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CONTRIBUTIONS IN MAMMALOGY

A Volume Honoring Professor E. Raymond Hall

EDITED BY

J. Knox Jones, Jr.

Museum of Natural History
The University of Kansas
1969

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*3. In memoriam, Charles Dean Bunker, 1870-1948. By E. Raymond Hall. Pp. 1-11, 1 figure in text. December 15, 1951.

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6. The barren ground caribou of Keewatin. By Francis Harper. Pp. 1-163, 28 figures. October 21, 1955. Copies, paper bound, $1.50 postpaid from the Arctic Institute of North America, 1619 New Hampshire Avenue, N. W., Washington, D. C. 20009.

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(Continued on inside back cover)

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PREFACE

This volume is dedicated to Professor E. Raymond Hall on the occasion of his retirement from the directorship of The University of Kansas Museum of Natural History on June 30, 1967. The word "retirement" for someone of Professor Hall's interests and energies has little meaning and the months following this event have witnessed a continuation of his active involvement in local, national, and international conservation activities, field work, scholarly research, and graduate teaching.

The fact that the Museum of Natural History continues to flourish in an academic world where museums are sometimes poorly understood is a tribute to Professor Hall's vision and the single-mindedness of his administrative activities through the years. More important surely is the fact that the community of faculty and graduate student scholars inhabiting the Museum is singularly well adapted to relate the field of vertebrate natural history in a museum environment to the larger problems and principles of modern biology. This circumstance is due in large measure to the personal philosophy which guided Professor Hall through his years as director.

The ensuing collection of articles in the field of mammalogy honoring Professor E. Raymond Hall was assembled under the editorial supervision of Professor J. Knox Jones and contains contributions from many of those who received advanced degrees with Professor Hall's guidance. This collection of papers, prepared especially in Professor Hall's honor, is not only an affectionate tribute to him but also an exhortation that he continue unabated the extraordinary research career that began more than 40 years ago.

As Director of The University of Kansas Museum of Natural History (1944-1967), Professor Hall was a scholar-administrator for 23 years with various intermittent administrative involvements for a much longer period. Professor Hall's career is proof-positive that scholarly research, teaching, public service, and administration can form a highly productive mix and one which his successors may have difficulty emulating.

Philip S. Humphrey

EDITOR'S NOTE

Shortly after E. Raymond Hall's retirement as Director of the Museum of Natural History at Kansas, several of his former graduate students met to discuss means of commemorating the occasion. It was decided that a "Festschrift" of papers in mammalogy, contributed by his students and honoring a lifetime of teaching and research, would be eminently appropriate. Officials at The University of Kansas, including Chancellor W. Clarke Wescoe, Provost James R. Surface, and Dean of Faculties Francis H. Heller, enthusiastically endorsed the project and have provided substantial financial support.

All those who received the Ph.D. degree under Professor Hall's guidance were asked to contribute to the proposed volume, as were two leading Mexican mammalogists who studied at Kansas and received the M.A. degree there. Some persons contacted understandably were unable to participate, principally because administrative or other duties long had deprived them of the opportunity for active research in mammalogy. Seventeen, however, agreed to do so, and were instructed to select from their own current research a contribution that they felt would be appropriate for the "Festschrift." In this way, it was hoped that the collected papers would reflect, indirectly, one aspect of Professor Hall's impact on the discipline of mammalogy.

Editing of the papers that comprise "Contributions in Mammalogy" was held to a minimum consistent with the established style of the publications of the Museum of Natural History. The present volume is number 51 of the Miscellaneous Publications of the museum, which is particularly pertinent in that E. Raymond Hall was instrumental in establishing this series as well as the familiar "University of Kansas Publications, Museum of Natural History."

The outstanding workmanship and cooperation of persons at The University of Kansas Printing Service in seeing this volume through to completion is gratefully acknowledged, as is the substantial editorial assistance provided by several of my graduate students, especially Elmer C. Birney, Hugh H. Genoways, Carleton J. Phillips, James D. Smith, and Ronald W. Turner.

J. Knox Jones, Jr.

CONTRIBUTIONS IN MAMMALOGY

E Raymond Hall

EUGENE RAYMOND HALL—BIOGRAPHY AND BIBLIOGRAPHY

BY

STEPHEN D. DURRANT

Professor E. Raymond Hall, honored by his students and to whom they dedicate this volume, was born in Imes, Kansas, on May 11, 1902, to Wilbur Downs and Susan Effie (Donovan) Hall; he married Mary Frances Harkey on August 9, 1924; three sons, William Joel, Hubert Handel, and Benjamin Downs were born to them.

