chiapas (Fig. 26). Series from the Isthmus contain: (1) Socialis forms similar to those from the Pacific coastal plain, (2) intergrades, and (3) mixtures of Socialis types and intergrades, as indicated below.

Differences in external and cranial dimensions between samples from Pacific and Gulf sides of the Isthmus are slight and average.

Oaxaca: An adult (LACM 13748) from three miles east of Matías Romero resembles some squirrels from near Tehuantepec; it has an indistinct nape patch (score 1), a moderate shoulder and costal patch (score 2), and orange underparts. An adult (AMNH 145196) from the southern slopes of Cerro Laollaga at Potrero Gueladú also resembles specimens from Tehuantepec in most features, but in addition to having a broad orange-red nape patch, it has an orange saddle (score 4) and orange underparts and tail. Two adults and one juvenile (AMNH 190245–7) from 20 miles northeast of La Ventosa fit within the range of variation of the series from southeastern Oaxaca near Tapanatapec and are good Socialis types. Of the two adults from Cerro Atravesado, one (AMNH 145199) is a Socialis type with black-flecked buffy underparts, an orange-red nape patch (score 1), and no Aureogaster traits, but the other (AMNH 145197), besides having an expansive orange-red nape patch, has a conspicuous orange shoulder and costal patch (score 3) and orange underparts and tail.

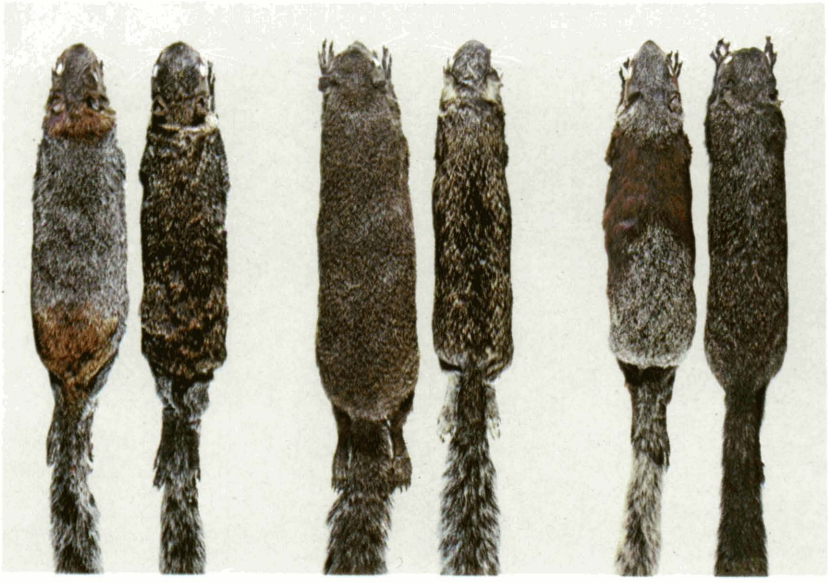
Chiapas: An adult (AMNH 147578) from Cinco Cerros near Cintalapa is like those from Arriaga or Tonalá—a good Socialis type with a broad orange nape patch and no shoulder or costal pattern; but an adult (CAS 10951) from twenty miles southwest of Cintalapa has an orange-red nape patch that is connected to a paler (orange) saddle (score 5).

Apparently at the present time there is continuous habitat suitable for tree squirrels across the Isthmus (see Duellman, 1960, for comments on vegetation of the Isthmus region) and no barriers to prevent gene flow.

FIGURES 28 AND 29

FIG. 28. Color and pattern of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis,* from left to right: *aureogaster* (sample 37; UMMZ 99949 ♀, Paso del Río, Colima) and *colliaei* (sample 59; UMMZ 113914 ♂, 17 mi SE Manzanillo, Colima), coastal plain of Colima; *aureogaster* (sample 19; AMNH 79357 ♂, San Lucas, Guatemala) and *variegatoides* (sample 63; AMNH 68528 ♂, Finca Salache, Guatemala), highlands and adjoining coastal plain of Guatemala; *aureogaster* (sample 15; KU 66542 ♀, 10 mi E, 19 mi N Macuspana, Tabasco) and *yucatanensis* (sample 65; LSU 8463 ♀, 12 mi NW Balancán, Tabasco), eastern Tabasco. See text.

FIG. 29. Categories of gradation from gray to blackish phases in samples of the Socialis Group from the Cordillera Volcánica in Michoacán, Estado de México, and Distrito Federal. From left to right, scores and phases are: (0) bright gray (UMMZ 109400 ♂, Lengua de Vaca, Estado de México); (1) dark gray (OC M-125 ♂, Puerto Morillos, Michoacán); (2) tawny (UMMZ 112586 ♂, E La Marquesa, Distrito Federal); (3) dirty-gray (UMMZ 112588 ♀, La Marquesa, Distrito Federal); (4) grizzled-black (UMMZ 102756 ♂, Lengua de Vaca, Estado de México); and (5) blackish (OC M-138 ♀, Lengua de Vaca, Estado de México). See Figure 23.



Cloud forest, which may be a barrier, is spotty in distribution (patches on Cerro Atravesado, Cerro Azul, and Cerro Baul, for example, as noted by Goodwin [in press]). Specimens from the Pacific lowlands and uplands are from dry pine-oak and scrub forests, and tall tropical broadleaf forest along streams and rivers. The majority of specimens from the Gulf side are from humid tropical, mostly evergreen, broadleaf forest. Those from intervening localities have been taken in both dry and humid oak-pine forests and in scrub forests, all on Pacific slopes.

NORTHERN CHIAPAS-GUATEMALA.—Some of the evidence for intergradation between populations of Aureogaster and Socialis in northern Chiapas is diagrammed in Figure 30. Shown there are frequencies of particular pelage features in samples from lowland Tabasco and Chiapas, Pueblo Nuevo, and the Mesa Central of Chiapas. Squirrels from the Gulf lowlands of Tabasco and Chiapas (sample 15) and from higher elevations in foothills of the Mesa Central (sample 16) are Aureogaster types. Most of the latter are slightly paler than those from lower elevations and there is no melanistic phase in the series.

The small sample from elevations of 5000–6000 feet, on the rim of the Mesa Central near Pueblo Nuevo (sample 17), varies in pelage pattern (Fig. 20) from an extreme (UMMZ 84118, for example) like the highland Socialis types in sample 18 (upper parts broken only by a nape patch, orange underparts) to those that resemble pale versions (UMMZ 114709, for example) of the Aureogaster types from lower elevations in the Gulf foothills of the Mesa Central (grayish dorsum broken by an orange saddle, orange-red underparts). Intermediate pattern combinations occur in the sample. Samples from regions to the southeast in the northern Chiapas highlands (sample 18) are Socialis types. The genetic influence of Aureogaster is still evident as judged by a pale shoulder and costal pattern—ranging from small (score 1) to expansive (score 4)—in 61 per cent of the sample.

All samples of Socialis available from the highlands of northern Chiapas—from near San Cristóbal to Lagos Montebello near the Chiapas-Guatemala border—show some pelage features of Aureogaster. Populations of the two forms may intergrade throughout northern Chiapas, for pine-oak forest occurs both in the highlands of the Mesa Central and at lower elevations below the cloud forest belt where it covers the higher ridges and interdigitates with tropical evergreen forest (Leopold, 1959; Dressler, 1957). I have no samples from intervening regions between the Mesa Central and the Gulf limestone ridges and tablelands from Simojovel to the Selva Lacandona in eastern Chiapas. The geographically closest samples are those of the Socialis-Aureogaster intergrades from Pueblo Nuevo taken in

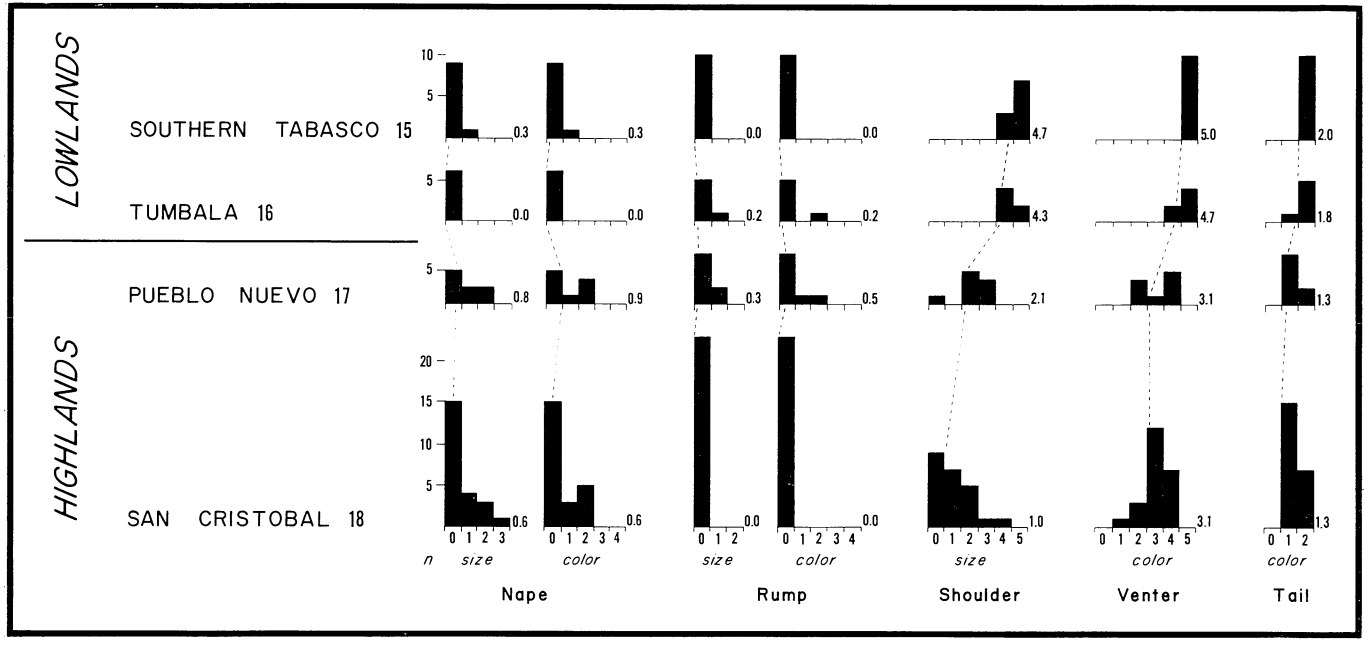


FIG. 30. Frequencies of some pelage traits in samples of the highland Socialis Group (samples 17 and 18) and lowland Aureogaster Group (samples 15 and 16) from the highlands of northern Chiapas and adjoining Gulf lowlands of Chiapas and southern Tabasco. See legend of Figure 25 for explanation.

humid oak and pine forest and one Aureogaster type from Simojovel, about eight airline miles to the northeast of Pueblo Nuevo at an elevation slightly above 2000 feet, from tropical evergreen forest (virgin forest according to the collector's notes on the skin label). These two localities are separated by rugged precipitous slopes once mostly covered by cloud forest.

Series from northwestern Chiapas and Guatemala include intergrades between Socialis and Aureogaster. For example, sample 21 from tropical deciduous and scrub forests in the region of Tuxtla Gutiérrez, Chiapas, is a *potpourri* that in features of pelage combines traits of the Socialis types from the Mesa Central and the Pacific side of the Isthmus of Tehuantepec, and features of Aureogaster from the Gulf lowlands and uplands.

The sample from the vicinity of San Juan Ixcoy, at elevations above 7000 feet in the Sierra de los Cuchumatanes of northwestern Guatemala (part of sample 19), contains at least one intergrade, an adult which is a duplicate in color and pattern of some intergrades from Cofre de Perote in central Veracruz.

RELATIONSHIPS OF *SCIURUS AUREOGASTER, S. COLLIAEI, S. VARIEGATOIDES,* AND *S. YUCATANENSIS*

Sciurus aureogaster (sensu latu), S. colliaei, S. variegatoides, and *S. yucatanensis* are morphologically close, and are mostly or entirely allopatric. Various interrelationships of these species are discussed below.

S. colliaei: Known distribution is along the lowlands and mountains of the Pacific Coast from southern Sonora through Sinaloa and Nayarit to northwestern Colima, and along the Pacific slopes of the Sierra Madre Occidental in Chihuahua, Durango, and parts of Sinaloa (Fig. 1). Known altitudinal range is from sea level (Barro de Navidad, Jalisco, for example) to 4300 feet in Chihuahua (Barranca de Cobre), 6600 feet in Sinaloa (south of Revolcaderos), 6500 and 7300 feet on the Sierra de Autlán and Sierra de Cuale, respectively, of Jalisco.

Habitat is primarily tropical or subtropical forests as follows: oil-palm forests intermixed with fig and other native tropical broadleaf trees surrounding lagoons (near Barro de Navidad for example, see Hooper, 1955:4); tropical deciduous forest on slopes below the oak-pine belt of the Sierra Madre Occidental and western margins of the Mexican Plateau; and cloud forests of pine, oak, fir, and hardwoods such as basswood, walnut, and alder on the Sierra de Autlán (Hooper, 1955:4). To the north *colliaei* occurs farther inland. In Sonora, for example, there are specimens from oak forests on upland slopes and from riparian formations in canyons that dissect the Sierra Madre (see Burt, 1938:38, for notes on habitat in Sonora).

Morphology of *colliaei* was described by Nelson (1899; under the names *truei, sinaloensis, colliaei,* and *nuchalis).* Size similar to *aureogaster;* upper parts variegated buff (or orange) and black; overhairs black, broken by a subterminal buffy band; shoulders, thighs, feet, and sometimes sides of the body gray; postauricular patches vary from white to buff; underparts usually white (whitish-orange or orange rare); tails white suffused with black dorsally, ventrally, variegated buff (or orange) and black midventral strip margined by black, then white; no melanistic phases. There are north-south clines of increasing size and pigmentation (Anderson, 1962).

S. colliaei is known to occur sympatrically with only one other species of *Sciurus,* a fox squirrel, *S. nayaritensis.* The two species have been taken in Jalisco on the Sierra de Cuale (according to the collector's notes, *colliaei* was collected in a canyon in subtropical broadleaf vegetation, *nayaritensis* was taken on the slopes in pine) and observed together in Sinaloa. They probably are sympatric elsewhere along the western margins of the Sierra Madre Occidental northward to Chihuahua.

S. colliaei is allopatric with the Socialis Group of *aureogaster* in Nayarit and Jalisco. There *colliaei* occurs in the lowlands and highland outliers of the Mexican Plateau and *aureogaster* is found only on the Plateau where it has been taken as low as 3500 feet near La Toma (1–2 miles north of Tequila, Jalisco). Altitudinal and ecologic limits of the two species are unknown. All specimens I have examined from this area are either *colliaei* or *aureogaster,* but the differences are not pronounced, particularly those between *aureogaster* from the Jalisco-Nayarit region on the Plateau (sample 41) and *colliaei* from adjoining lowlands of the Pacific coastal plain and highland spurs of the Plateau. The two series are similar in external and cranial dimensions, and in many features of pelage. In *colliaei,* however, the variegated, blended buff and black extends over the back from nape to rump, upper parts are brighter and darker than in *aureogaster,* and pelage is shorter and thinner than in that species. In the Plateau sample of *aureogaster* the variegated buff and black is restricted to the nape and rump forming either distinct or pale and inconspicuous patches. The back is gray in most specimens but some have a buff suffusion between nape and rump patches. These are the major pelage differences between the two species.

Since I have not worked in the Jalisco-Nayarit area I have no first hand knowledge of the ecological distribution of the two species. If interbreeding occurs at all between *aureogaster* and *colliaei* I would expect to find evidence of it in this region and not in Colima where the two species are closely allopatric and morphologically distinctive.

On the coastal plain of Colima populations of *colliaei* and *aureogaster*

occupy similar habitats and are represented by samples taken about three airline miles apart (Fig. 1). James H. Brown and I worked in the region in the latter half of May, 1964. We obtained samples of both populations from oil-palm forests intermixed with figs and other native tropical broadleaf trees along the northeastern margin of the Laguna de Cuyutlán. Both species were feeding on nuts of coquito palms and figs. Large globular leaf nests were common in the tall figs and other broadleaf trees.

This population of *colliaei,* geographically closest to *aureogaster,* consists of large dark squirrels (described under the name *nuchalis)* that represent the southern end of a cline in color and size within the species (Anderson, 1962). In this region, *colliaei* is larger than *aureogaster* (e.g., in cranial length, Figs. 6 and 31; Table 6) and the two species differ in color and pattern as listed below (sample 59 versus sample 37 and Figure 28).