His grammar school education was obtained in Kansas, as was his high school with the exception of the third year, which was taken at Yakima, Washington. He was awarded the A.B. degree from The University of Kansas in 1924. His M.A. and Ph.D. degrees were awarded by the University of California at Berkeley in 1925 and 1928, respectively (see "Who's Who in America").

He has held 80 appointments and positions of local, state, university, national, and international scope. Certainly those of greatest significance to him and to his contemporaries in his chosen field are Associate Professor of Vertebrate Zoology (1937-1944), Curator of Mammals (1927-1944) and Acting Director of the Museum of Vertebrate Zoology (1938-1944) at the University of California, Berkeley, and Professor of Zoology (1944-1958), Chairman, Department of Zoology (1944-1961), Director, Museum of Natural History (1944-1967), and Summerfield Distinguished Professor (1958-present) at The University of Kansas.

Under his guidance and through his efforts, the collection of mammals and the output of published information forged ahead at the Museum of Vertebrate Zoology, University of California. This was perhaps the most prolific period (1928-1944) of this museum, both in the acquisition of specimens of mammals and in the published works upon them.

He returned to his Alma Mater, The University of Kansas, in 1944, as Director of the Museum of Natural History and Chairman of the Department of Zoology, which, in many ways, was perhaps the beginning of his finest hour. This museum, in 24 short years, has matured and grown in stature and recognition in all phases until at present it is one of the truly great institutions of our land. The expansion of the physical plant, the remarkable acquisitions in kinds and numbers of specimens, the gathering of outstanding scholars to conduct its activities, the number and quality of its graduate students, the hundreds of pages of printed results, and the educational opportunities provided for the entire citizenry bear direct testimony of Professor Hall's industry, devotion, and dedication.

He is a member of 25 scientific societies and has held important positions in several, being a Fellow in the American Society for the Advancement of Science and Past President and Honorary Member of the American Society of Mammalogists. Moreover, he has traveled widely in North America, Central America, and Europe.

While these accomplishments are remarkable and depict great energy and purpose, they are far from his greatest, which are his contributions through his students, especially his graduates, and by the printed word. The latter, as of 1968, consisted of 309 titles involving some 5400 pages. The outstanding are "Mammals of Nevada," "The Weasels of North America," and the two volume "Mammals of North America" with K. R. Kelson (see attached Bibliography). It is impossible to totally assess his impact upon the field of taxonomic mammalogy through his students, but the fruits of his personal efforts are well known. He has named and described nine new genera, a new subgenus, 23 new species, and 138 new subspecies of both fossil and Recent mammals. Four kinds, *Lutravus halli* Furlong, *Perognathoides halli* Wood, *Microtus longicaudus halli* Ellerman, and *Taxidea taxus halli* Schantz, have been named in his honor, and another is named in this volume.

Investigations have failed to disclose another person of our time who sits so high in the saddle or who has cast a wider or longer shadow of accomplishment over this field of endeavor. In the field of taxonomic mammalogy, he and his intellectual sons and grandsons are in the forefront in positions and prestige. Anywhere where taxonomic mammalogy is pursured his influence is felt by his writings, his students, or his students' students and their total productivity.

Penetrating studies of his disposition and capacities enable one to understand and evaluate the personal characteristics that have aided him to mount such a high pinnacle of achievement. Doctor Hall has an extremely intense dedication to his work, a nearly fierce belief in the efficacy of the problem at hand and his position with reference to it, and unlimited determination and physical capacity to see projects established and carried to completion.

In many respects he is a stormy petrel or at least a highly controversial figure. Once committed to a course of action, his dogged persistence, his unrelenting attack, his singleness of purpose, and his characteristic shouldering aside of opposition usually have led him to the attainment of his goals. If thwarted in one approach, he stubbornly launches a new attack from a new, different stance. To friend, he is a great source of support and encouragement; his opponents soon learn they have a man to be measured and an adversary worthy of their steel.

To him, the written word, whether in manuscript, galley, page proof, or printed, possesses a certain sanctity. His students well remember some of his idiosyncrasies in his efforts to arrive at excellence. Comments like: "You cannot encounter a mouse"; "To begin a sentence with 'however' is poor"; "Be careful of the use of 'due to,' especially with an adverbial modifier"; "Use first usages in the dictionary"; "Be careful of the use of the word 'type.'" Whether they agreed or not, all his students were impressed by the fact that when their manuscripts were returned, they were the best he was capable of making them. In some ways, he had a sixth sense of timing to keep a student totally productively occupied (sometimes fretfully) from the inception of his study to just a few moments before the deadline.

To all these accomplishments there are many as yet unsensed and uncatalogued to be brought into full fruition in decades to come. It has often been stated that no one can ever know the total effects of a stone thrown into a quiet pool. Likewise, it would be impossible to completely assess the total impact of our man of the hour upon the hundreds of persons with whom he has come into contact both in and out of his chosen field. Moreover, the situation is not to be likened to that of a quiet pool and the effects in a turbulent one undoubtedly would be tremendously pronounced and increased both in scope and intensity.