Feature	*aureogaster*	*colliaei*
Postauricular patches	white, usually conspicuous	whitish but often tinged with buff and less distinct
Upper parts	frosted blue-gray broken by orange nape and rump patches; overhairs of back either black with white tips or black with wide subterminal orange bands; hairs of nape and rump gray basally, then orange tipped with black	unpatterned; most overhairs black with narrow subterminal buffy bands, white-tipped hairs restricted to sides of body, thighs and feet, sometimes scattered over back; backs often blackish resulting from overlay of long black tips of overhairs
Underparts	usually white (1 out of 25 specimens is whitish-orange)	usually white (of 37 specimens, 9 are whitish-orange, 1 is chestnut)
Tail	variegated grayish-buff	variegated orange or chestnut

In summary, *aureogaster* and *colliaei* occupy similar habitats along the Pacific coastal plain of Colima. *S. colliaei* is large and dark with variegated buff and black upper parts, white underparts, and an orange tail; *aureogaster* is smaller, with distinct bright nape and rump patches, a blue-gray back, white underparts, and a grayish tail. Distributional limits of the two species are incompletely known. If the species are sympatric, overlap is probably narrow. The range of *colliaei* may extend along the southwest margins of the Laguna de Cuyutlán and meet that of *aureogaster* again somewhere along the southeastern coastal plain of Colima. These aspects require further study.

S. variegatoides: Known geographic range is from southeastern Chiapas to Panama (Hall and Kelson, 1959:381). The segment geographically closest

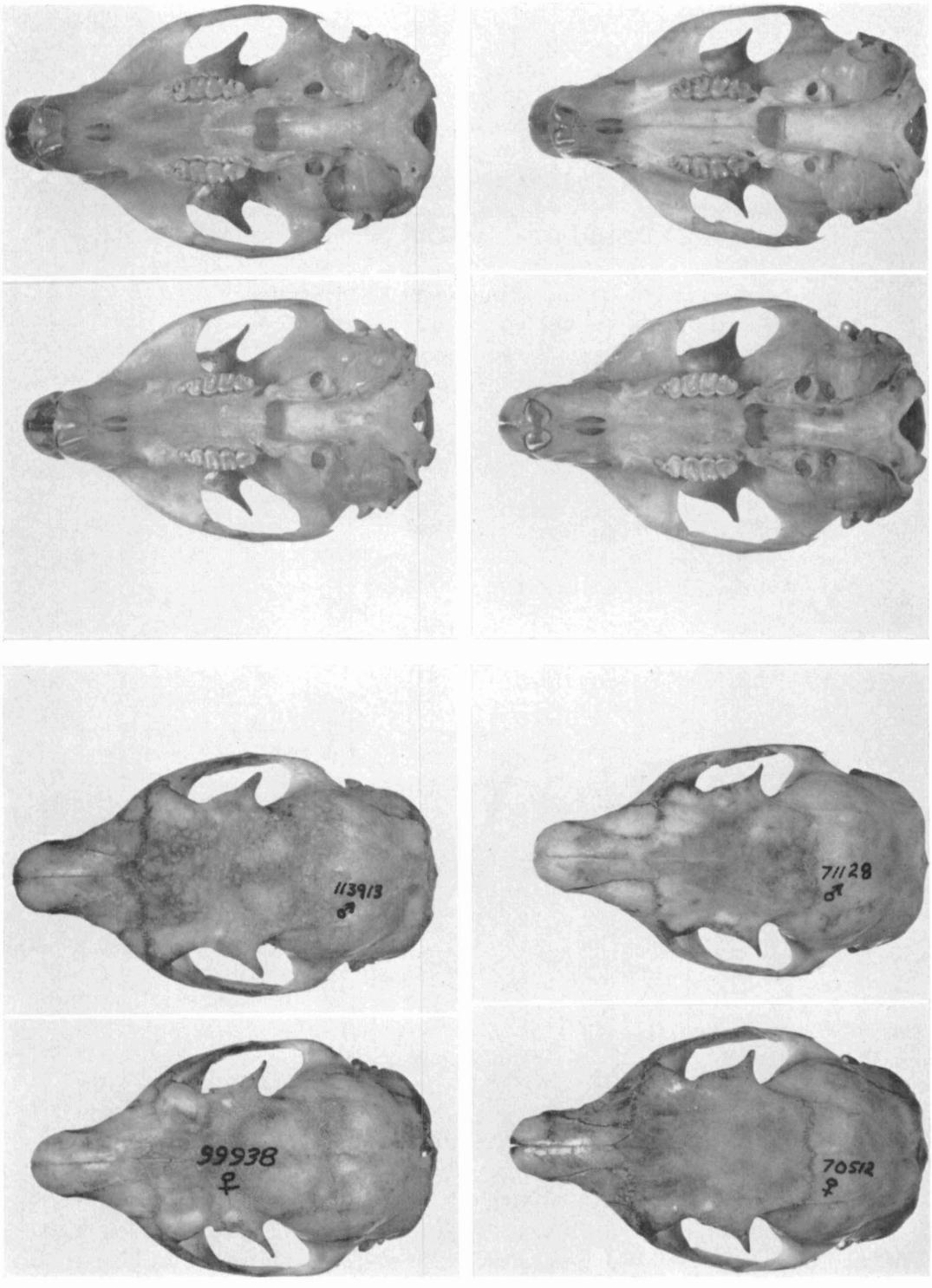


FIG. 31. Ventral (above) and dorsal (below) cranial views (natural size) contrasting *Sciurus aureogaster* (lower figure in each set of views) with *S. colliaei* (left-hand column) and *S. variegatoides* (right-hand column). Left, *aureogaster* (sample 37; UMMZ, Paso del Río, Colima) and *colliaei* (sample 59; UMMZ, 17 mi SE Manzanillo, Colima) from coastal plain of Colima. Right, *aureogaster* (sample 19; AMNH, Chichicastenango, Guatemala) and *variegatoides* (sample 63; AMNH, Finca Cipres, Chiapas) from southeastern Chiapas and Guatemala.

to *aureogaster* (Socialis Group) occurs along the Pacific coastal plain and uplands of southeastern Chiapas and Guatemala. Originally described as *S. goldmani* (Nelson, 1898:149; 1899:82), but later considered a subspecies of *variegatoides* (Harris, 1937) with which it fully intergrades.

My comments pertain only to this *(goldmani)* segment of *S. variegatoides.* Known geographic range extends from southeastern Chiapas through southern Guatemala (Fig. 1). Known altitudinal range is from near sea level along the coast (25 feet, south of Mapastepec, Chiapas, for example) to 4900 feet (San Pedro Yepocapa in Guatemala) along the flanks of the Guatemalan highlands. All known specimens are either from tropical evergreen and rain forests or from drier and partly deciduous tropical forests surrounding lagoons. We have taken them south of Mapastepec (Chiapas) in forests of nut palms intermixed with figs and other tropical broadleaf trees on the coastal plain. Farther inland, the species occurs in tropical rain forest that has been thinned to shade coffee and cacao. This habitat is typical of most of the collecting sites in Chiapas and Guatemala (see Griscom, 1932, for Guatemalan sites Finca Cipres, Hacienda California, and Finca Carolina). *S. variegatoides* has not been taken in the pine and oak forests above the rain forest or cafetal zone in Chiapas or Guatemala, though it lives in pine-oak habitats farther south in Honduras and Nicaragua.

In color and pattern, *S. variegatoides* from Chiapas and Guatemala closely resembles the southernmost population of *S. colliaei (nuchalis).* Like that form, *variegatoides* has variegated buff and black upper parts (which cover the sides and thighs that are grayish in *colliaei).* White or buff-tinged postauricular patches are larger and more distinct than in *colliaei,* upper parts are paler (not as black), feet are white and slightly peppered instead of frosted black or black, underparts are white, and the tail is variegated buff. There is no known melanistic phase. Nelson (1899:83) lists other minor differences, among which are coarseness and stiffness of pelage, which I do not appreciate. The Chiapas-Guatemala population of *variegatoides* also resembles *colliaei* in external dimensions but is appreciably smaller in cranial measurements (Fig. 6), and sphenopalatine vacuities occur more frequently (Fig. 7).

In the Chiapas-Guatemala region *S. variegatoides* is sympatric with *S. deppei* (at least at Finca Carolina; Goodwin, 1934:25), and is allopatric with *S. aureogaster.* In southern Guatemala, *aureogaster* occupies forests of pine-oak and fir in the highlands and has not been taken in the lower belt of either tropical evergreen or rain forest. Specimens of *aureogaster* from the Sierra Madre de Chiapas are also from dry or wet oak-pine forest. In southwestern Chiapas, however, *aureogaster* occurs in tropical forest on the coastal plain. In the latter part of March, 1965, John Hubbard and I collected along a transect from Cacahuatán, about 2000 feet, near the

Chiapas-Guatemala border, northward to the flanks of Volcán Tacaná, 4000 feet, above Unión Juárez. The habitat at Cacahuatán is thinned rain forest that shades coffee, cacao, and mango groves. The few squirrels collected and seen were *variegatoides*. Unión Juárez is also in the cafetal belt. There, on the steep and deeply dissected flanks of the Volcán, remnants of rain forest persist in deep canyons—the slopes cleared and planted to coffee—and ridges are covered with oak and pine which merge with cloud forests of pine, oak, fir, and alder at higher elevations. We collected both *aureogaster* and *S. deppei* above Unión Juárez in oak and pine forest along the ridges, and all large squirrels seen there were *aureogaster*. In the steep canyons below the ridges we saw and obtained only *deppei*, which was common. We saw no squirrels between Unión Juárez and Cacahuatán.

In the Chiapas-Guatemala area, neither *aureogaster* nor *variegatoides* is strikingly patterned. *S. aureogaster* has a longer head and body, longer feet, shorter tail, and larger skull (Figs. 6 and 31; Table 6) with a greater frequency of open, larger sphenopalatine vacuities (Fig. 7). Contrasting pelage features are shown in Figure 28 and listed below (samples 19 and 63).

Feature	*aureogaster*	*variegatoides*
Postauricular patches	either dirty white and indistinct or absent	large white conspicuous tufts, sometimes tinged with buff
Upper parts	usually without pattern; sometimes indistinct nape and rump patches, or only nape patch; back is either buff flecked with black (overhairs with alternating black and buffy bands) or frosted blue-gray suffused with orange (hairs alternately black and orange banded but white-tipped)	unpatterned as in *colliaei;* hairs of back black with subterminal buff or orange band, some black; overall effect is blended variegated buff and black
Feet	frosted buffy black or blackish	whitish, slightly speckled with black
Underparts	orange or chestnut, often black-flecked	white, rarely pigmented
Pelage	long, soft, dense; abundant underfur	slightly coarser and shorter; little underfur

Northwestern distributional limits of *variegatoides* along the Pacific coastal plain in Chiapas and its distributional relations with *aureogaster* from the lowlands of southwestern Chiapas are unknown. The northwestern-most sample of *variegatoides* is from the coastal plain about 19 kilometers south of Mapastepec. We hunted farther north in the forests sur-

TABLE 6

EXTERNAL AND CRANIAL MEASUREMENTS (MM) OF *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis*

Species and Locality	Lengths: M.±S.D., 95% C.L., (Extremes), and N.				
	Head and Body	Tail	Hind Foot	Ear	Cranium
aureogaster	253.9± 9.7	263.0±15.8	64.8±2.2	32.0±1.9	59.99± .74
Colima (37)	249.1–258.7	254.9–271.1	62.7–65.8	31.1–32.9	59.62–60.36
	(237–273)	(235–291)	(61–68)	(29–35)	(58.2–60.9)
	18	17	20	20	18
colliaei	268.5±11.9	275.8±14.6	67.8±2.7	33.3±1.7	62.88±1.09
Jalisco-Colima (59)	263.8–273.1	270.3–281.4	66.9–68.7	32.8–33.9	62.50–63.26
	(226–295)	(247–305)	(63–73)	(30–36)	(61.3–64.9)
	28	29	34	33	34
aureogaster	254.6± 6.8	234.2±10.3	62.8±2.7	29.6±1.2	58.87± .89
Chiapas-Tabasco (15)	250.8–258.2	228.7–239.7	61.3–64.2	28.9–30.2	58.35–59.39
	(242–265)	(206–247)	(57–66)	(28–31)	(57.5–60.2)
	16	16	16	16	14
yucatanensis	232.5± 9.2	250.0±11.3	61.5± .7		55.40± .56
Tabasco (65)					54.02–56.78
	(226–239)	(242–258)	(61–62)		(54.8–55.9)
	2	2	2		3

TABLE 6 (Cont.)

Species and Locality	Lengths: M.±S.D., 95% C.L., (Extremes), and N.				
	Head and Body	Tail	Hind Foot	Ear	Cranium
yucatanensis	242.1±14.3	241.5±11.3	58.3±3.1	20.8±3.2	55.34±1.13
Chiapas-Guatemala (64)	231.8–252.4	233.4–249.6	56.1–60.5	18.5–23.1	54.39–56.29
	(208–260)	(220–255)	(53–62)	(17–28)	(53.7–56.9)
	10	10	10	10	8
aureogaster	273.1±14.7	243.7±17.3	68.5±2.6	32.1	60.80±1.23
Chiapas-Guatemala	268.4–277.8	238.1–249.2	67.6–69.4		60.41–61.18
Highlands (19)	(249–310)	(208–277)	(65–74)	(29–35)	(57.9–64.2)
	40	40	33	8	41
variegatoides	260.7±15.1	270.8±14.5	64.4±3.1	32.2	59.38± .81
Chiapas-Guatemala	255.2–266.1	265.5–276.1	63.3–65.5		59.10–59.65
Coastal Plain (63)	(210–291)	(240–305)	(60–70)	(29–34)	(57.8–60.8)
	32	31	31	11	33
aureogaster	264.5±12.3	273.6±23.3	68.3±2.3	31.1±2.2	61.24±1.17
Chiapas Coastal	260.9–268.0	266.8–276.3	67.6–69.0	30.0–32.1	60.87–61.61
Plain (22)	(232–291)	(235–315)	(64–72)	(27–34)	(58.9–63.9)
	49	48	43	18	42

rounding the lagoons on the coastal plain southwest of Pijijiápan, found leaf nests but saw no squirrels. People living in the area told us that squirrels were uncommon, but did occur in small groups where the forest had not been completely destroyed. Their descriptions of those squirrels fit *variegatoides*. The species may extend in suitable habitat along the coastal plain to the southeastern flanks of Pico Vernal (see Selander, 1964:80), a small mountainous mass bounding the southeastern margin of Laguna de la Joya, but it is unlikely that it occurs farther to the northwest.

In summary, the Chiapas-Guatemala populations of *variegatoides* occur in tropical broadleaf forests while *aureogaster* occupies either the pine and conifer forests of the Sierra Madre de Chiapas and Guatemalan highlands or the lowland scrub and tropical deciduous forests west of Pico Vernal. The two species differ in size, but neither has strikingly patterned pelage. Vertical and horizontal distributional limits of each along the coastal plain of Chiapas to the northwest are unknown. Though the two species overlap altitudinally, nowhere have they been found to be sympatric.

S. yucatanensis: This species occurs in the Yucatán Peninsula, the Petén of northern Guatemala (Hall and Kelson, 1959:377), and eastern Tabasco and Chiapas (Fig. 1). Known altitudinal range of *yucatanensis* in areas geographically closest to *aureogaster* extends from about 200 feet (Monte Cristo, Tabasco) to 1600 feet (Secanquim, Guatemala). Habitat is primarily tropical broadleaf forest (either deciduous, evergreen, or rain forest), but the species also frequents semiarid pine-oak woodlands.

S. yucatanensis resembles *S. variegatoides* (Chiapas-Guatemala population) and *S. colliaei* in color and pattern, but is much smaller than either (Figs. 31 and 32; Table 6). In features of pelage *yucatanensis* from the northern segment of its range resembles *variegatoides* from the Pacific lowlands and uplands of southeastern Chiapas and Guatemala. Upper parts are variegated buff and black; postauricular patches conspicuous, either white or tinged with buff; shoulders, thighs, legs, and feet grayish; underparts white, usually flecked with black; and the tail variegated grayish or pale buff (Nelson, 1899:70, provides more details). To the south pelage is darker; appendages, ears, bellies, and tails tend to be melanistic; postauricular patches either dingy buff or obscured; and underparts buff flecked with black rather than white and black-flecked (where melanism doesn't obscure the color). These southern segments of *yucatanensis* have been described under the names *baliolus* (Nelson, 1901:131), which includes examples from Tabasco, and *phaeopus* (Goodwin, 1932 and 1934), applied to specimens from eastern Chiapas and Guatemala.

Throughout its range, *yucatanensis* is sympatric with *S. deppei*; both are found in similar habitats. Ranges of *yucatanensis* and *aureogaster,* however, are mostly allopatric. Available samples of *yucatanensis* and *aureogas-*

ter that are geographically closest to each other are from eastern Tabasco, where *aureogaster* (Aureogaster Group) may be narrowly sympatric with *yucatanensis*. I have not worked in that region and the only data available to me are based on nine specimens of *aureogaster* and one of *yucatanensis*, collected at Monte Cristo (about 200 feet elevation) by E. W. Nelson in May, 1900. In an annotated checklist of mammals collected at Monte Cristo (manuscript in the files of the U. S. Fish and Wildlife Services, Washington, D. C.), Nelson wrote that *aureogaster* (which he called *Sciurus hypopyrrhus*) was "rather common about a cacao plantation below Montecristo but scarce elsewhere." *S. yucatanensis* consisted of "A single specimen shot from a small tree where it was lying stretched out asleep one afternoon. Its nest of twigs and leaves in a fork of the tree top was only a few feet away and the squirrel had evidently left it on account of the heat. They are very scarce here and this must be about the extreme limit of the range of this species."

Though habitat information is meager, morphology of the two species in this area may be compared: *yucatanensis* is smaller than *aureogaster* in most dimensions, but has a slightly longer tail (Figs. 6 and 32; Table 6) and more frequently closed and smaller sphenopalatine vacuities (Fig. 7). The two are strikingly dissimilar in color and pattern (Figure 28), as indicated below (comparing sample 15 and 65).

Feature	*aureogaster*	*yucatanensis*
Eye ring	orange	dingy buff or blackish
Ears	margined with orange that connects via an orange stripe with eye rings	blackish
Postauricular patches	white and indistinct	usually absent, dingy buff when present
Upper parts	crown, nape (sometimes), and rump are frosted blue-gray (overhairs are orange basally, followed by a black band, tipped with white); crown and rump separated by broad chestnut saddle sometimes extending onto nape (scores 4, 5)	unpatterned; variegated buff and black like *variegatoides* or *colliaei* (hairs black with subterminal pale or rich buffy bands)
Underparts	chestnut	pale buff speckled with black
Tail	chestnut	blackish or variegated buff and black, like *colliaei* and *variegatoides*
Melanism	about half the sample are completely melanistic or nearly so	usually confined to ears, feet and legs, belly and tail, sometimes head

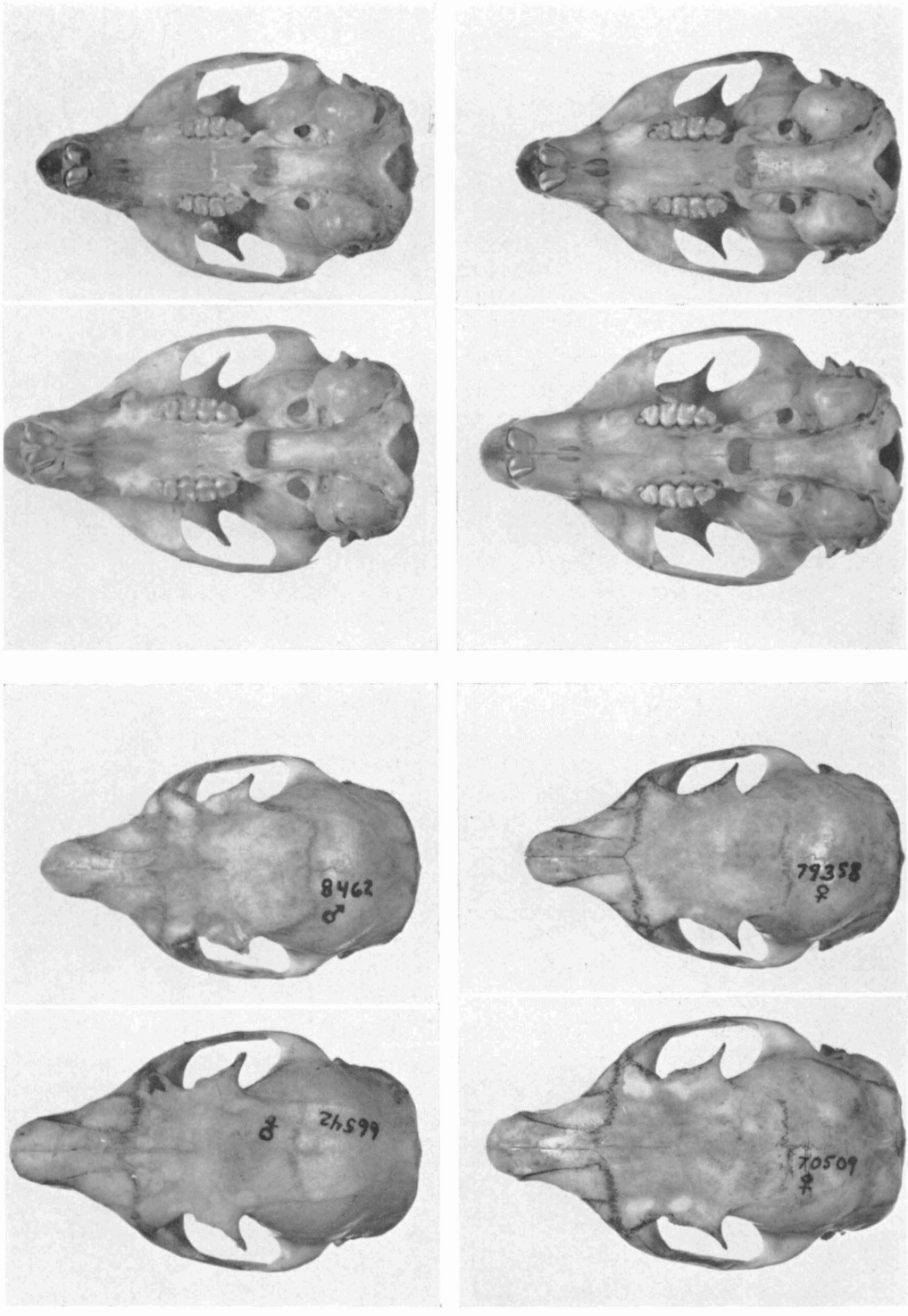


FIG. 32. Ventral (above) and dorsal (below) cranial views (natural size) contrasting *Sciurus aureogaster* (lower figure in each set of views) with *S. yucatanensis*. Left, *aureogaster* (sample 15; KU, 10 mi E, 19 mi N Macuspana, Tabasco) and *yucatanensis* (sample 65; LSU, 22 mi N Balancán) from eastern Tabasco. Right, *aureogaster* (sample 19; AMNH, La Primavera, Guatemala) and *yucatanensis* (sample 64; AMNH, Finca Chama, Guatemala) from eastern Chiapas and northern Guatemala.

S. yucatanensis is also allopatric with the Socialis Group of *aureogaster* in eastern Chiapas and Guatemala. There *yucatanensis* inhabits lowland forests and *aureogaster* occurs in the highlands, but precise distributional relations between the two are unknown. In Chiapas, *yucatanensis* has been taken near Sabana de San Quintin (215 meters) in tropical broadleaf forest. Samples from Guatemala (Alta Verapaz) are from two localities, Finca Chamá and Secanquim. They were obtained by A. W. Anthony in 1926 and 1928. His description of each locality (from Griscom, 1932:13, 15) follows:

"Chama.—A coffee finca thirty miles northwest of Coban, on the Rio Negro, here called the Rio Chixoy; altitude 1200 feet. The coffee plantation furnished most of the ground required for collecting, the shade growth being rubber and cacao, with a sprinkling of the native forest.

"Secanquim.—Ten miles north of Sepacuite; altitude 1600 feet. Pine and oak forest and considerable brush-land in abandoned fields." Goodwin (1934:Plate II) provides an illustration of the habitat at Secanquim.

The closest samples of the two species from this area are a series of *yucatanensis* from Finca Chamá and two specimens of *aureogaster* from the highlands south of Chamá, collected by Anthony at Finca La Primavera. He described the locality (in Griscom, 1932:13) as:

"La Primavera.—A sugar finca some fifteen miles east of Finca El Soche, and the same distance south of Coban, in Alta Vera Paz. Forest of pine, oak, and alder, with rain forest along the ridges, where the heavy rains fell. Altitude 3200 feet." Griscom (1932:79) and Goodwin (1934:pl. IV, fig. 1) provide illustrations of the habitat at La Primavera. See also Stuart (1950) for a broader discussion of the Alta Verapaz region.

S. yucatanensis is smaller than *aureogaster* from the Alta Verapaz region (Figs. 6 and 32; Table 6). Differences between the two species in color and pattern are of the same kind and degree as those between *aureogaster* from the Guatemalan highlands and *variegatoides* from southeastern Chiapas and Guatemala, except that the appendages, ears, belly, and tail are either partially or completely melanistic in *yucatanensis,* the postauricular patches are obscure, and the belly is grizzled-buff (if not melanistic).

In summary, *yucatanensis* is morphologically a small version of *variegatoides* and ecologically similar to it. *S. yucatanensis* is also smaller than *aureogaster*. Geographic ranges of *yucatanensis* and *aureogaster* (Aureogaster Group) overlap slightly in lowlands of eastern Tabasco; ecological relations between the two species there are unclear. Color and pattern of the two are strikingly different. In eastern Chiapas and the Alta Verapaz of Guatemala, *yucatanensis* occupies the lowlands, and the Socialis Group of *S. aureogaster* occurs in the highlands. There, too, habitat relations

between the two are obscure. Neither *yucatanensis* nor *aureogaster* is strikingly patterned or colored. There is no evidence in available samples that *yucatanensis* interbreeds with either the Aureogaster or Socialis groups of *S. aureogaster*.

CONCLUSIONS AND QUESTIONS

By studying the ecologic and geographic distribution of size, color, and pattern of pelage, it has been possible to define morphological limits of *S. aureogaster*. Those limits embrace two major segments within the species, the Aureogaster Group of eastern México and the Socialis Group of western México and Guatemala. As judged from morphological data, there is gene flow within each segment and between some populations of each segment (Fig. 33).

The evidence for intergradation between the Aureogaster and Socialis groups is based on pelage features, principally rump, nape, and shoulder patterns. The areas of intergradation are: (1) along the Gulf foothills of the Mexican Plateau in northern Veracruz and eastern Puebla; (2) on

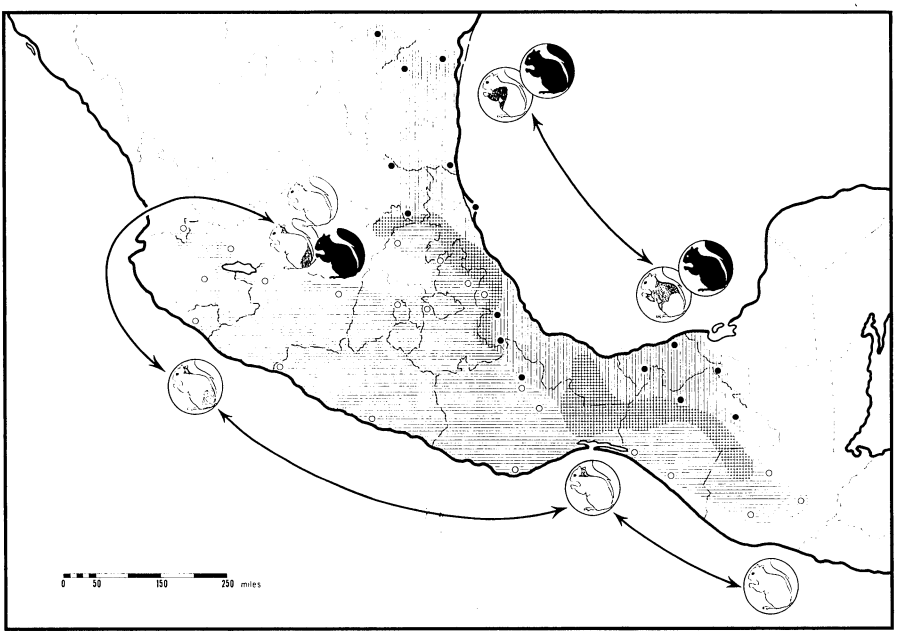


FIG. 33. Geographic ranges of the Aureogaster (dots, vertical lines) and Socialis (circles, horizontal lines) segments of *Sciurus aureogaster* and areas of intergradation between the groups.

the Gulf slopes of the Cofre de Perote and Pico de Orizaba; (3) across the Isthmus of Tehuantepec; and (4) along Gulf margins of the Mesa Central in Chiapas. In northern Oaxaca, however, the two groups act as allopatric species and apparently do not intergrade. This, plus peculiarities of intergradation between the groups, suggests that the two were once geographically (and apparently ecologically) isolated and have diverged almost to the species level, yet not to the point of reproductive isolation.

Though factors responsible for the distribution of size and most pelage features of *aureogaster* and their adaptive significance are unclear or unknown, some correlations seem likely. For example, variation in length and density of the pelage appears to be related to factors that vary with altitude, such as temperature and humidity. Length and density of the pelage probably play an important role in the thermoregulatory capabilities of the squirrels. The difference in tail length between montane populations of *S. aureogaster* and populations of the hot Pacific lowlands may also be partly related to thermoregulatory function. Length of the tail—relative to length of head and body—also is probably related to degree of agility and balance involved in movement through treetops. But what are the explanations for distributions of color and pattern? Is the distribution of pigmented underparts a result of introgression from the red-bellied populations of Aureogaster into the populations of Socialis or is its variance related to other factors? Are the nape and rump or shoulder and costal patterns cryptic—especially the patterns that are deeply pigmented and contrast sharply with grayish backs? Are such patterns particularly advantageous in forests where light penetrates the canopy (tropical deciduous forests, for example), producing an effect of alternating light and shadowed areas?

Factors controlling frequency of melanism in the populations are also unknown. Why are samples of the Aureogaster segment from Tamaulipas, San Luis Potosí, Querétaro, northern Veracruz, and Tabasco comprised primarily of either gray or black phases while in Gulf regions of the Isthmus of Tehuantepec the variation ranges from gray to black through an intermediate spectrum of partial melanistic gradations? Are those partial melanistic phases intensively selected against in the northern and southeastern populations and selectively neutral elsewhere? Or is melanism genetically linked with other characteristics and thus a phenotypic expression of a process or character which is actually the trait under selective pressure? Similar questions apply to the distribution of melanism in populations of Socialis types. Is the increase in frequency and kinds of melanistic phases across the Cordillera Volcánica a response to the increased frequency of cold and wet boreal forest formations in that area (see the discussion of

vegetation zones in Leopold, 1959)? Is frequency of pelage phases related to forest types as Serebrennikov (1931) suggested for *Sciurus vulgaris*? I don't know. Available data are insufficient to provide answers to these questions.

Several important conclusions result from study of relations between *S. aureogaster* and the other three Middle American gray squirrels, *S. colliaei, S. variegatoides,* and *S. yucatanensis.* First, the distribution of contrasting characters between *aureogaster* and each of the latter forms at contiguous zones is exclusive. At each of those areas the distinguishing features of *aureogaster* and its allopatric congener change in geographic directions away from the contiguous regions and not across them (Fig. 34). There is an indication that though there is gene flow in various directions within populations of *aureogaster, colliaei, variegatoides,* and *yucatanensis,* there is none between populations of *aureogaster* and the other three. This conclusion reflects the morphology of available samples and does not exclude the possibility that *aureogaster* hybridizes with those species. If it does, where and to what extent are presently unknown.

Secondly, the degrees of difference between *S. aureogaster* and the three kinds are unequal. Both the Aureogaster and Socialis groups of *S.*

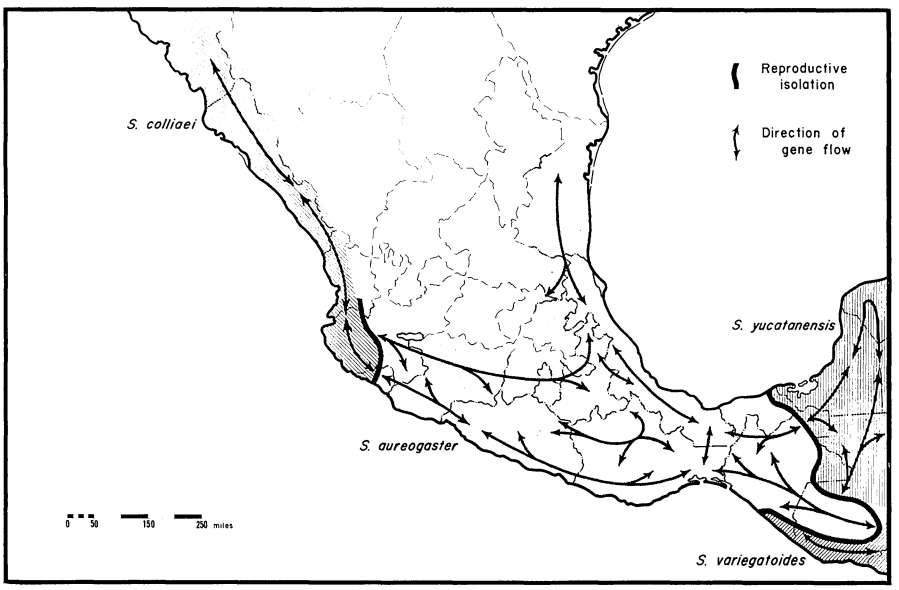


FIG. 34. Geographic ranges of *Sciurus aureogaster, S. colliaei, S. variegatoides,* and *S. yucatanensis,* and estimates of directions of gene flow as indicated by skin and skull and distribution of suitable habitats.

aureogaster are morphologically well differentiated from *yucatanensis* and *variegatoides* in size, color and pattern, and habitat between certain populations. The magnitude of differences between the Socialis segment of *aureogaster* and *colliaei* where populations of each occur on the coastal plain of Colima is similar to that between *aureogaster* and the *yucatanensis-variegatoides* populations. Indeed, if *aureogaster* and *colliaei* are sympatric in Colima, the character divergence between the two species in that area may be related to mechanisms involving species reinforcement. However, morphological differences between *colliaei* from western Jalisco and Nayarit and the Socialis segment of *aureogaster* from fringes of the Mexican Plateau in southern Nayarit and northwestern Jalisco are not as pronounced. There, the two species are similar in size and cranial configuration. Primary discriminating features between the two involve pattern of pelage and habitat. Total morphological and distributional aspects of *aureogaster* and *colliaei* in this region suggest that the two were once part of the same interbreeding population and have been separated for a shorter time, compared with other populations in areas of contact between *aureogaster* and *colliaei,* and between *aureogaster* and *yucatanensis* and *variegatoides.* Aspects of those populations suggest a much longer period of separation with accompanying marked divergence and the attainment of full reproductive isolation.