His students and colleagues stand in his honor, respect his contributions, hope for his continued productivity, and dedicate this volume to him as a monument to his endeavors and accomplishments. It might be said of him that he belongs to that select few who during their lifetime have seen their realizations far exceed their fondest expectations.

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80. Statement of Dr. E. Raymond Hall on grazing of sheep on the public domain and in the National Forests. Pp. 176-177, *in* Grazing Sheep in National Forests, Hearing before the Special Committee on Conservation of Wild Life Resources, United States Senate, Seventy-third Congress, second session.

81. Two new rodents of the genera Glaucomys and Zapus from Utah. Occas. Papers, Mus. Zool., Univ. Michigan, 296:1-6, November 2.

82. Mammals collected by T. T. and E. B. McCabe in the Bowron Lake region of British Columbia. Univ. California Publ. Zool., 40:363-386, 1 fig., November 5.

1935

83. Geographic distribution of pocket gophers (genus Thomomys) in Nevada. Univ. California Publ. Zool., 40:387-402, 1 fig., March 13 (with W. B. Davis).

84. A new mustelid genus from the Pliocene of California. Jour. Mamm., 16:137-138, 3 figs., May 15.

85. Occurrence of the spotted bat at Reno, Nevada. Jour. Mamm., 16:148, May 15.

86. A new weasel from Peru. Proc. Biol. Soc. Washington, 48:143-146, August 22.

87. Nevadan races of the Microtus montanus group of meadow mice. Univ. California Publ. Zool., 40:417-428, 1 fig., October 25.

1936

88. A new meadow mouse from Bowen Island, British Columbia. Murrelet, 17:15-16, March 7.

89. Identity of the Bowron Lake moose of British Columbia. Murrelet, 17:17, March 7.

90. A new pocket gopher from New Mexico. Jour. Washington Acad. Sci., 26:296-298, July 15.

91. Ranges and relationships of certain mammals in southwestern Utah. Proc. Utah Acad. Sci., Arts and Letters, 13:211-213, September 15 (with C. C. Presnall).

92. Mustelid mammals from the Pleistocene of North America with systematic notes on some Recent members of the genera Mustela, Taxidea and Mephitis. Publ. Carnegie Inst. Washington, 473:41-119, pls. 1-5, 6 figs., November 20.

1937

93. Mustela cicognanii, the short-tailed weasel, incorrectly ascribed to Ohio. Amer. Midland Nat., 18:304, March.

94. Lafayette sunshine. Lafayette Sun, 1 p. (with M. F. Hall).

95. [Review of] October farm, from the Concord Journals of William Brewster. Jour. Mamm., 18:245, May 14.

96. A new kangaroo mouse (Microdipodops) of Utah and Nevada. Jour. Mamm., 18:357-359, August 14 (with S. D. Durrant).

97. Deleterious effects of preservatives on study specimens of mammals. Jour. Mamm., 18:359-360, August 14.

1938

98. Fur and the public domain. The trapper and sportsman, 1(1):12-14, January.

99. A new pocket gopher from Nevada. Proc. Biol. Soc. Washington, 51: 15-16, February 18 (with F. E. Durham).
100. A new weasel from Bolivia and Peru. Proc. Biol. Soc. Washington, 51: 67-68, March 18.
101. Gestation period in the long-tailed weasel. Jour. Mamm., 19:249-250, May 14.
102. Notes on the spotted skunks (genus *Spilogale*), with accounts of new subspecies from Mexico and Costa Rica. Ann. Mag. Nat. Hist., ser. 2, 1:510-515, May.
103. Notes on the meadow mice Microtus montanus and M. nanus with description of a new subspecies from Colorado. Proc. Biol. Soc. Washington, 51:131-134, August 23.
104. Mammals from Millard County, Utah. Proc. Utah Acad. Sci., Arts and Letters, 15:121-122, June (with D. H. Johnson).
105. Variation among insular mammals of Georgia Strait, British Columbia. Amer. Nat., 72:453-463, 2 figs., September 10.
106. Mammals from Touchwood Hills Saskatchewan. Canadian Field-Nat., 52:108-109, October.
107. A new pika from southeastern Idaho with notes on nearby subspecies. Univ. California Publ. Zool., 42:335-340, 1 fig., October 12 (with H. L. Bowlus).
108. Inyo screech owl at Fallon, Nevada. Condor, 40:259, November 15.
109. Broad-tailed hummingbird attracted to food of red-naped sapsucker. Condor, 40:264, November 15.