The third conclusion is that *colliaei, variegatoides,* and *yucatanensis* are strikingly similar in color and pattern of pelage, though they differ in size. For example, the range of variation in pelage features of some samples of *yucatanensis* from Yucatán fall within that of samples of *colliaei* from northern Nayarit and Sinaloa; specimens of each species are practically indistinguishable from one another. *S. yucatanensis* is also essentially a smaller version of the western and southwestern populations of *variegatoides.* Differences in pelage features between the two are of the same magnitude as those between adjacent, slightly differentiated and intergrading subspecies of *variegatoides* (between *goldmani* and *bangsi,* for example). But *yucatanensis* is smaller in cranial and external dimensions than nearby populations of *variegatoides.* Individual and geographic variation in *yucatanensis,* as well as aspects of its ecology and geographic distribution, are poorly known; the form is in need of systematic review. Judging from my studies there are indications that *yucatanensis* and *variegatoides* may intergrade.

Differences in pelage features between the western segment of *variegatoides* in southeastern Chiapas and southern Guatemala and the southernmost population of *colliaei* on the coastal plain of Jalisco and Colima are of the magnitude found between adjacent intergrading subspecies within both *variegatoides* and *colliaei.* Size is the most conspicuous difference between these geographically closest populations of each form,

The three forms, *colliaei, variegatoides,* and *yucatanensis* may be fragmented segments of a single species whose geographic range once extended along the Pacific lowlands and uplands from Sonora to southern Guatemala, across eastern Guatemala into the Yucatán Peninsula and throughout Central America to Panamá. Geographic distributions of segments now represented by *yucatanensis* and *variegatoides* remain relatively intact and the two may still connect (geographically and genetically) through eastern Guatemala and northwestern Honduras. The Pacific segment in México, however, was fragmented and the northwestern populations now represented by *colliaei* are at present separated from the southeastern populations *(variegatoides)* by a different but closely related species, *aureogaster.* Pelage features and known ecology of *colliaei, variegatoides,* and *yucatanensis* are in harmony with this hypothesis. So too is the geographic distribution of external and cranial dimensions in the three forms. Though the three differ in these features, the extremes are encompassed in *colliaei* which grades clinally from a small squirrel about the size of *yucatanensis* to one larger than *variegatoides.* The original, continuously distributed species may have been as variable in external and cranial dimensions.

The various biological interrelations between populations of *aureogaster* and those of *colliaei, variegatoides,* and *yucatanensis* merit further and detailed study to answer various questions. Is *aureogaster* sympatric in a microgeographic sense with any of the other three kinds? If so, how is the habitat utilized by each species in terms of food availability, establishment of home ranges and territories, and availability of nesting sites? Is pelage color and pattern important in species recognition, thereby reinforcing reproductive isolation between two sympatric forms? Or are other cues, such as vocal, olfactory, and behavioral, more important in pair formation? If *aureogaster* is not closely sympatric with any of the other three kinds, but is instead allopatric with them, does one species compete more aggressively for the available habitat to the exclusion of the other? And what is the effect of population size on competition between them? Does reproductive isolation ever break down? And if *aureogaster* does hybridize with any of the other three, what is the extent of that hybridization? Answers to these and other questions will greatly increase biological knowledge of Middle American gray squirrels.

TAXONOMY

The oldest name available for the species comprised of the Aureogaster and Socialis populations is *aureogaster,* a name that has been in the taxonomic literature since 1829 (Nelson, 1899:44). In my opinion, the geographic

variation within this species can be taxonomically treated by employing one of four alternatives.

At one extreme is to treat *aureogaster* as a monotypic species, formally recognizing no subspecies. Geographic variation within the species would then be documented by description and illustration as I have done in the previous sections on Morphological Variation, and Geographic Variation and Intergradation. My informal Aureogaster and Socialis "groups" would be recognized as segments of the species that designate populations which apparently act as allopatric species in some regions, but intergrade in other areas where barriers to reproductive continuity have been broken. Each segment contains different levels of variation, ranging from the local population to broader-based geographic variants, each level connected by gradual intergradation. This is a reasonable and defensible alternative. It will especially satisfy those workers who do not find the subspecies a useful concept and would rather abandon its usage.

Recognizing the 19 subspecies of Nelson and later workers (as listed in Hall and Kelson, 1959) represents an extreme choice. Consistency with this classification would require subspecific recognition of at least three more populations, those of Cruz Alta (sample 51), Zacapoaxtla (sample 52), and the Sierra de Coalcomán (sample 36), for example. If this alternative is employed the subspecies within the two major "groups" would be generally weakly differentiated, their boundaries vague, and the transition in characters between them usually gradual. Character discordance rather than concordance would be emphasized. In effect, this classification would formally recognize every slightly differentiated local population. The subspecies would serve only as a vehicle for describing the geographic variation of a particular character or the frequency and distribution of a pelage phase (melanism, for example). My interpretation of available data suggests that of all possible taxonomic arrangements, this alternative seems least desirable and unwarranted.

I think there are two reasonable alternatives between these extremes. One is to recognize four subspecies of *S. aureogaster*. The squirrels of eastern México in my Aureogaster Group would be listed as the subspecies *aureogaster*. Populations of the Mexican Plateau (including the Sierra de Coalcomán, Michoacán) and central México (including the Sierra de Miahuatlán, Oaxaca, and the mountains near Santa María Ozolotepec, Oaxaca) would be placed together under the name *poliopus*. The Pacific coastal populations would be called *socialis*. And the name *griseoflavus*, would be applied to populations of eastern Chiapas and Guatemala. The latter three subspecies would generally correspond to divisions of my Socialis Group. This is preferable to recognizing 19 or more subspecies and

better indicates the relationships between populations than does the latter choice. The arrangement of four subspecies, however, emphasizes only one level in a continuum of intraspecific variation and not the most important level. These subspecies would represent broad, relatively well-differentiated segments of the species, but the intergradation between them is so broad in some geographic regions that it would be difficult and in some cases arbitrary to assign populations to a given subspecies. Also, this choice does not point up the relations of the Aureogaster segment of the species to the Socialis segment.

The last alternative, and the one I prefer, is to recognize formally two geographic races, each corresponding to one of my two major "groups." This arrangement seems the most objective taxonomic interpretation of the available data. The trinomial then designates populations that apparently behave as separate morphologically and ecologically distinct species in some localities, but interbreed freely in other regions. The various levels of geographic variation within each subspecies are documented by description and illustration as I suggested for the first alternative. The various interrelationships of populations in the Aureogaster Group are then best expressed by including all of them under one subspecific name, *aureogaster* (which includes *hypopyrrhus,* but not *frumentor,* which is placed in the Socialis Group). The name *socialis* would be applied to populations in the Socialis Group (and would include *cervicalis, colimensis, effugius, hernandezi, nemoralis, perigrinator, poliopus, senex, tepicanus, cocos, littoralis, griseoflavus, chiapensis, nelsoni, hirtus,* and *frumentor).* Nomenclatorial aspects of this arrangement are presented in the following annotated synonymy. Listed there are only the first synonymous uses of names or combinations of names for each taxon that I have recognized.

Sciurus aureogaster aureogaster F. Cuvier

Sciurus aureogaster F. Cuvier, 1829. The whereabouts of the type is unknown. Although "California" was given as the type locality by Cuvier, the animal he figured is obviously a red-bellied gray squirrel from eastern México. Nelson (1899:38) with ample reason restricted the type locality to Altamira, Tamaulipas. He also noted that the type may be in the Paris Museum, but Rode (1945) does not list it or refer to it. I have examined Cuvier's colored plate of the *"Ecureuil de la Californie"* that is the basis for the name *aureogaster,* and I. Geoffroy (1855:156; see also Plate II of the Atlas, 1846) and Nelson (1899:41) provide further comment about Cuvier's original description and illustration.

Sciurus niger Erxleben, 1777:417 (part). Under this name Erxleben listed the melanistic form of *Sciurus mexicanus* or Quauhtechalotl thliltic of Hernandez (1651) and Nelson (1899:38) placed it in the synonymy of *S. aureogaster.* Hernandez (1651:582) illustrated and wrote of long-tailed black *tree* squirrels and could reasonably have been referring to the melanistic tree squirrels of eastern México.

Sciurus rafiventer Lichtenstein (1830:116). Noting that ". . . Herrn Geoffroy's *Sc. rafiventer* höchstwahrscheinlich diese mexicanische Art, . . ," Lichtenstein indicated that the name was based upon a young immature animal. Nelson (1899:38) listed *rafiventer* as a synonym of *aureogaster*.

Sciurus leucogaster F. Cuvier, 1831 (published in Suppl. d'Hist. Nat. Buffon, pp. 300–301). I have not seen the publication in which the name *leucogaster* appears. In listing it as a synonym of *aureogaster,* I follow Nelson (1899:38 and 41) and Kelson (1952:249).

Sciurus hypopyrrhus Wagler, 1831:510. Whereabouts of the type specimen is unknown though Nelson (1899:42) suggested it is probably in the Berlin Museum. The type is from "Mexico." Nelson (1899:42) restricted the type locality to Minatitlan, Veracruz.

Sciurus mustelinus Audubon and Bachman, 1841:100. This name is based upon an apparently completely melanistic squirrel thought to have been obtained in "California." Judging from Audubon and Bachman's description of the animal and from Audubon's colored plate (Audubon and Bachman, 1854:pl. 152, fig. 1) the animal is most likely a melanistic specimen of *S. aureogaster* from the lowlands of eastern México, as Nelson (1899:41) indicated.

Sciurus ferruginiventris Audubon and Bachman, 1841:101. The authors state that all their specimens were received from "California." But the animals they describe and those drawn by Audubon (Audubon and Bachman, 1849:pl. 38) are clearly *S. aureogaster*. One of the three specimens figured by Audubon has a large rump patch and a diffuse nape patch. The three animals could have been collected from the same locality; they match the variation seen in series from lowlands of central and southeastern Veracruz.

Sciurus ferrugineiventris: Schinz, 1845:14. Apparently a variant spelling of Audubon and Bachman's name, *ferruginiventris*.

Sciurus aurogaster: Audubon and Bachman, 1854:344. These authors indicate *aurogaster* to be synonymous with *"Ferruginiventer."*

Sciurus hypoxanthus (Lichtenstein MS), I. Geoffroy, 1855:158. Lichtenstein's name on labels of squirrels from Berlin Museum that were received and reported upon by I. Geoffroy.

Sciurus chrysogaster Giebel, 1859:650 (footnote). Apparently a substitute for the name *aureogaster*.

Sciurus variegatus: Saussure, 1861:4. Apparently this is the first restricted application of the name *variegatus* to gray squirrels with reddish underparts and shoulder patches and is a synonym of *S. aureogaster* F. Cuvier. Saussure listed Wagner's forms, *albipes, varius,* and *socialis,* names that apply to squirrels in my Socialis Group, under *variegatus,* but Saussure's description clearly fits squirrels in my Aureogaster Group. Nelson (1899:38) implied that Desmarest (1817:103), in part, first applied the name *variegatus* to squirrels which Nelson called *S. a. aureogaster,* but Desmarest's description is too general to be clearly linked with the gray squirrels of eastern México.

Macroxus aureogaster: Gray, 1867:423. Gray described two varieties stating that the second one resembled I. Geoffroy's figure (1846:pl. II of Atlas) of a female *S. aureogaster;* Nelson (1899:38) considered "variety 2" a synonym of *S. aureogaster*.

Sciurus hypopyrrhous: Gray, 1867:424. A variant spelling of *hypopyrrhus*.

Macroxus morio Gray, 1867:424. The type locality is unknown. Nelson (1899:44) gives reason for allocating this name to the synonymy of *S. aureogaster*.

Macroxus maurus: Gray, 1867:425. The type locality is Oaxaca (Sallé), Mexico. Nelson (1899:44) explains why this name is a synonym of *S. aureogaster*.

Sciurus aureigaster: Allen, 1877:750 (part: specimens from Orizaba, Cordoba, and Mirador). A variant spelling of *aureogaster*.

Sciurus rufiventris? Rovirosa, 1887:360. Rovirosa apparently applied "SCIURUS RUFIVENTRIS?" and "SCIURUS CINEREUS?" to gray squirrels of the Macuspana region of Tabasco.

Sciurus aureogaster aureogaster: Nelson, 1899:38 (part: all specimens listed by Nelson except those from Jalapa and Xico).

Sciurus aureogaster hypopyrrhus: Nelson, 1899:42. Applied by Nelson to squirrels of "Humid tropical forests of southern Vera Cruz, adjacent parts of extreme southeastern Oaxaca, Tabasco, eastern Chiapas, and perhaps extreme northwestern Guatemala (below 4000 feet)." Nelson (1952) synonymized *hypopyrrhus* with *S. a. aureogaster.*

Sciurus aureigaster hypopyrrhus: Elliot, 1904:116. The variant spelling of *aureogaster* used in combination.

Sciurus oculatus: Nelson, 1899:88, Part: melanistic specimen from Pinal de Amoles, Querétaro; see p. 68 of this report (not *S. oculatus* Peters, 1863).

Sciurus aureogaster socialis Wagner

Sciurus socialis Wagner, 1837:88. The type is in the Berlin Museum (*fide* Nelson, 1899:63) and is from the vicinity of Tehuantepec, Oaxaca, México. I have not seen the specimen upon which the name *socialis* is based. However, I have before me Wagner's original description and accompanying color plate of the animal he described as *socialis.* Pelage features of the squirrel depicted in that plate would fit within the range of variation of my sample 24 from the Tehuantepec region. See Nelson (1899:64) for further comment on the type specimen.

Sciurus albipes Wagner, 1837:85. The type is in the Berlin Museum (*fide* Nelson, 1899:45) and is probably from Cerro San Felipe, Oaxaca, as Nelson (1899:48) indicated. Although the name *albipes* has page priority over *socialis,* Allen (1898:453) noted that it was preoccupied by *Sciurus albipes* Kerr, 1792.

Sciurus varius Wagner, 1843:168. A renaming of material that Wagner had earlier (1837) called *S. albipes;* correctly listed in synonymy of *S. poliopus poliopus* by Nelson (1899:47).

Sciurus aureogaster: I. Geoffroy, 1855:156. Specimens, some with white underparts, described by Geoffroy and figured in Plate 10 of the Atlas (1846). Considered a synonym of *S. socialis cocos* by Nelson (1899:65).

Sciurus ludovicianus: Tomes, 1861:281. Applied to specimens from Dueñas, Guatemala, by Tomes and listed under *S. griseoflavus* by Nelson (1899:67).

Sciurus variegatus poliopus Fitzinger, 1867:478. Based on a variety of *S. varius* that was originally described by Wagner (1843). Nelson (1899:46) lists the name in the synonymy of *S. poliopus.*

Sciurus variegatus rufipes Fitzinger, 1867:478. Based on another variety that Wagner (1843) included under *S. varius;* listed in the synonymy of *S. poliopus* by Nelson (1899:46).

Macroxus griseoflavus Gray, 1867:427. The type is from "Guatemala." Specimens from near Dueñas are typical (Nelson, 1899:67).

Macroxus leucops Gray, 1867:427. Type is from Oaxaca, México. Nelson (1899:46) considers specimens upon which this name is based to be *S. poliopus.*

Sciurus aureigaster: Allen, 1877:750 (part: specimen from Guatemala). Listed in synonymy of *S. griseoflavus* by Nelson (1899:67).

Sciurus leucops: Allen, 1877:753. Of the six specimens that Allen listed under *leucops,* Nelson (1899) listed the one from Río Coahuyana, Colima, under *S. poliopus colimensis,* the three from Tehuantepec under *S. socialis socialis,* and two from "Sierra Madre, Dur-

ango, Mexico," as actually being from the "Sierra Madre of Colima," and included them under *S. poliopus cervicalis*.

Sciurus variegatus: Alston, 1878:660 (part: the *"leucops"* type of southern México). Alston considered this name to apply to two types of squirrels: the *"aureogaster"* types with red bellies and shoulder patterns, and the *"leucops"* type with nape and rump patterns and either red, orange, or white underparts.

Sciurus affinis (Reinhardt, MS), Alston, 1878:660. Referring to *S. griseoflavus,* Alston noted: ". . . and a Mexican specimen in the Copenhagen Museum, labelled *'Sc. affinis,* an sp. nov.? Reinh.,' does not appear to be separable [from *S. griseoflavus*]."

Sciurus aureogaster leucops: Allen, 1889:166. Specimens from the vicinity of the Nevado de Colima, Jalisco. Considered as *S. poliopus cervicalis* by Nelson (1899:51).

Sciurus cervicalis Allen, 1890:183. Type is from the Hacienda San Marcos, Jalisco, México. Considered a subspecies of *S. poliopus* by Nelson (1899:51).

Sciurus nelsoni Merriam, 1893:144. The type is from Huitzilac, Morelos, México. The name is based on melanistic phases.

Sciurus albipes quercinus Nelson, 1898:150. Type is from the mountains on west side of the Valley of Oaxaca de Juárez, Oaxaca, México.

Sciurus albipes nemoralis Nelson, 1898:151. Type is from Pátzcuaro, Michoacán, México.

Sciurus albipes colimensis Nelson, 1898:152. Type is from the Hacienda Magdalena (now called Pueblo Juárez), Colima, México.

Sciurus albipes effugius Nelson, 1898:152. Type is from mountains near Chilpancingo, Guerrero, México.

Sciurus nelsoni hirtus Nelson, 1898:153. Type is from Tochimilco, Puebla, México.

Sciurus aureogaster frumentor Nelson, 1898:154. Type is from Las Vigas, Veracruz, México. Included are the specimens that Nelson listed from Las Vigas, near and above Xico, and Jalapa, and the two specimens from Jalapa that Allen and Chapman (1897:198) listed under *S. leucops*.

Sciurus socialis cocos Nelson, 1898:155. Type is from Acapulco, Guerrero, México.

Sciurus wagneri Allen, 1898:453. Here Allen showed that Wagner's names *albipes* and *varius* were preoccupied and he proposed the name *wagneri* to replace them, overlooking Fitzinger's name, *poliopus*. The taxa, *quercinus, nemoralis, colimensis, effugius,* and *cervicalis* were then listed by Allen as subspecies of *wagneri*.

Sciurus albipes hernandezi Nelson, 1898:783. A renaming of *S. albipes quercinus*.

Sciurus aureogaster aureogaster: Nelson, 1899:42 (part: specimens from Jalapa and Xico that Nelson earlier [1898:154] included in *S. aureogaster frumentor).*

Sciurus poliopus: Nelson, 1899:46 (see above).

Sciurus poliopus hernandezi: Nelson, 1899:48 (see above).

Sciurus poliopus nemoralis: Nelson, 1899:50 (see above).

Sciurus poliopus cervicalis: Nelson, 1899:51 (see above).

Sciurus poliopus colimensis: Nelson, 1899:52 (see above).

Sciurus poliopus effugius: Nelson, 1899:54 (see above).

Sciurus griseoflavus chiapensis Nelson, 1899:69. Type is from San Cristóbal, Chiapas, México.

Sciurus aureigaster frumentor: Elliot, 1904:117. A variant spelling of *aureogaster*.

Sciurus griseiflavus: Elliot, 1904:124. A variant spelling of *griseoflavus*.

Sciurus griseiflavus chiapensis: Elliot, 1904:125. The variant spelling of *griseoflavus* used in combination.

Sciurus poliopus senex Nelson, 1904:148. Type is from La Salada, 40 miles south of Uruapan, southern Michoacán, México.

Sciurus poliopus perigrinator Nelson, 1904:149. Type is from Piaxtla, Puebla, México.

Sciurus poliopus tepicanus Allen, 1906:243. Type is from Rancho Palo Amarillo, near Amatlan de Cañas, Nayarit, Mexico.

Sciurus socialis littoralis Nelson, 1907:87. Type is from Puerto Angel, Oaxaca, México.

Sciurus oculatus tolucae Nelson, 1899:89 (part: melanistic specimen from north slope of the Volcán de Toluca; see p. 52 of this report).

APPENDIX

SPECIMENS EXAMINED

AMNH	American Museum of Natural History
CAS	California Academy of Sciences
FMNH	Field Museum of Natural History
IB	Instituto de Biologia, Universidad Nacional Autónoma de México
KU	University of Kansas, Museum of Natural History
LACM	Los Angeles County Museum
LSU	Louisiana State University, Museum of Zoology
MCZ	Museum of Comparative Zoology, Harvard University
MSU	The Museum, Michigan State University
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley
OC	Occidental College, Moore Laboratory of Zoology
SDM	San Diego Museum of Natural History
TCWC	Texas Agricultural and Mechanical College Cooperative Wildlife Collections, College Station
UMMZ	University of Michigan, Museum of Zoology
USNM	United States National Museum

Specimens that were part of the basis for E. W. Nelson's (1899) revision of Latin American squirrels are included in this study. Much of that material was collected towards the end of the nineteenth century by Nelson and E. A. Goldman during their biological surveys in México for the United States Fish and Wildlife Service. Those specimens, usually adequately prepared, are still useful in any analysis of morphologic variation. I compared them with recent examples (i.e., collected within the last five years) from the same localities. I found few important color alterations resulting from effects of time and storage in museum cases. The pelage discoloration present was usually a result of the accumulation of dirt, particularly evident on white venters, and dried blood encrusted on the hair. Some specimens that Nelson described as having white underparts now have pale dirty yellow underparts, but most series are as he described them. Most squirrels collected shortly after 1900 that are housed in other institutions were useable, but specimens obtained much earlier, in the mid 1800's for example, were less reliable. They are usually poorly prepared, faded, and dirty. Generally the locality information is meager and even when available is often inaccurate. For these and other reasons I excluded from detailed analysis the majority of specimens collected before the turn of the century. Most of the examples of *Sciurus aureogaster (sensu latu)* were collected within the last 20 years, many within the last two to three years.

I have not provided a gazetteer of collecting sites because many published zoogeographic and faunistic studies relating to México and Central America contain maps, gazetteers, and adequate descriptions of many sites of collections. Some of those pertinent to this study follow.

Adler, 1965: descriptions of localities in Guerrero and Oaxaca; UMMZ specimens.

Allen, 1906: descriptions of localities in Sinaloa and Jalisco; AMNH specimens.

Alvarez, 1963: map and gazetteer for Tamaulipas; KU specimens.

Burt, 1938: map of localities in Sonora; UMMZ and MVZ specimens. 1961: map and gazetteer of region near Cerro de Tancítaro, Michoacán; UMMZ specimens.

Dalquest, 1953: gazetteer and map for San Luis Potosí; KU and LSU specimens.

Davis, 1944: descriptions of collection sites in México; TCWC specimens.

Davis and Dixon, 1959: map of localities in the Chilpancingo region, Guerrero; TCWC specimens.

Duellman, 1960: gazetteer and map for the Isthmus of Tehuantepec. 1961: excellent gazetteer for localities in Michoacán.

Goldman, 1951: descriptions of collection sites of most USNM specimens from México and Guatemala.

Goodwin, 1954: descriptions of localities in Tamaulipas; AMNH specimens.

Griscom, 1932: map and gazetteer for collection sites in Guatemala; AMNH specimens.

Hall and Dalquest, 1963: map and gazetteer for localities in Veracruz; KU specimens.

Hooper, 1952: an excellent gazetteer in his review of *Reithrodontomys;* UMMZ specimens as well as those from other institutions. 1947, 1953, 1955, 1957, and 1961: habitat descriptions; UMMZ specimens.

Jones, 1963: KU specimens from Durango.

Martin, 1958: map and description of localities near Gómez Farías, Tamaulipas.

Musser, 1964: descriptions of localities in Guerrero, Hidalgo, Oaxaca, and Puebla; UMMZ specimens.

Paynter, 1957: description of a collection site in the Selva Lacandona of Chiapas; MCZ specimens.

Rowley, 1966: map and description of localities in the Sierra Madre del Sur of Oaxaca.

Schaldach, 1963: gazetteer and maps for sites in Colima and adjacent parts of Jalisco; AMNH and LACM specimens.

Stuart, 1951, 1954, and 1963, and in other reports cited therein: maps, gazetteers and descriptions of collection sites in Guatemala.

Following are localities from which specimens of *Sciurus aureogaster, colliaei, variegatoides,* and *yucatanensis* were examined. Most are mapped in Figure 1. Collecting sites within one to five miles of a mapped locality which could not be mapped separately are included under the same symbol. In the following lists, those localities are italicized and follow the mapped locality.

Under each species and subspecies, localities and number of specimens examined in the numbered "sample groups" are listed first (alphabetically by state and country and generally from north to south within each of those political boundaries) then those outside the grouped localities (listed alphabetically by state and country only).

Distances are those originally recorded on the specimen tags in miles (mi), kilometers (km), or time by mule-back (hr, min). Altitudes, when given, are in feet (ft) or meters (m) and are approximate. Distances are airline unless otherwise indicated. Sources of place names and some elevations are from topographic maps (1:500,000)

issued by the Comisíon Intersecretarial Coordinadora del Levantamiento de la Carta Geográfica de la República Mexicana and from American Geographical Society maps, scale one to one million.

Sciurus aureogaster aureogaster (total 530)

1. General Terán.—**Nuevo Leon:** 20 km NW General Terán, 900 ft, 1 (UMMZ); La Unión, 20 km NE General Terán, 1000 ft, 1 (MVZ).

2. Ciudad Victoria.—**Tamaulipas:** Santa Engracia, 10 mi W Carmen, 25 mi N Ciudad Victoria, 2 (UMMZ); 3 mi NE Guemes, 4 (KU); 9.5 mi SW Padilla, 800 ft, 4 (KU); Rancho Santa Rosa, 25 km N, 13 km W Ciudad Victoria, 260 m, 8 (KU).

3. Gómez Farias.—**Tamaulipas:** 43 km S Ciudad Victoria, 1 (KU); 70 km S (hwy), 6 km W Ciudad Victoria, 5 (2 AMNH, 3 KU); *2 km W El Carrizo,* 7 (KU); near headwaters Río Sabinas, 8 km W, 10 km N El Encino, 400 ft, 1 (KU); Ejido Santa Isabel, 2 km W Panamerican Hwy, 2000 ft, 5 (KU); Rancho Pano Ayuctle, 6 mi N Gómez Farías, 300 ft, 3 (KU); *5 mi NE Gómez Farias, Río Sabinas at Pano Ayuctle, 4* (3 AMNH, 1 UMMZ); near Gómez Farías, 300 ft, 10 (8 AMNH, 2 LACM).

4. Altamira.—**Tamaulipas:** Aldama, 2 (AMNH); Altamira, 75 ft, 17 (USNM); Tampico, 10 (7 AMNH, 3 MCZ). **Veracruz:** Pánuco, 1 (AMNH).

5. Eastern San Luis Potosi.—**San Luis Potosí:** vicinity of El Salto Falls (Salto del Agua) on the Río Salto, 11 (10 AMNH, 1 LSU); *Rancho Martinez on Río Salto, 30 km E Ciudad Maiz, 1600 ft,* 1 (MVZ); Tamuin, 6.4 mi W on hwy to Ciudad de Valles, 1 (LSU); Ciudad de Valles, 3 (2 AMNH, 1 USNM); Huichihuayán, 1 (LSU); Río Axtla, 3 km W Axtla, 300 ft, 6 (KU); Xilitla, 3 (LSU); *1.5 mi NNW Xilitla, 2300 ft,* 1 (LSU); *2 mi N Xilitla,* 1 (LSU); *3.5 rd mi SW Xilitla, 740 m,* 6 (UMMZ); *Rancho Miramar,* 1 (LSU); 12 mi NW Tamazunchale, 1 (AMNH); Tamazunchale, 1 (AMNH); *3 km N Tamazunchale,* 3 (KU); *1 mi N Tamazunchale,* 1 (LSU); Ejidi Jalpilla, 1 (AMNH).

6. Pinal de Amoles.—**Querétaro:** Pinal de Amoles, 8000 ft, 4 (USNM).

7. Papantla.—**Puebla:** near Metlaltoyuca, 800 ft, 7 (USNM); Apapantilla, 1000 ft, 1 (LACM); *5 mi N Apapantilla, 2200 ft,* 1 (OC); 30 mi E Huauchinango, 1200 ft, 3 (OC). **Veracruz:** 17 mi W Poza Rica, 300 ft, 1 (OC); Papantla de Olarte, 600 ft, 11 (USNM); *9 and 4 km E Papantla de Olarte, 300 and 400 ft,* 2 (KU); 10 mi S Papantla de Olarte, 400 ft, 3 (UMMZ).

8. San Marcos.—**Veracruz:** 3 km SW San Marcos, 200 ft, 2 (KU).

9. Central Veracruz Coastal Plain.—**Veracruz:** Puenta Nacional, 1 (TCWC); 20 mi W Ciudad Veracruz, 200 ft, 2 (OC); Río Atoyac, 7 and 8 km NW Potrero, 1700 ft, 17 (16 KU, 1 MSU); Río Blanco, 20 km WNW Piedras Negras, 4 (KU); *Río Blanco, 20 km W Piedras Negras, 400 ft,* 6 (KU); *Río Blanco, 15 km W Piedras Negras, 300 ft,* 2 (KU).

10. Valle Nacional.—**Oaxaca:** Toro Bravo, 5 km N Tuxtepec, 1 (KU); *Rancho Palo Blanco, 3 km W Tuxtepec,* 2 (KU); *3–4 km NNW Tuxtepec, 40 m,* 5 (KU); 5 mi W San José Chiltepec, 43 (AMNH); 1 mi S San Juan Bautista Valle Nacional, 100 m, 3 (UMMZ); 11 mi (Oaxaca de Juárez-Tuxtepec rd) SW San Juan Bautista Valle Nacional, 760 m, 1 (UMMZ).

11. Catemaco.—**Veracruz:** Tecolapan, 34 mi SE Alvarado, 2500 ft, 2 (SDM); Santiago Tuxtla, 750 ft, 1 (USNM); 3 km E San Andrés Tuxtla, 2 (KU); *San Andrés Tuxtla, 1500 ft,* 1 (USNM); Catemaco, 1000–1500 ft, 8 (USNM); *1 mi N Catemaco,* 1 (AMNH); *Laguna Catemaco,* 1 (AMNH); 7 mi (hwy 180) S Catemaco, 1650 ft, 21 (UMMZ).

12. Southeastern Veracruz.—**Veracruz:** Pasa Nueva (see Selander, 1964:152, and Hall and Dalquest, 1963:184, for comments on geographic area of this locality), 23 (AMNH); Jimba, 350 ft, 1 (KU); 20 mi W Rodriguez Clara, 500 ft, 4 (OC); 35 km ENE Jesús

Carranza, 150 ft, 2 (KU); 20 km ENE Jesús Carranza, 200–300 ft, 5 (KU); 40 mi S Acayucan, 3 (AMNH); *45 mi S Acayucan,* 1 (AMNH); *Río Jaltepec,* 2 (1 AMNH, 1 MVZ).

13. Sarabia.—**Oaxaca:** 30 mi N Matías Romero, 1 (LACM); 2 mi S Tollocito (Tollosa), 150 ft, 1 (KU); Sarabia, 20 mi N Matías Romero, 200 ft, 3 (2 AMNH, 1 SDM); *17–18 mi N Matías Romero,* 9 (4 AMNH, 5 SDM); San Juan Guichicovi, 2 (USNM); mountains near Santo Domingo, 1600 ft, 8 (USNM); Santo Domingo, 2 (AMNH).

14. Minatitlán.—**Tabasco:** La Venta, 6 (USNM). **Veracruz:** 14 km SW Coatzacoalcos, 100 ft, 1 (KU); 10 km NW Minatitlán, 100 ft, 1 (KU); Minatitlán, 75–100 ft, 14 (USNM); Buena Vista, 20 (USNM).

15. Southern Tabasco.—**Chiapas:** Palenque, 800 ft, 2 (USNM); *1.5 km N Ruinas de Palenque,* 2 (KU). **Tabasco:** Monte Cristo Emiliano Zapata, 200 ft, 9 (1 MCZ, 8 USNM); 6 mi S Cardenas, 5 (KU); 10 mi E, 19 mi N Macuspana, 7 (KU); Macuspana, 4 (KU); *3 mi E Macuspana,* 1 (KU); 5 mi SE Macuspana, 3 (KU); 1 mi E Teapa, 800 ft, 5 (3 LSU, 2 USNM); 7 mi W Teapa, 3 (LSU).

16. Tumbalá.—**Chiapas:** Tumbalá, 1500 m, 1 (USNM); Simojovel, 660 m, 1 (UMMZ); La Florida, 50 km E Altamirano, 525 m, 1 (TCWC); El Real, 35 km NE Altamirano, 580 m, 1 (TCWC); Laguna Ocotal, 950 m, 3 (MCZ).

Specimens from the following localities are not included in the sample groups listed above.

Chiapas.—Monte Libano, 100 km NE San Cristóbal de las Casas (15 km SE El Real), 2500 ft, 1 (MVZ)—not mapped.

Oaxaca.—The following localities are not mapped: Chacalapa, 650 ft, 1 (KU); La Soledad, 1 (KU); Matías Romero, 1 (AMNH).

San Luis Potosi.—Ebano Region, 1 (LSU); *2 mi S Ajinche, Ebano Region,* 1 (LSU). The following localities are not mapped: 1 mi NE Rancho Sabinal, 1 (LSU); Cuestro de los Cedros (½ mi E on hwy), 1 (LSU).

Tabasco.—½ mi W Miramar, 2 (LSU).

Tamaulipas.—San Fernando, 180 ft, 2 (KU); San Carlos Mountains, Marmolejo, 1 (UMMZ); 7 mi W La Pesca, 25 ft, 2 (MSU); 3 mi N Soto La Marina, 500 ft, 6 (KU); Sierra de Tamaulipas, 10 mi W, 2 mi S Piedra, 1200 ft, 6 (KU); Forlón, 3 (USNM); Sierra de Tamaulipas, Hacienda de Acuña, 3000 ft, 1 (MVZ); Río Guayilejo, 20 mi E El Mante, 400 ft, 1 (OC); Santa María, 2 (AMNH).