1939

110. The spotted bat in Kern County, California. Jour. Mamm., 20:103, February 14.
111. Deux sous-especes nouvelles du rongeur *Dipodomys ordii* de l'ouest des Etats-Unis D'Amerique. Mammalia. 3:10-16, 1 pl., March (with S. D. Durrant).
112. Three new pocket gophers (mammalian genus Thomomys) from Washington. Murrelet, 20:3-5, April 30 (with W. W. Dalquest).
113. Extension of the known geographic range of the striated chipmunk (Tamias straitus). Amer. Midland Nat., 21:766, May.
114. On the characters of the pocket gopher Thomomys talpoides couchi Goldman. Murrelet, 20:38-39, August (with W. W. Dalquest).
115. Joseph Grinnell—obituary. Murrelet, 20:46-47, 1 photograph, August.
116. A new subspecies of beaver from Colorado. Jour. Mamm., 20:358-362, 1 fig., August 14 (with E. R. Warren).
117. The grizzly bear of California. California Fish and Game, 5:237-244, 2 pls., 1 fig., September.
118. Remarks on the primitive structure of Mustela stolzmanni with a list of the South American species and subspecies of the genus *Mustela.* Physis (Revista de la Sociedad Argentina de Ciencias Naturales), 16:159-178, 2 maps, 1 pl.
119. [Review of] Revision of the North American ground squirrels with a classification of the North American Sciuridae. Saugetierk., 13:184-188, September 1.
120. Joseph Grinnell [obituary notice]. Jour. Wildlife Mgt., 3:366-368, October.
121. Una nueva especie de comadreje de Bolivia y del Peru. Bol. Mus. Hist. Nat., Javier Prado, 3:95-97, October [translation of contribution no. 100].
122. Geographic races of the kangaroo rat, Dipodomys microps. Occas. Papers Mus. Zool.. Louisiana State Univ., 4:47-62, 3 figs., November 10 (with F. H. Dale).
123. Joseph Grinnell (1877 to 1839)—biographical notes. Jour. Mamm., 20: 409-417, November 14.
124. Utah jumping mouse recorded from Idaho. Murrelet, 20:71, December.

1940

125. An ancient nesting site of the white pelican in Nevada. Condor, 42:87-88, 1 fig., January 19.
126. A new race of beaver from Oregon. Jour. Mamm., 21:87-89, February 14 (with S. G. Jewett).
127. Gifts of specimens to the California Museum of Vertebrate Zoology, June 1, 1936, to June 30, 1939. Univ. California Press, pp. 1-21, March 1.
128. Supernumerary and missing teeth in wild mammals of the orders Insectivora and Carnivora, with some notes on disease. Jour. Dental Res. 19:103-119, pls. 1-12, April.
129. The Pinyon mouse (Peromyscus truei) in Nevada, with description of a new subspecies. Univ. California Publ. Zool., 42:401-405, 1 fig., April 30 (with D. F. Hoffmeister).
130. Pribilof fur seal on California Coast. California Fish and Game, 26:76-77.
131. Transplantation of the Douglas Ground Squirrel. California Fish and Game, 26:77.
132. A curious mutation in a coyote from Kern County, California. California Fish and Game, 26:393-395, 2 figs., December.
133. Capture of a coati *(Nasua narica)* in San Diego County, California. California Fish and Game, 26:395, December.
134. A new chipmunk of the Eutamias amoenus group from Nevada. Proc. Biol. Soc. Washington, 53:155-156, December 19 (with D. H. Johnson).
135. A new race of Belding ground squirrel from Nevada. Murrelet, 21:59-61, 1 fig., December 20.

1941

136. Freak antlers of mule deer. California Fish and Game, 27:37-39, 2 figs., March 27.
137. Deer has no gall bladder. Pacific Rural Press, 131:289, April.
138. Two new kangaroo mice from Utah. Murrelet, 22:5-7, April 30 (with S. D. Durrant).
139. New heteromyid rodents from Nevada. Proc. Biol. Soc. Washington, 54: 55-62, May 20.
140. Three new mammals (Microtus and Ochotona) from Utah. Great Basin Nat., 2:105-108, July 20 (with L. C. Hayward).
141. [Review of] Distribution and variation in the native sheep of North America. Jour. Mamm., 22:332, August 14.
142. [Review of] Bibliography of fossil vertebrates. Jour. Mamm., 22:333, August 14.
143. Revision of the rodent genus Microdipodops. Field. Mus. Nat. Hist., Zool. Ser., 27:233-277, 8 figs., December 8.

1942

144. The type specimen of Aplodontia rufa californica (Peters). Murrelet, 22:45-51, January 20.
145. Geographic variation in the canyon mouse, Peromyscus crinitus. Jour. Mamm., 23:51-65, 1 fig., February 14 (with D. F. Hoffmeister).
146. [Review of] Mammalia [being part 65 of the zoology of the Faroes]. Jour. Mamm., 23:100-101, February 14.
147. Joseph Grinnell, 1877 to 1939. Boone and Crockett Club, officers, by-laws, treasurer's report and list of members for the years 1940-1941, pp. 32-33, July 1, 1941 [unsigned].
148. A new race of wood rat (Neotoma lepida). Univ. California Publ., Zool., 46:369-370, July 3.
149. Gestation period in the fisher with recommendations for the animal's protection in California. California Fish and Game, 28:143-147, 1 fig., August.

150. Fur bearers and the war. Trans. 7th N. Amer. Wildlife Conf., pp. 472-475, and discussion, pp. 474-480, November.

1943

151. New genus of American Pliocene badger, with remarks on the relationships of badgers of the northern hemisphere. Abstr. Soc. Vert. Paleo., pp. 1841-1842.
152. [Review of] The Ohio Recent mammal collection in the Cleveland Museum of Natural History. Jour. Mamm., 24:105, February 20.
153. [Review of] Furred animals of Australia. Jour. Mamm., 24:105-106, February 20.
154. Cranial characters of a dog-coyote hybrid. Amer. Midland Nat., 29:371-374, 2 figs., March.
155. Intergradation versus hybridization in ground squirrels of the western United States. Amer. Midland Nat., 29:375-378, 1 fig., March.
156. Criteria for vertebrate subspecies, species and genera: the mammals. Ann. New York Acad. Sci., 44:141-144, June 8.
157. U.S. textbooks for students in Latin American universities. Science, 98: 15-16, July 2.
158. [Review of] Joseph Grinnell's philosophy of nature. Audubon Mag., 45: 252-253, August.
159. Oscar Perry Silliman—obituary notice. Jour. Mamm., 24:420, August 17.

1944

160. Pelicans of the past. Nature Mag., 37:156, 162, March.
161. Four new ermines from the islands of southeastern Alaska. Proc. Biol. Soc. Washington, 57:35-42, June 28.
162. A new genus of American Pliocene badger, with remarks on the relationships of badgers of the Northern Hemisphere. Publ. Carnegie Inst. Washington, 551:9-23, 2 pls., 2 figs., July 18.
163. Classification of the ermines of eastern Siberia. Proc. California Acad. Sci., 23:555-560, 1 fig., August 22.
164. Speciation in the American genus Mustela. Anat., Rec., 89:550, August.
165. [Review of] The armadillo: its relation to agriculture and game. Jour. Wildlife Mgt., 8:342-343, October.

1945

166. Four new ermines from the Pacific Northwest. Jour. Mamm., 26:78-85, February 27.
167. Chase Littlejohn, 1854 to 1943: observations by Littlejohn on hunting sea otters. Jour. Mamm., 26:89-91, February.
168. [Review of] The mammals of Chile. Jour. Mamm., 26:97-98, February 27.
169. Dental caries in bears. Trans. Kansas Acad. Sci., 48:79-85, 4 pls.
170. Some mammals of Ozark County, Missouri. Jour. Mamm., 26:142-145, July 13 (with A. S. Leopold).
171. A revised classification of the American ermines with description of a new subspecies from the western Great Lakes region. Jour. Mamm., 26:175-182, 1 fig., July 13.

1946

172. The Museum of Natural History, The University of Kansas. Misc. Publ., Mus. Nat. Hist., Univ. Kansas, 1:1-16, illustrated, January 5.
173. Mammals of Nevada. Univ. California Press, Berkeley, xi + 710 pp. frontispiece, 11 pls., 485 numbered figs. and 54 unnumbered figs., 2 charts, July 1.
174. [Review of] The principles of classification and a classification of mammals. Jour. Mamm., 27:287-288, August 14.

175. Zoological subspecies of man at the peace table. Jour. Mamm., 27:358-364, 2 figs., November 25.

1947

176. [Review of] Atlas des mammiferes de France. Jour. Mamm., 28:69, February 17.
177. [Review of] The California ground squirrel. Ecology, 28:211, April.
178. [Review of] Catalogue of Canadian Recent mammals. Jour. Mamm., 28: 304, August 19.
179. Subspeciation in pocket gophers of Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 1:217-236, 2 figs., November 29 (with B. Villa-R.).
180. A new bat (genus Myotis) from Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 1:237-244, 6 figs., December 10 (with W. W. Dalquest).
181. Tadarida femorosacca (Merriam) in Tamaulipas, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 1:245-248, 1 fig., December 10 (with W. W. Dalquest).
182. Obituary [Ralph Ellis (1908-1945)]. Proc. Linnean Soc. London, 159: 158-159, December 30.
183. Geographic range of the hairy-legged vampire in eastern Mexico. Trans. Kansas Acad. Sci., vol. 50:315-317, December 30 (with W. W. Dalquest).