Veracruz.—1 mi E Higo, 500 ft, 1 (KU); Hacienda Tamiaha, Cabo Rojo, 1 (KU); Platón Sanchez, 800 ft, 3 (KU); 35 km NW Tuxpan, 1 (KU); 17 km NW Tuxpan, 2 (KU); 12.5 mi N Tihuatlán, 300 ft, 2 (KU); Mirador, 3800 ft, 3 (1 MCZ, 2 USNM); Orizaba, 7 (3 MCZ, 4 USNM); *Barrio Nuevo, vicinity of Orizaba, 3500 ft,* 3 (CAS); Cordoba, 2 (1 AMNH, 1 MCZ); Xuchil, 1 (AMNH); Presidio, 35 km S Cordoba, 1000 ft, 5 (2 MCZ, 3 OC); *Motzorongo, 800 ft,* 1 (USNM); *2 km N Motzorongo, 1500 ft,* 1 (KU); 24 mi S Veracruz, 9 (AMNH); Otatitlan, 4 (USNM). The following localities are not mapped: Tapalapan, 500 ft, 2 (MVZ); Chichicaxtle, 1 (USNM); 5 km S Tihuatlán, 700 ft 1 (KU); Ojochico, 1500 ft, 2 (FMNH).

S. a. socialis (total 1184)

17. Pueblo Nuevo.—**Chiapas:** vicinity of Pueblo Nuevo Solistahuacán, 10 (1 KU, 3 UMMZ, 6 AMNH).

18. San Cristóbal.—**Chiapas:** near San Cristóbal de las Casas, 8200–8500 ft, 11 (USNM); 20 mi SE Teopisca, 7200–8500 ft, 2 (USNM); Lagos Montebello, 4350 ft, 10 (UMMZ); 18 mi E Zapaluta, 5400 ft, 2 (TCWC).

19. CHIAPAS-GUATEMALA HIGHLANDS.—**Chiapas:** Cerro Mozotal, 3021 m, 2 (UMMZ); Volcán de Tacaná (includes Aguacaliente and Chiquihuite), 2600–3800 m, 5 (1 OC, 4 UMMZ); 2 mi N Unión Juárez, 400 ft, 2 (UMMZ). **Guatemala:** ALTA VERAPAZ: La Primavera, 2 (AMNH). HUEHUETENANGO: vicinity of San Juan Ixcoy, 2200 m, 4 (UMMZ); Hacienda Chancol, 11,000 ft, 6 (USNM). EL QUICHE: Nebaj, 5 (1 AMNH, 4 USNM); Sacapulus, 1 (USNM). HUEHUETENANGO: Calel, 3 (USNM). TOTONICAPAN: Momostenango, 3 (AMNH); *7 mi W Momostenango,* 1 (AMNH). SAN MARCOS: Zanjon, 4 (AMNH). BAJA VERAPAZ: Sierra de las Minas, La Montañita, 1 (AMNH). TOTONICAPAN: 5 mi ESE Totonicapan, 1 (KU). SAN MARCOS: S slopes Volcán Tajumulco, 8500–10,650 ft, 8 (4 FMNH, 4 UMMZ). EL QUICHE: Chichicastenango, 3 (AMNH). CHIMALTENANGO: Sierra Santa Elena, 9500 ft, 1 (FMNH); *Santa Elena, 8500 ft,* 1 (FMNH); Tecpam, 7 (6 AMNH, 1 FMNH). QUEZALTENANGO: Volcán de Santa María, 2 (USNM). SOLOLA: San Lucas, 2 (AMNH). SACATEPEQUEZ: Antigua, 1 (AMNH);*San Antonio,* 1 (AMNH).

20. SOCONUSCO.—**Chiapas:** between Mapastepec and Paral, 450 m, 2 (UMMZ); Distrito Soconusco, Finca Juárez (about 14 km E Escuintla), 1200 m, 1 (UMMZ).

21. TUXTLA GUTIÉRREZ.—**Chiapas:** 3 mi S San Fernando, Las Vistas, 2 (UMMZ); *3 mi N San Fernando, 2400 ft,* 4 (UMMZ); El Suspiro, 5 mi N Berriozábal, 4500 ft, 4 (UMMZ); El Ocote, Ocozocoautla de Espinoza, 740 m, 2 (FMNH); 11 km W Tuxtla Gutiérrez, 800 m, 1 (UMMZ); *Tuxtla Gutiérrez, 2600 ft,* 3 (USNM); El Canelar, 10 mi S Ocozocoautla de Espinoza, 750 m, 4 (UMMZ); San Bartolomé, 3000 ft, 2 (USNM).

22. OAXACA-CHIAPAS COASTAL PLAIN.—**Oaxaca:** vicinity of Santa Efigenia, 8–12 mi NW Tapanatepec, 550–800 ft, 12 (3 SDM, 9 USNM); *Río Ostuta, 4 mi W and N Zanatepec,* 2 (AMNH); *Zanatepec,* 1 (AMNH); 4 mi WNW Tapanatepec, 2 (AMNH); *2 mi W Tapanatepec,* 1 (LACM); *Tapanatepec,* 17 (16 AMNH, 1 IB); *1 mi W El Jicaro,* 4 (AMNH). **Chiapas:** La Calara, 1200 ft, 1 (USNM); Arriaga, 100 m, 1 (UMMZ); 9 mi SW Arriaga, 2 (SDM); Tonala, 13 (USNM).

23. CHICAPA.—**Oaxaca:** San Geronimo (Ixtepec), 3 (FMNH); 18 mi S Matías Romero, 1 (LACM); Chicapa de Castro, 100 ft, 2 (USNM).

24. TEHUANTEPEC.—**Oaxaca:** Magdalena Tequisistlán, 600 ft, 2 (USNM); Salazar, 200 ft, 4 (AMNH); *Las Cuevas, 9 mi NW Tehuantepec at edge of Río Tehuantepec,* 6 (AMNH); Cerro San Pedro, 10 mi W Mixtequilla, 3700 ft, 1 (AMNH); *Guiengola, 7 mi W Mixtequilla, 3000–3500 ft,* 1 (AMNH); *Escuarano, near slopes of Cerro San Pedro, 12 mi W Mixtequilla, 1500 ft,* 1 (AMNH); vicinity of Tehuantepec, 3 (1 MVZ, 2 UMMZ); *5 mi NW Tehuantepec,* 5 (KU); *San Pablo,* 5 (AMNH); *La Presa, 3 mi W Mixtequilla,* 1 (AMNH); Las Tejas, 8 mi NW Tehuantepec at highway crossing over Río Tejas, 5 (AMNH); *San Antonio, 15 mi W Tehuantepec near Río Las Tejas,* 3 (AMNH); San Miguel Tenango, 25 mi W Tehuantepec, 5000 ft, 1 (AMNH); *La Concepción, 7 mi NE San Miguel Tenango, 3500 ft,* 1 (AMNH); *El Limón,* 3 (AMNH); San Pedro Huilotepec, 14 (USNM).

25. PUERTO ANGEL.—**Oaxaca:** Colotepec, 2 (USNM); vicinity of Puerto Angel, 100–400 ft, 18 (8 KU, 3 UMMZ, 7 USNM); Santa Cruz Bay, 1 (UMMZ).

26. OZOLOTEPEC.—**Oaxaca:** mountains near Santa María Ozolotepec, 10,000 ft, 3 (USNM).

27. SAN GABRIEL MIXTEPEC.—**Oaxaca:** 2 mi (Hwy 131) N San Gabriel Mixtepec (or *ca.* 11 mi S San Pedro Juchatenango, on some specimen labels), 5600 ft, 7 (1 CAS, 6 UMMZ).

28. GUERRERO-OAXACA COASTAL PLAIN.—**Guerrero:** near Ometepec, 200 ft, 3 (USNM). **Oaxaca:** Pinotepa Nacional, 700 ft, 1 (USNM); Jamiltepec, 1 (USNM); eastern margin of Laguna Mantialtepec, 11 rd mi W Puerta Escondida, 3 (UMMZ).

29. ACAPULCO.—**Guerrero:** vicinity of Acapulco, sea level–300 ft, 28 (6 UMMZ, 22 USNM); Río Aguacatillo, 1000 ft, 30 km N Acapulco, 2 (TCWC); *Aguacatillo,* 1 (USNM).

30. Agua de Obispo.—**Guerrero:** Agua de Obispo, 3000 ft, 18 (9 TCWC, 9 UMMZ); *Acahuizotla, 2800 ft,* 21 (2 KU, 14 TCWC, 3 UMMZ, 2 USNM).

31. Omilteme.—**Guerrero:** vicinity of Omilteme, 64 (3 MVZ, 54 USNM, 7 UMMZ); Coapongo, 16 (4 MVZ, 12 UMMZ); mountains near Chilpancingo, 8 (USNM); Puerto Chico, 8400 ft, 13 (UMMZ); *12 mi SW Xochipala, 8200 ft,* 1 (MSU); Cerro Teotepec, 1 (OC).

32. San Andrés de la Cruz.—**Guerrero:** 1 mi E San Andrés de la Cruz, 700 m, 19 (UMMZ); *1 mi SE San Vicente de Jesús, 1000 m,* 1 (UMMZ).

33. Southwestern Guerrero Coastal Plain.—**Guerrero:** Zihuatenejo, 1 (USNM); 6 rd mi NW San Jéronimito, 100 m, 2 (UMMZ); Petatlán, 3 (USNM); Tecpan de Galeana, 2 (USNM); *Rancho Tortuga, 5 mi NW Tecpan de Galeana,* 1 (OC).

34. Zacatula.—**Guerrero:** 5 rd mi E Zacatula, 50 m, 3 (UMMZ); 2 mi NE Petacalco, 50 m, 4 (UMMZ).

35. Southeastern Michoacán.—**Michoacán:** 30 rd mi N Playa Azul, 200 m, 5 (UMMZ).

36. Dos Aguas.—**Michoacán:** Sierra Barolosa, 1.5 hrs (by mule) S WRancho Barolosa, 7800 ft, 3 (UMMZ); vicinity and 3 mi N Rancho Reparto, 6 hrs, 20 min (by mule) E Coalcomán, 6000 ft, 2 (UMMZ); vicinity, 6.3, and 8.4 rd mi WSW Dos Aguas, 20 (UMMZ).

37. Colima Coastal Plain.—**Colima:** 23 mi (Hwy 80) SE Manzanillo, 50 m, 2 (UMMZ); Armería, sea level–200 ft, 2 (USNM); Paso del Río, 200–300 ft, 22 (UMMZ).

38. Pueblo Juárez.—**Colima:** Pueblo Juárez (Hacienda La Magdalena), 1500 ft, 25 (7 AMNH, 13 LACM, 5 USNM).

39. Platanar.—**Jalisco:** Platanar, 4000 ft, 3 (USNM).

40. Nevado de Colima.—**Jalisco:** Tuxpan, 1 (AMNH); slopes of Nevado de Colima, 4000–10,000 ft, 78 (9 AMNH, 20 LACM, 34 UMMZ, 15 USNM); *Las Canoas,* 1 (AMNH); *Tanko Riparti, Volcán de Nieve,* 6 (AMNH); *Volcán de Nieve,* 1 (AMNH); *Los Masos,* 5 (AMNH); *Volcán de Fuego,* 48 (AMNH); *8 mi W Atenquique, 9100 ft,* 1 (MSU); Tonila (including Hacienda San Marcos), 4 (AMNH).

41. Ameca.—**Jalisco:** Cerro Viejo de Magdalena, 6500 ft, 3 mi NE Magdalena, 1 (KU); Cerro Tequila, 7 mi S, 2 mi W Tequila, 10,000 ft, 1 (KU); 5 mi N Ameca, 6000 ft, 1 (KU); Ameca, 5000 ft, 4 (USNM); 13 mi WSW Ameca, 5100 ft, 2 (KU); La Cienega, 700 ft, 1 (AMNH); *Wakenakili Mountains,* 6 (AMNH); *La Laja, 9000–10,000 ft,* 1 (AMNH). **Nayarit:** 6 mi S Ixtlan del Río, 6800 ft, 1 (KU); Rancho Palo Amarillo, near Amatlan de Cañas, 5000 ft, 4 (AMNH); *Estancia,* 5 (AMNH); *Arroyo de Platanar,* 1 (AMNH); *Río Santa María,* 3 (AMNH). Elevations for localities of AMNH specimens are given by Allen (1906).

42. Mazamitla.—**Jalisco:** 4 mi W Mazamitla, 6600 ft, 2 (KU); *3 mi WSW Mazamitla,* 1 (KU); *3 mi SW Mazamitla, 1900 m,* 1 (UMMZ).

43. Patamban.—**Michoacán:** near Patamban, 9000 ft, 7 (USNM); *Sierra Patamban, 9000 ft,* 4 (KU).

44. Cerro de Tancitaro.—**Michoacán:** 6 mi W Quiroga, 2 (UMMZ); Pátzcuaro, 7000 ft, 20 (1 AMNH, 19 USNM); *9 km S Pátzcuaro (hwy to Tacambaro),* 1 (UMMZ); Volcán Parícutin, 1 (UMMZ); 4 mi E Uruapan, 1 (OC); Cerro de Tancítaro, 8000–8500 ft, 10 (USNM); *Tancítaro, 6000 ft,* 17 (FMNH); *vicinity of Apo on Cerro de Tancítaro, 2600 m,* 12 (UMMZ); *2 mi N Apo, Rancho Escondido,* 2 (UMMZ); *¾ mi N San Juan,* 1 (UMMZ); 12 mi S Pátzcuaro, 9000 ft, 1 (UMMZ).

45. La Salada.—**Michoacán:** 10 km W Apatzingán, 1040 ft, 5 (FMNH); La Salada, 2000 ft, 15 (USNM); near La Huacana, 2000 ft, 1 (USNM).

46. E Morelia.—**Michoacán:** Puerto Morillos, 37 rd mi E Morelia, 9500 ft, 5 (2 MVZ, 3 OC); *30 mi E Morelia, 8500 ft,* 1 (MVZ); 15 mi ESE Morelia, 7300 ft, 1 (MVZ); Puerta

de Garnica, 10 mi W Mil Cumbres, 9400 ft, 1 (UMMZ); 12 mi W Ciudad Hidalgo, 9150 ft, 2 (KU).

47. LENGUA DE VACA.—**Estado de México:** Puerta Lengua de Vaca, 47 rd mi W Toluca, 9200 ft, 15 (4 OC, 1 IB, 10 UMMZ); Refugio San Cayetano, 3 mi S Bosencheve, 8200 ft, 2 (UMMZ); *Criadero de Fauna Cinegética de San Cayetano, 8 km SSW Villa Victoria,* 1 (IB).

48. VOLCÁN DE TOLUCA.—**Estado de México:** Volcán de Toluca, 9000, 11,000, and 11,500 ft, 10 (1 OC, 9 USNM).

49. DISTRITO FEDERAL.—**Distrito Federal:** 2 mi E La Marquesa (Hwy 15), 10,000 ft, 3 (UMMZ); *Salazar,* 1 (USNM); *1 mi W Salazar, 9850 ft,* 1 (KU); *2 mi E Salazar, 10,200 ft (Estado de México),* 1 (MSU); *Parque de Hidalgo, 20 km W Ciudad de México, 9500 ft,* 1 (MVZ); *10 mi W Ciudad de México,* 1 (AMNH); Santa Rosa, 2700 m, 2 (UMMZ); Desierto de los Leones, Cruz de Coloxtitla, 3600 m, 1 (UMMZ); *Desierto de los Leones, Cruz Blanca,* 1 (IB); *Desierto de los Leones,* 4 (3 AMNH, 1 USNM); *Pico San Miguel, 3500 m,* 1 (UMMZ); *Ajusco, 7600 and 9000 ft,* 9 (1 IB, 8 USNM). Morelos: kilometer 46 (Ciudad de México-Cuernavaca Federal Hwy), ½ mi SW Distrito Federal-Morelos boundary, 1 (UMMZ); Tres Cumbres, 20 km N Cuernavaca, 9800 ft, 5 (2 MVZ, 3 CAS); *5 km N Tres Cumbres (Tres Marías), 10,000 ft,* 1 (TCWC); Huitzilac, 5 (1 IB, 4 USNM); *5 km SW Huitzilac,* 2 (IB); *Kilometers 7 and 10 de la carretera Huitzilac-Zempola,* 4 (IB); *Cerro Cuatepetl, Lagunas de Zempola, 3100–3200 m,* 6 (IB).

50. VOLCÁN POPOCATEPETL.—**Estado de México:** Monte Río Frío, 45 km ESE Ciudad de México, 2 (TCWC); *55 km SE Ciudad de México, 10,500 ft,* 8 (TCWC); *Rancho Cordoba, 2700 m,* 1 (UMMZ); *pine forest 3 mi W Río Frío,* 1 (CAS); Paso Cortez, 10,500 ft, 1 (UMMZ); *N slope Volcán Popocatepetl, 13000 ft,* 2 (OC); *Volcán Popocatepetl, 11,500 ft,* 1 (USNM); *W slope Volcán Popocatepetl, 72 km SE Ciudad de México, 10,000 ft,* 1 (TCWC); *83 km SE Ciudad de México, 13,500 ft,* 2 (1 MVZ, 1 TCWC). **Morelos:** Tetela del Volcán, 8500 ft, 1 (USNM). **Puebla:** Tochimilco, 7500 ft, 4 (USNM).