1948

184. Pipistrellus cinnamomeus rediscovered. Jour. Mamm., 29:180, May 14 (with W. W. Dalquest).
185. A new pocket gopher (Thomomys) and a new spiny pocket mouse (Liomys) from Michoacán, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 1:249-256, 6 figs., July 26 (with B. Villa-R.).
186. Two new meadow mice from Michoacán, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 1:423-427, 6 figs., December 24.

1949

187. [Review of] Ecology of the California ground squirrel on grazing lands. Ecology, 30:112, January.
188. Paul Rode: 1901-1948. Science, 110:51, July 8.
189. Paul Rode: 1901-1948. Jour. Mamm., 30:341-342, August 17.
190. A new subspecies of the cotton rat, Sigmodon hispidus, from Michoacán, México. Proc. Biol. Soc. Washington, 62:149-150, 3 figs., August 23.
191. A new subspecies of funnel-eared bat (Natalus mexicanus) from eastern Mexico. Proc. Biol. Soc. Washington, 62:153-154, August 23 (with W. W. Dalquest).
192. A new harvest mouse from Michoacan, Mexico. Proc. Biol. Soc. Washington, 62:163-164, August 23.
193. Un nuevo ratón de campo genero Reithrodontomys de Michoacán, México. Anuarie por 1947 de la Comisión Impulsora y Coordinadora de la Investigación Científica, pp. 173-175, September 18 (with B. Villa-R.).
194. Five bats new to the known fauna of Mexico. Jour. Mamm., 30:424-427, November 14 (with W. W. Dalquest).
195. Observaciones acerca de la preparación de trabajos científicos. Univ. Nac. México, Publ. Inst. Biol., 44:1-10, December 3.
196. An annotated list of the mammals of Michoacán, México. Univ. Kansas Publ., Mus. Nat. Hist., 1:431-472, 2 pls., 1 fig., December 27 (with B. Villa-R.).

1950

197. Geographic range of the hooded skunk, Mephitis macroura, with description of a new subspecies from Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 1:575-580, 1 fig., January 20 (with W. W. Dalquest).
198. Pipistrellus cinnamomeus Miller 1902 referred to the genus Myotis. Univ. Kansas Publ., Mus. Nat. Hist., 1:581-590, 5 figs., January 20 (with W. W. Dalquest).

199. A synopsis of the American bats of the genus Pipistrellus. Univ. Kansas Publ., Mus. Nat. Hist., 1:591-602, 1 fig., January 20 (with W. W. Dalquest).

200. Speciation in American weasels (genus Mustela). Proc. 13th Internat. Cong. Zool., pp. 404-405.

201. Lista anotada de los mammíferos de Michoacán, México. An. Inst. Biol., 21:159-214, 5 figs., September 28 (with B. Villa-R.).

202. State administration of wildlife, a natural resource. Trans. Kansas Acad. Sci., 53:295-301, October 3.

203. Kansas wildlife can be saved. Southwest Farmer, Wichita Beacon, p. 11, 1 fig., November 5.

1951

204. Two new pocket gophers from Wyoming and Colorado. Univ. Kansas Publ., Mus. Nat. Hist., 5:25-32, February 28 (with G. H. Montague).

205. A northern record for *Centronycteris maxmiliani centralis* with a key to the skulls of the North American emballonurine bats. An. Inst. Biol., 21:431-433, March 6 (with W. W. Dalquest and W. G. Frum).

206. The gross anatomy of the tongues and stomachs of eight New World bats. Trans. Kansas Acad. Sci., 54:64-72, 34 figs., March 17 (with H. Park).

207. An instance of coyote-dog hybridization. Trans. Kansas Acad. Sci., 54: 73-77, 4 figs., March 17 (with J. W. Bee).

208. Mammals collected by Dr. Curt von Wedel from the barrier beach of Tamaulipas, Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 5:33-47, 1 fig., October 1.

209. Comments on the taxonomy and geographic distribution of some North American rabbits. Univ. Kansas Publ., Mus. Nat. Hist., 5:49-58, October 1 (with K. R. Kelson).

210. A new subspecies of Microtus montanus from Montana and comments on Microtus canicaudus Miller. Univ. Kansas Publ., Mus. Nat. Hist., 5:73-79, October 1 (with K. R. Kelson).

211. A new pocket gopher from eastern Colorado. Univ. Kansas Publ., Mus. Nat. Hist., 5:81-85, October 1.

212. An hypothesis to account for the winter whitening of Arctic mammals. Anat. Rec. 3:no page number, November.

213. A synopsis of the North American Lagomorpha. Univ. Kansas Publ., Mus. Nat. Hist., 5:119-202, 68 figs., December 15.

214. A new pocket gopher (genus Thomomys) from Wyoming and Colorado. Univ. Kansas Publ., Mus. Nat. Hist., 5:219-222, December 15.