51. NORTHERN PUEBLA HIGHLANDS.—**Puebla:** Mesa de la Tuca (W Rancho Ocotal Colorado) 10,000 ft, 1 (UMMZ); *Cruz Alta (S. Aquixtla), 9000 ft,* 7 (UMMZ).

52. HIDALGO-PUEBLA EASTERN HIGHLANDS.—**Hidalgo:** 13 mi NE Metepec (Hwy 53), 6600 ft, 1 (UMMZ). **Puebla:** 2 rd mi NW Zacapoaxtla, 1520 m, 6 (UMMZ); *Apulco, 5.5 rd mi NW Zacapoaxtla, 1375 m,* 3 (UMMZ); Scapa, 3 mi NE Huauchinango, 4000–4600 ft, 1 (OC).

53. LAS VIGAS.—**Veracruz:** Las Vigas, 7400–8500 ft, 16 (1 AMNH, 1 MCZ, 14 USNM); *3 mi N Las Vigas,* 3 (UMMZ); *3 km E Las Vigas, 8000 ft,* 1 (KU); ½ mi NE Las Minas, 1400 m, 6 (USNM).

54. XICO.—**Veracruz:** Xico, 5000–6500 ft, 23 (USNM).

55. JALAPA.—**Veracruz:** 5 mi N Jalapa, 4500 ft, 6 (1 OC, 5 TCWC); *Jalapa,* 2 (AMNH).

56. TLAPANCINGO.—**Puebla:** Piaxtla, 3900 ft, 2 (USNM). **Oaxaca:** Tlapancingo, 7500 ft, 3 (USNM); 2 km NE San Andrés Chicahuastla, 2300 m, 5 (UMMZ).

57. W OAXACA DE JUÁREZ.—**Oaxaca:** Rancho de las Rosas, 46 mi (Panamer-hwy) NW Oaxaca de Juárez, 1 (OC); 15 mi W Oaxaca de Juárez, 8800–9500 ft, 15 (1 AMNH, 14 USNM).

58. SIERRA DE JUÁREZ.—**Oaxaca:** S slope Cerro Pelon (13 rd mi NE Llano de las Flores), 2700 m, 4 (UMMZ); Llano de las Flores, 12 mi N Ixtlán de Juárez, 9500 ft, 7 (UMMZ); *4 rd mi SW Llano de las Flores, 8700 ft,* 2 (UMMZ); vicinity of Cerro San Felipe, 8000–10,000 ft, 14 (1 FMNH, 1 MVZ, 9 USNM, 3 UMMZ); *La Cumbre, 5 mi NE Cerro San Felipe,* 2 (1 CAS, 1 MVZ).

None of the following localities are included in the sample groups listed above.

CHIAPAS.—20 mi WSW Cintalapa, 4200 ft, 1 (CAS); Cinco Cerros, 1 (AMNH); San Vicente, 4000 ft, 3 (USNM); Mapastepec, 1 (UMMZ). None of the following localities are mapped in Figure 1: 6 mi NW Tonala, 1 (KU); Finca San Salvador, 15 km SE San Clemente, 1000 m, 1 (KU); Pinabete, 8200 ft, 2 (USNM); Morelia, 4700 ft, 2 (KU); San Jose, 28 mi ESE Comitan, 4900 ft, 2 (MVZ); Finca El Paraiso, 4050 ft, 1 (KU); 4 km N Finca Prusia, 1160 m, 1 (IB); Finca Esperanza, 45 km (by rd) N Huixtla, 770 m (apparently not the "Finca Esperanza" at 250 m where *Sciurus variegatoides* occurs [see Hooper, 1947]), 1 (IB); Finca Cacahuatl, 1 (SDM); Cacahuatl, 4 km E Rizo de Oro, 4 (IB).

COLIMA.—Plains of Colima, 1 (AMNH); Río de Coahuayana, 1 (USNM); 5 km NE Comala, 1 (LACM, not mapped).

GUERRERO.—Apipilulco, 1 (FMNH); 12 mi S Zirandaro (El Rancho Portrero de los Indios), 1200 ft, 1 (OC); El Zopilote, 1 (USNM); El Naranjo, 1 (USNM); Papayo, 3 (USNM); San Marcos, 200 ft, 1 (USNM).

HIDALGO.—10 mi NNE Zimapán, 7000 ft, 1 (UMMZ).

JALISCO.—Barranca Ibarra, 3000 ft, 1 (USNM); 1 mi N Tapalpa, 7800 ft, 1 (OC). The following localities are not mapped in Figure 1: Etzatlán, 1 (USNM); 1.5 and 2 mi N Tequila, 3500 and 3700 ft, 2 (UMMZ).

ESTADO DE MÉXICO.—none of the following localities are mapped: Volcán Popocatepetl, 22 km N Amecameca, 3425 m, 1 (KU); 5 km W Río Frío, 10,000 ft, 1 (KU); 7 mi W San Jose Allende, 4 (KU).

MICHOACÁN.—Coalcomán, 3500 ft, 2 (UMMZ); Ojos de Agua, near Cabeza Negra (Punta San Juan de Lima), 100 ft, 1 (UMMZ). The following localities are not mapped: Nahuatzin, 8500 ft, 2 (USNM); 1.5 km N San Juan, 2250 m, 1 (KU); 4 mi SE Angahuan, 7500 ft, 3 (KU).

MORELOS.—pine woods above Cuernavaca, 2 (CAS, not mapped).

OAXACA.—Reyes Pápalo, 6700 and 9200 ft, 3 (USNM); Cerro Zempoaltepec, 1 (USNM); near La Parada, 8500 ft, 1 (USNM); 45 mi NW Sola de Vega, 1 (AMNH); 3.5 mi E Matías Romero, 1 (LACM); Cerro Atravesado, 2 (AMNH); 20 mi NE La Ventosa, 3 (AMNH); Potrero Gueladú, 10 mi E Jalapa de Diaz, 1 (AMNH); Chontecomatlán, 1 (AMNH); Santiago Astata, 1 (AMNH); Pluma Hidalgo, 3000 ft, 1 (USNM). The following localities are not mapped in Figure 1: Llano Grande, 1 (USNM); La Reforma, 1 (FMNH).

PUEBLA.—26 mi NW San Martin Texmelucan, 9000 ft, 1 (OC).

VERACRUZ.—N slope Cofre de Perote, 10,500 ft, 1 (TCWC); S slope Volcán Citlaltepetl (Pico de Orizaba), vicinity of Malacara, 9600 ft, 2 (CAS).

GUATEMALA.—HUEHUETENANGO: San Mateo, 2 (AMNH); Nenton, 3500 ft, 1 (USNM). JALAPA: San Lorenzo, 4 mi NE Volcán de Jumay, 5900–6000 ft, 3 (FMNH). SAN MARCOS: 3 mi N, 1 mi S San Marcos, 9500 ft, 1 (KU, not mapped).

S. colliaei (total 314)

59. JALISCO-COLIMA COASTAL PLAIN.—**Colima:** 9.5 mi (Hwy 80) E Manzanillo, 1 (UMMZ); 13 mi (Hwy 80) SE Manzanillo, 10 (UMMZ); 17 mi (Hwy 80) SE Manzanillo, 14 (UMMZ). **Jalisco:** Tenacatita Bay, 4 (UMMZ); vicinity–5 mi NE Barra de Navidad, 23 (3 LACM, 4 KU, 16 UMMZ).

60. SAN BLAS.—**Nayarit:** vicinity of San Blas, 37 (15 USNM, 22 UMMZ); 10 mi E San Blas, 200 ft, 1 (LACM); 5 mi SE San Blas, 3 (KU).

61. SOUTHERN SINALOA.—**Sinaloa:** 20 mi SE Mazatlán, 4 (UMMZ); Escuinapa, 14 (AMNH); Juan Lisiarraga Mountain, 3 (AMNH); Los Peiles, 3 (AMNH; the last two localities are not mapped in Figure 1).

62. SONORA-CHIHUAHUA.—**Chihuahua:** Carimecchi, Rio Mayo, 4 (UMMZ). **Sonora:** San Javier, 3 (Anderson, 1962:13); Río Mayo, 800 ft, 4 (USNM); Agua Marin, 8.3 mi WNW Alamos, 6 (MVZ); Chinobampo, 3 (Anderson, 1962:13); 3 mi E Guirocoba, 9 (MVZ).

The following localities are not included in the grouped samples listed above.

CHIHUAHUA.—Barranca de Cobre, 4300 ft, 1 (LACM); 40 km N, 6 km W Choix (in Sinaloa), 2400 ft, 1 (KU).

COLIMA.—(none of the following localities are mapped in Figure 1) 4 km ENE Santiago, 1 (KU); 1 mi NE Santiago, 10 ft, 1 (KU); Manzanillo, sea level–50 ft, 3 (USNM).

DURANGO.—Chacala, 6 (USNM); Santa Ana, 1300 ft, 7 (KU); *12 km E Cosalá, 1300 ft,* 4 (KU); *6 km E Cosalá, 1500 ft,* 3 (KU).

JALISCO.—San Sebastián, 3000–7500 ft, 7 (USNM); 4 mi NNE Puerto Vallarta, 50 ft, 2 (KU); Ixtapa, 300 ft, 2 (USNM); Las Palmas, 1000 ft, 1 (USNM); Mascota, 4700 ft, 1 (USNM); Sierra de Cuale, 6500, 7300 ft, 7 (KU); 10 mi SE Talpa de Allende, 5350 ft, 1 (KU); 15 mi S, 9 mi E Talpa de Allende, 6500 ft, 1 (KU); 5 mi S, 1 mi E El Arado, 4 (KU); 18 km NW Purificacion, 1 (KU); *20 km WNW Purificacion, 1400 ft,* 1 (KU); Sierra de Autlán, 20 mi SSE Autlán, 6500 ft, 3 (UMMZ); Sierra de Autlán, 12 mi SSW Ahuacapán, 4 (LACM); 9 mi SSW Ahuacapán, 1 (LACM); Sierra de Autlán, La Cumbre, 9 mi SSW Autlán de Navarro, 4 (LACM); *11 mi SW Autlán de Navarro, 2000 ft,* 2 (KU). The next two localities are not mapped in Figure 1: 1 mi E Malaque, 2 (LACM); 7 mi NE Malaque (N Cihuatlán), 1 (LACM).

NAYARIT.—Acaponeta, 200 ft, 2 (USNM); Platanares, 10 mi E Ruiz, 12 (KU); *2 mi E El Venado, 200 ft,* 2 (KU); Las Varas, 1 (USNM); 8 mi SSW las Varas, 2 (KU); *5 mi S Las Varas, 150 ft,* 5 (KU); Banderas Bay, Mita Point, 1 (UMMZ). The next locality is not mapped: Santiago Ixcuintia, 200 ft, 6 (USNM).

SINALOA.—13 km NNE Vaca, 1300 ft, 2 (KU); 15 km N, 65 km E Sinaloa, 4700 ft, 8 (KU); 10 km S, 38 km E Sinaloa, 800 ft, 1 (KU); 20 km N, 5 km E Badiraguato, 1800 ft, 4 (KU); 1.5 mi N Badiraguato, 750 ft, 5 (KU); 13 mi ESE Badiraguato, 800 ft, 4 (KU); 32 mi SSE Culican, 3 (KU); 1.5 mi E San Lorenzo, 1 (KU); San Ignacio, 700 ft, 2 (KU); ½ mi (hwy) S Revolcaderos, 6600 ft, 1 (UMMZ); near Mazatlán, 1–300 ft, 6 (USNM); *Presidio propre Mazatlán,* 1 (AMNH); 8 km N Villa Unión, 450 ft, 3 (KU); 7 mi ENE Plomosas, 6000 ft, 1 (KU); vicinity of Plomosas (Plomosas, 22 km E Matatan, 2500 ft, 4; 2 mi SW Plomosas, 3050 ft, 2; 3 mi SE Plomosas, 1), 7 (KU); Palmito, 20 ft, 6 (KU); Isla Palmito del Verde (middle), 2 (KU). The following localities are not mapped; 2 mi E Aguacaliente, 800 ft, 3 (KU); 5 km SW Santa Lucia, 2150 ft, 1 (KU); Tatemales, 3 (AMNH).

SONORA.—8 mi SE Alamos, 1 (KU).

S. variegatoides (total 80)

63. CHIAPAS-GUATEMALA COASTAL PLAIN.—**Chiapas:** 19 km S Mapastepec, 25 ft, 1 (UMMZ); Distrito Soconusco, Finca Esperanza (*ca.* 4 mi NE Escuintla; apparently not the same "Finca Esperanza" where Villa-R [1949] worked), 200 m, 2 (UMMZ); 8 km NE Huixtla, 160 m, 1 (UMMZ); Huehuetán, 300 and 500 ft, 8 (1 AMNH, 7 USNM); Cacahuatán, 4 (2 OC, 2 UMMZ). **Guatemala:** RETALHULEU: Salache, 1000 ft, 1 (AMNH).

SUCHITEPEQUEZ: Finca Cipres, 2000 ft, 15 (AMNH). SAN MARCOS: Finca Carolina, 3500 ft, 4 (AMNH); Hacienda California, sea level, 2 (AMNH). ESCUINTLA: Finca San Victor, 11 mi SW of Escuintla, 700 ft, 13 (6 FMNH, 7 UMMZ); Concepcion del Mar, 2 (FMNH).

The following sites are not included in the grouped localities listed above.

CHIAPAS.—7 mi ENE Tapachula, 2 (KU, not mapped).

GUATEMALA: CHIQUIMULA: Chiquimula, Linda Vista, 200 ft, 2 (FMNH). JUTIAPA: Santa Catarina Mita, 2450 ft, 1 (FMNH); 5 mi SE Asunción Mita, 1800 ft, 1 (FMNH); Amayito, 4.5 mi W Jutiapa, 1 (FMNH). CHILMALTENANGO: San Pedro Yepocapa, 4900 ft, 1 (FMNH). SANTA ROSA: Finca El Zapote, 3200 ft, 2 (UMMZ); Finca El Cacahuito, Taxisco, 1300 ft, 1 (FMNH); Astillero (42 mi SE Esquintla, on coast), 25 ft, 11 (KU). ESQUINTLA: San Jose (25 mi S Esquintla, on coast), 5 (USNM).

S. yucatanensis (total 70)

64. NORTHERN CHIAPAS-GUATEMALA.—**Chiapas:** 4 km SW Sabana de San Quintin, 215 m, 1 (KU). **Guatemala:** ALTA VERAPAZ: Finca Chama, 8 (7 AMNH, 1 UMMZ); Secanquim, 5 (AMNH).

65. EASTERN TABASCO.—**Tabasco:** 22 mi N Balancán, 1 (LSU); 12 mi NW Balancán, 1 (LSU); Monte Cristo Emiliano Zapata, 200 ft, 1 (USNM).

The following localities are not included in the sample groups listed above.

CAMPECHE.—S Campeche, 2 (UMMZ); 7 km N, 51 km E Escarcega, 2 (KU); 7.5 km W Escarcega de Metamoras, 65 m, 1 (KU); Apazote, near Yohaltun, 5 (USNM); La Tuxpena, Champotón, 5 (USNM); *5 km S Champotón,* 1 (KU).

QUINTANA ROO.—Pueblo Nuevo X-Can, 10 m, 8 (KU, not mapped); 4 km NNE Felipe Carrillo Puerto, 30 m, 2 (KU, not mapped).

YUCATÁN.—Merida, 2 (USNM); Chichén Itzá, 14 (9 AMNH, 5 USNM); Puerto Morelos, 1 (USNM, not mapped); La Vega, 2 (USNM, not mapped).

BRITISH HONDURAS.—El Cayo, 3 (UMMZ).

GUATEMALA.—PETEN: Remate, 1 (USNM); Tikal, 1 (UMMZ); Sayaxché, 1 (KU); Chuntuqui, 1 (USNM, not mapped); Pacomon, 1 (USNM, not mapped).

LITERATURE CITED

ADLER, K. 1965. Three new frogs of the genus *Hyla* from the Sierra Madre del Sur of México. Occ. Pap. Mus. Zool. Univ. Mich., 642:1–18, 4 figs., 1 pl.

ALLEN, J. A. 1877. Sciuridae. Monographs of North American Rodentia, No. 11, Pp. 631–939. *In:* Report of the United States Geological Survey of the Territories, 9:xii + x + 1091, 7 pls.

———— 1899. Notes on a collection of mammals from southern Mexico, with descriptions of new species of the genera Sciurus, Tamias, and Sigmodon. Bull. Amer. Mus. Nat. Hist., 2:165–181.

———— 1890. Notes on collections of mammals made in central and southern Mexico, by Dr. Audley C. Buller, with descriptions of new species of the genera Vespertilio, Sciurus, and Lepus. *Ibid.,* 3:175–194.

———— 1898. Nomenclatorial notes on certain North American mammals. *Ibid.,* 10:449–461.

———— 1906. Mammals from the states of Sinaloa and Jalisco, Mexico, collected by J. H. Batty during 1904 and 1905. *Ibid.,* 22:191–262, 3 figs., 14 pls.

ALLEN, J. A., AND F. M. CHAPMAN. 1897. On a collection of mammals from Jalapa and Las Vigas, state of Vera Cruz, Mexico. Bull. Amer. Mus. Nat. Hist., 9:197–208.

ALSTON, E. 1878. On the squirrels of the Neotropical Region. Proc. Zool. Soc. London, 2:656–670, 1 pl.

ALVAREZ, T. 1961. Sinopsis de las ardillas arbóreas del género *Sciurus* en México (Mamm. Sciuridae). Ann. Esc. nac. Cienc. biol., Méx., 10:123–148, 3 figs.

———— 1963. The recent mammals of Tamaulipas, México. Univ. Kans. Publ. Mus. Nat. Hist., 14:363–473, 5 figs.

ANDERSON, S. 1962. Tree squirrels (*Sciurus colliaei* Group) of western Mexico. Amer. Mus. Nov., 2093:1–13.

AUDUBON, J. J., AND J. BACHMAN. 1841. Descriptions of new species of quadrupeds inhabiting North America. Proc. Acad. Nat. Sci. Phila., 1:92–103.

———— 1849. Quadrupeds of North America. Vol. I. V. G. Audubon, New York. Pp. viii + 384. Numerous pls. and figs.

———— 1854. *Ibid.* Vol. III. Pp. v + 348. Numerous figs. and pls.

BOGERT, C. M., AND W. E. DUELLMAN. 1963. A new genus and species of colubrid snake from the Mexican state of Oaxaca. Amer. Mus. Nov., 2162:1–15, 7 figs.

BROWN, L. G., AND L. E. YEAGER. 1945. Fox squirrels and gray squirrels in Illinois. Bull. Ill. Nat. Hist. Surv., 23:443–536, 42 figs.

BURT, W. H. 1938. Faunal relationships and geographic distribution of mammals in Sonora, Mexico. Misc. Publ. Mus. Zool. Univ. Mich., 39:1–77, 26 figs.

———— 1961. Some effects of Volcán Parícutin on vertebrates. Occ. Pap. Mus. Zool. Univ. Mich., 620:1–24, 1 fig., 2 pls.

CUVIER, F. 1829. *In:* Histoire Naturelle des Mammifères, by M. Geoffroy-Saint-Hilaire and M. Frédéric Cuvier, vol. 3.

DALQUEST, WALTER W. 1953. Mammals of the Mexican state of San Luis Potosí. La. State Univ. Stud. Biol. Sci. Ser., 1:1–229, 1 fig.

DAVIS, W. B. 1944. Notes on Mexican mammals. Jour. Mamm., 25:370–403, 1 fig.

DAVIS, W. B., AND J. R. DIXON. 1959. Snakes of the Chilpancingo region, Mexico. Proc. Biol. Soc. Wash., 72:79–92, 2 figs.

DESMAREST, A. G. 1817. Nouveau Dictionnaire D'Histoire Naturelle, Paris. 10:103–104.

DRESSLER, R. L. 1957. The vegetation about Laguna Ocotal. *In:* Biological investigations in the Selva Lacandona, Chiapas, Mexico (R. A. Paynter, Jr., ed.). Bull. Mus. Comp. Zool. Harv. Coll., 116:290–298.

DUELLMAN, W E. 1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. Univ. Kans. Publ. Mus. Nat. Hist., 13:19–72, 3 figs., 8 pls.

———— 1961. The amphibians and reptiles of Michoacán, México. *Ibid.,* 15:1–148, 11 figs., 6 pls.

ELLIOT, D. G. 1904. The land and sea mammals of Middle America and the West Indies. Publ. Field Columbian Mus., Zool. Ser., 4:xxi + 439 + xlix, 130 figs.

ERXLEBEN, C. P. 1777. Systema Regni Animalis per Classes, Ordines, Genera, Species Varietates cvm Synonymia et Historia Animalivum. Classis I Mammalia. Lipsiae. Pp. 1636.

FITZINGER, L. J. F. J. 1867. Versuch einer natürlichen Anordnung der Nagethiere (Rodentia). Sitzungsberichte der Chematisch-Naturwissenschaftlichen Classe, Akad. Wiss., 55:453–515.

GEOFFROY SAINT-HILAIRE, I. 1846. Voyage Autour du Monde sur la frégate La Venus, pendant les années 1836–1839, Publie Par Ordre Du Roi, sous les auspices du Ministre de la Marine, par M. Abel Du Petit-Thouars, Capitaine de Vaisseau, Grand-officier de la Légion-D'Honneur. Atlas de Zoologie, (Gide et Cie, editors). Paris. Pls. 1–13.

——— 1855. Mammiferes. *In:* Voyage Autour du Monde sur la frégate La Venus commandee par Abel Du Petit-Thouars. Tome 5, part 1, Zoologie (Gide et J. Baudry, editors). Paris. Pp. 1–351.

GIEBEL, C. G. 1859. Die Säugethiere in Zoologischer, Anatomischer und Palaeontologischer Beziehung. Verlag Von Ambrosius Abel, Leipzig. Pp. xvi + 1–1108.

GOLDMAN, E. A. 1951. Biological investigations in México. Smithsonian Misc. Coll., 115:xiii + 476, 70 pls., frontis.

GOODWIN, G. G. 1932. A new squirrel from Guatemala. Amer. Mus. Nov., 57:1–2.

———— 1934. Mammals collected by A. W. Anthony in Guatemala, 1924–1928. Bull. Amer. Mus. Nat. Hist., 68:1–60, 5 pls.

———— 1954. Mammals from Mexico collected by Marian Martin for the American Museum of Natural History. Amer. Mus. Nov., 1689:1–16.

———— Oaxacan Mammals in the American Museum of Natural History. Bull. Amer. Mus. Nat. Hist. [In Press]

GRAY, J. E. 1867. Synopsis of the species of American squirrels in the collection of the British Museum. Ann. Mag. Nat. Hist., 20 (3rd ser.):415–434.

GRISCOM, L. 1932. The distribution of bird-life in Guatemala. Bull. Amer. Mus. Nat. Hist., 64:ix + 439, 11 figs. 2 maps.

GUTHRIE, D. A. 1963. The carotid circulation in the Rodentia. Bull. Mus. Comp. Zool. Harv. Coll. 128:455–481, 5 figs.

HALL, E. R., AND W. W. DALQUEST. 1963. The mammals of Veracruz. Univ. Kans. Publ. Mus. Nat. Hist., 14:165–362, 2 figs.

HALL, E. R., AND K. R. KELSON. 1959. The mammals of North America. Vol. I. New York: Ronald Press. Pp. xxx + 312, 79 figs.

HARRIS, W. P., JR. 1937. Revision of *Sciurus variegatoides,* a species of Central American squirrel. Misc. Publ. Mus. Zool. Univ. Mich., 38:1–39, 3 pls., 3 figs., 1 map.

HERNANDEZ, F. 1651. Nova Plantarum, Animalium et Mineralium Mexicanorum Historia. Rome.

HOOPER, E. T. 1947. Notes on Mexican mammals. Jour. Mamm., 28:40–57.

———— 1952. A systematic review of the harvest mice (genus *Reithrodontomys*) of Latin America. Misc. Publ. Mus. Zool. Univ. Mich., 77:1–255, 9 pls., 24 figs.

———— 1953. Notes on mammals of Tamaulipas, Mexico. Occ. Pap. Mus. Zool. Univ. Mich., 544:1–12.

———— 1955. Notes on mammals of western Mexico. *Ibid.*, 565:1–26.

———— 1957. Records of Mexican mammals. *Ibid.*, 586:1–9.

———— 1961. Notes on mammals from western and southern Mexico. Jour. Mamm., 42:120–122.

JONES, J. K., JR. 1963. Additional records of mammals from Durango, Mexico. Trans. Kans. Acad. Sci. 66:750–753.

KELSON, K. R. 1952. The subspecies of the Mexican red-bellied squirrel, Sciurus aureogaster. Univ. Kans. Publ. Mus. Nat. Hist., 5:243–250, 1 fig.

LEOPOLD, A. S. 1959. Wildlife of Mexico. The game birds and mammals. Univ. Calif. Press, Berkeley and Los Angeles, xiii + 568, numerous figs. and pls.

LICHTENSTEIN. 1830. Erläuterungen der Nachrichten des Franc. Hernandez von den vierfüssigen Thieren Neuspaniens. Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin:89–127.

MARTIN, P. S. 1958. A biography of reptiles and amphibians in the Gomez Farias region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool. Univ. Mich., 101:1–102, 7 figs., 4 maps, 7 pls.

MERRIAM, C. HART. 1893. Preliminary descriptions of four new mammals from southern Mexico collected by E. W. Nelson. Proc. Biol. Soc. Wash., 8:143–146.

MOORE, J. C. 1959. Relationships among living squirrels of the Sciurinae. Bull. Amer. Mus. Nat. Hist., 118:153–206, 7 figs.

MUSSER, G. G. 1964. Notes on geographic distribution, habitat, and taxonomy of some Mexican mammals. Occ. Pap. Mus. Zool. Univ. Mich., 636:1–22, 1 fig.

NELSON, E. W. 1898. Descriptions of new squirrels from Mexico and Central America. Proc. Biol. Soc. Wash., 12:145–156.

———— 1899. Revision of the squirrels of Mexico and Central America. Proc. Wash. Acad. Sci., 1:15–106, 1 pl.

———— 1901. Descriptions of two new squirrels from Mexico. Proc. Biol. Soc. Wash., 14:131–132.

———— 1904. Descriptions of new Squirrels from Mexico. *Ibid.*, 17:147–150.

———— 1907. Descriptions of two new subspecies of North American mammals. *Ibid.*, 20:87–88.

PAYNTER, R. A., JR. (ed). 1957. Biological investigations in the Selva Lacandona, Chiapas, Mexico. Bull. Mus. Comp. Zool. Harv. Coll., 116:191–298.

RODE, P. 1945. Catalogue des types de mammifères du Muséum National D'Histoire Naturelle; IV, ordre des Rongeurs. Bull. Mus. Nat. Hist. Natur., 17:131–182.

ROVIROSA, J. N. 1887. Apuntes para la zoologia de Tabasco. Vertebrados observados en el territorio de Macuspana. La Naturaleza, 7:345–389.

ROWLEY, J. S. 1966. Breeding records of birds of the Sierra Madre del Sur, Oaxaca, Mexico. Proc. West. Found. Vert. Zool., 3:103–204, 48 figs.

SAUSSURE, H. DE 1861. Note complémentaire sur quelques Mammifères du Mexique. Revue et Magasin de Zoologie, 13:3–5.

SCHALDACH, W. J., JR. 1963. The avifauna of Colima and adjacent Jalisco, Mexico. Proc. West. Found. Vert. Zool., 1:1–100, 2 maps.

SCHINZ, H. 1845. Synopsis Mammalium. J. Gassman, Sohn, in Solothurn. Pp. iv + 1–574.

SELANDER, R. K. 1964. Speciation in wrens of the genus Campylorhynchus. Univ. Calif. Publ. Zool., 74:iv + 305 pp., numerous figs. and pls.

SEREBRENNIKOV, M. K. 1931. On the polychromatism and albinism of the Siberian squirrels. Proc. Zool. Soc. London, Pt. 2:493–495, 3 pls.

SIBLEY, C. G. 1950. Species formation in the red-eyed towhees of Mexico. Univ. Calif. Publ. Zool., 50:109–194, 6 pls., 18 figs.

SIMPSON, G. G., A. ROE, AND R. C. LEWONTIN. 1960. Quantitative Zoology. New York: Harcourt, Brace and Co. Pp. vii + 440, Figs. 1–64.

STUART, L. C. 1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Cont. Lab. Vert. Biol. Univ. Mich., 45:1–87, 9 pls.

———— 1951. The herpetofauna of the Guatemalan Plateau, with special reference to its distribution on the southwestern highlands. *Ibid.*, 49:1–71, 2 maps, 7 pls.

———— 1954. Herpetofauna of the southeastern highlands of Guatemala. *Ibid.*, 68:1–65, 2 maps, 4 pls.

———— 1963. A checklist of the herpetofauna of Guatemala. Misc. Publ. Mus. Zool. Univ. Mich., 122:1–150, 1 map, frontis.

TOMES, R. F. 1861. Report of a collection of mammals made by Osbert Salvin, Esq., F.Z.S., at Dueñas, Guatemala; with notes on some of the species, by Mr. Fraser. Proc. Zool. Soc. London, pp. 278–288.

VILLA R., B. 1949. Mamíferos del Soconusco, Chiapas. Annl. Inst. Biol., 19:485–528, 1 map.

WAGLER. 1831. Einige Mittheilungen uber Thiere Mexicos. Isis von Oken: 510–535.

WAGNER, J. A. 1837. Beitrage zur kenntnis der warmblutigen wirbelthiere Amerika's. (Abhandlungen der Mathematische-Physikalischen Classe der Königlich Bayerischen Akademie der Wissenschaften München. Band 2:1–94 [repaged], 5 pls.).

——— 1843. Die Beutelthiere und Nager. *In:* Schreber, Johann Christian Daniel von, Die Säugethiere in Abbildungen nach den Natur, mit Beschreibungen. Supplement band, pts 3 + 4, pp. xiv + 523.

WEBER, W. A. 1945. Wildlife of Tabasco and Veracruz. Nat. Geog. Mag., 87:187–216, 8 photo., 15 pls.

Accepted for publication February 22, 1968

No. 79. An analysis of some physical factors affecting the local distribution of the shorttail shrew (*Blarina brevicauda*) in the northern part of the Lower Peninsula of Michigan. By WILLIAM O. PRUITT, JR. (1953) 39 pp., 9 figs. $0.75

No. 80. A comparative study of the osteology and myology of the cranial and cervical regions of the shrew, *Blarina brevicauda*, and the mole, *Scalopus aquaticus*. By GEORGE R. L. GAUGHRAN. (1954) 82 pp., 67 figs. $1.00

No. 82. The meibomian glands of voles and lemmings (Microtinae). By WILBUR B. QUAY. (1954) 24 pp., 3 pls., 3 figs. $0.25

No. 83. The comparative myology of the mammalian Genera *Sigmodon, Oryzomys, Neotoma,* and *Peromyscus* (Cricetinae), with remarks on their intergeneric relationships. By GEORGE C. RINKER. (1954) 124 pp., 18 figs. $1.50

No. 86. The anatomy of the diastemal palate in microtine rodents. By WILBUR B. QUAY. (1954) 41 pp., 4 pls., 12 figs. $0.50

No. 95. Survival rates, longevity, and population fluctuations in the white-footed mouse, *Peromyscus leucopus,* in southeastern Michigan. By DANA P. SNYDER. (1956) 33 pp., 3 figs. $0.50

No. 99. Dental patterns in mice of the Genus *Peromyscus*. By EMMET T. HOOPER. (1957) 59 pp., 24 figs. $0.75

No. 103. Life history and ecology of the chipmunk, *Eutamias amoenus,* in eastern Washington. By HAROLD E. BROADBOOKS. (1958) 48 pp., 3 pls., 6 figs. .. $0.95

No. 105. The male phallus in mice of the Genus *Peromyscus*. By EMMET T. HOOPER. (1958) 24 pp., 14 pls., 1 fig. $1.15

No. 106. The mammals of Iraq. By ROBERT T. HATT. (1959) 113 pp., 6 pls., 1 map $1.50

No. 109. Microclimates and local distribution of small mammals on the George Reserve, Michigan. By WILLIAM O. PRUITT, JR. (1959) 27 pp., 6 figs. $0.60

No. 113. Bacula of North American mammals. By WILLIAM HENRY BURT. (1960) 75 pp., 25 pls. $3.00

No. 117. The mammals of El Salvador. By WILLIAM HENRY BURT AND RUBEN A. STIRTON. (1961) 69 pp., 2 figs. $1.60

No. 120. A Synopsis of Recent North American microtine rodents. By EMMET T. HOOPER AND BARBARA S. HART. (1962) 68 pp., 11 figs. $1.30

No. 123. The glans penis in Neotropical cricetines (Family Muridae) with comments on classification of muroid rodents. By EMMET T. HOOPER AND GUY G. MUSSER. (1964) 57 pp., 9 figs. $1.35

No. 124. The comparative myology of four dipodoid rodents (Genera *Zapus, Napaeozapus, Sicista,* and *Jaculus*). By DAVID KLINGENER (1964) 100 pp., 15 figs. $1.85

No. 134. Behavioral and physiological influences on the distribution of the flying squirrel, *Glaucomys volans*. By ILLAR MUUL (1968) 66 pp., 26 figs. $1.85

No. 135. Adaptation to environmental temperature in two species of woodrats, *Neotoma cinerea* and *N. albigula*. By JAMES H. BROWN (1968) 48 pp., 18 figs. $1.50

No. 137. A systematic study of the Mexican and Guatemalan gray squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae). By GUY G. MUSSER (1968) 112 pp., 34 figs. $2.25