215. A new name for the Mexican red bat. Univ. Kansas Publ., Mus. Nat. Hist., 5:223-226, December 15.

216. In memoriam. Charles Dean Bunker 1870-1948. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 3:1-11, 1 fig., December 15.

217. American weasels. Univ. Kansas Publ., Mus. Nat. Hist., 4:1-466, 41 pls., 31 figs., December 27.

1952

218. Taxonomic notes on Mexican bats of the genus Rhogeessa. Univ. Kansas Publ., Mus. Nat. Hist., 5:227-232, April 10.

219. Comments on the taxonomy and geographic distribution of North American microtines. Univ. Kansas Publ., Mus. Nat. Hist., 5:293-312, November 17 (with E. L. Cockrum).

220. The subspecific status of two Central American sloths. Univ. Kansas Publ., Mus. Nat. Hist., 5:313-317, November 21 (with K. R. Kelson).

221. Comments on the taxonomy and geographic distribution of some North American marsupials, insectivores and carnivores. Univ. Kansas Publ., Mus. Nat. Hist., 5:319-341, December 5 (with K. R. Kelson).

222. Comments on the taxonomy and geographic distribution of some North American rodents. Univ. Kansas Publ., Mus. Nat. Hist., 5:343-371, December 15 (with K. R. Kelson).

1953

223. A synopsis of the North American microtine rodents. Univ. Kansas Publ., Mus. Nat. Hist., 5:373-498, 149 figs., January 15 (with E. L. Cockrum).
224. A westward extension of known geographic range for the timber rattlesnake in southern Kansas. Trans. Kansas Acad. Sci., 56:89, March 21.
225. Seventeen species of bats recorded from Barro Colorado Island, Panama Canal Zone. Univ. Kansas Publ., Mus. Nat. Hist., 5:641-646, December 1 (with W. B. Jackson).

1954

226. Occurrence of the harbor porpoise at Point Barrow, Alaska. Jour. Mamm., 35:122-123, February 10 (with J. W. Bee).
227. A new subspecies of pocket mouse from Kansas. Univ. Kansas Publ., Mus. Nat. Hist., 7:587-590, November 15.

1955

228. On the legitimacy of scientific authorship. Science, 121:40-41, January 7.
229. Nuevos murciélagos para la fauna Mexicana. Acta Zool. Mexicana, 1(3): 1-2, September 10.
230. A new subspecies of wood rat from Nayarit, Mexico, with new name-combinations for the Neotoma mexicana group. Jour. Washington Acad. Sci., 45:328-332, 1 fig., October 31.
231. Handbook of mammals of Kansas. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 7:1-303, illustrated, December 13.

1956

232. What goes on under your farm? Capper's Farmer, 67(3):37, 129-131, 1 colored two-page illustration, February 13.
233. Harry Harris [obituary notice]. Burrough Club Bull., 7(4):3-4, February.
234. Future fishing and hunting in Kansas. Kansas Sportsman, 2(11):4-5, 10-11, February.
235. Mammals of northern Alaska. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 8:1-309, 1 colored frontispiece, 4 pls., 127 figs., March 10 (with J. W. Bee).
236. Animals that keep house below ground give nature a helping hand. Topeka Daily Capital, p. 13A, 1 fig., April 8 [essentially a reprint of no. 232 above, but without colored illustration].
237. Remarks on mammalian ecology and germ warfare. Pp. 101-102, *in* Symposium on ecology of disease transmission in native mammals, 6 + 122 pp., July 6.
238. The biological relationships between American weasels (genus *Mustela*) and nematodes of the genus *Skrjabingylus* Petrov, 1927 (Nematoda: Metastrongylidae), the causitive organisms of certain lesions in weasel skulls. Revista Ibérica de Parasitologia, Granada (España). Tomo Extraordinario, pp. 531-576, 8 figs., August (with E. C. Dougherty).
239. Arctic to tropics in America. Proc. XIV Internat. Cong. Zool., Copenhagen, p. 125, December 31.
240. Speciation in American microtine rodents. Proc. XIV Internat. Cong. Zool., Copenhagen, pp. 160-162, December 31.
241. Systematics of American Lagomorpha. Proc. XIV Internat. Cong., Zool., Copenhagen, pp. 521-522, December 31.

1957

242. Kansas Natural Resources Conference. Spec. Rept., 82:15-19, April 1.
243. Museum of Natural History. An unpaged, illustrated "flier," Mus. Nat. Hist., Univ. Kansas, June 1 (with R. R. Moore).

244. Vernacular names for North American mammals north of Mexico. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 14:1-16, June 19 (with S. Anderson, J. K. Jones, Jr., and R. L. Packard).

245. [Functions of a museum of natural history]. Pp. 108-110, *in* Cultural Leadership in the Great Plains—a report of the Great Plains Conference on Higher Education held at Univ. Oklahoma, Norman, P. G. Ruggiers (ed.), Univ. Oklahoma Press, viii + 191 pp., about November 1.

1958

246. Teachers, conservation and native resources. Kansas Sportsman, 4(9): 4-5, 13, January 28.

1959

247. Introduction [Geographic distribution of contemporary organisms]. Publ. Amer. Assoc. Adv. Sci., 51:371-373, January 16.

248. Publications, University of Kansas Museum of Natural History. Pp. 1-4, February 7.

249. [Review of] A guide to Saskatchewan mammals. Blue Jay, 17:44, March.

250. The mammals of North America. Ronald Press Co., New York, 1:xxx + 546 + 79, and 2:ix + 547-1083 + 79), 1231 illustrations, March 31 (with K. R. Kelson).

251. Natural History Museum, University of Kansas. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 19:unpaged, illustrated "flier," May 29 (with R. R. Moore).

252. Additional evidence indicating that *Sorex hydrodromus* Dobson is a member of the *Sorex arcticus* group of shrews. Pp. 263-265, *in* Fauna of the Aleutian Islands and Alaska Peninsula, by O. J. Murie, N. Amer. Fauna, 61:xiv + 1-364, November 4.

1960

253. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. Univ. Kansas Publ., Mus. Nat. Hist., 9:513-518, 1 map, January 14 (with M. B. Ogilvie).

254. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. Univ. Kansas Publ., Mus. Nat. Hist., 9:531-538, 1 fig., January 14.

255. Elm spray peril: child safety [letter to the editor]. Lawrence Daily Journal-World, p. 4, January 14.

256. [Review of] A revision of American bats of the genera Euderma and Plecotus. Jour. Mamm., 41:144-145, February 20.

257. Publications, University of Kansas Museum of Natural History. Pp. 1-4, May 2 (with E. Hudson).

258. The red fig-eating bat *Stenoderma rufum* Desmarest found alive in the West Indies. Mammalia, 24:65-67, 2 figs., May 27 (with J. W. Bee).

259. A new subspecies of pocket gopher (Thomomys umbrinus) from Sinaloa, Mexico, with comments on T. u. sinaloae and T. u. evexus. Proc. Biol. Soc. Washington, 73:35-38, August 10 (with C. A. Long).

260. Zoological subspecies of man. Mankind Quart., 1:113-119, 2 figs., October 31.

261. Oryzomys couesi only subspecifically different from the marsh rice rat, Oryzomys palustris. Southwestern Nat., 5:171-173, November 1.

262. ". . . *Dama* as the generic name of North American deer." Jour. Mamm., 41:537-538, November 11.

263. ". . . use of the generic name *Spermophilus* F. Cuvier, 1825, for *Mus citellus* Linnaeus and for other ground squirrels of the same genus." Jour. Mamm., 41:538-539, November 11 (with others).

264. Guide to the panorama of North American mammals. Misc. Publ. Mus. Nat. Hist., Univ. Kansas, 25:1-31, illustrated, December 15.

1961

265. Degrees and titles. Science, 133:1630-1631, May 19.
266. *Bison bison* in Nevada. Jour. Mamm., 42:279-280, 1 fig., May 20.
267. Rare books in scientific investigation. Books and Libraries at the University of Kansas, 26:7-8, May 22.
268. A new species of mouse (Peromyscus) from northwestern Veracruz, Mexico. Proc. Biol. Soc. Washington, 74:203-205, August 11 (with T. Alvarez).
269. Prairie National Park. Trans. Kansas Acad. Sci., 64:265-266, November 1.
270. Dutch elm disease and DDT spray. Kansas State Biol. Surv., Service Leaflet, no. 961-1-12, 1 p., December 15.
271. A new subspecies of pocket gopher *(Heterogeomys)* from northern Veracruz. An. Escuela Nac. Ciencias Biol., 10:121-122, December 20 (with T. Alvarez).
272. A new subspecies of black myotis (bat) from eastern Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 14:69-72, 1 fig., December 29 (with T. Alvarez).
273. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. Univ. Kansas Publ., Mus. Nat. Hist., 14:73-98, 4 figs., December 29 (with J. K. Jones, Jr.).

1962

274. The Prairie National Park. Natl. Parks Mag., 36(173):4-8, 3 photographs, 2 figs., January 26.
275. Weasel. Encyclopedia Americana. 1962 ed., 28:532, March 15.
276. A new doglike carnivore, genus Cynarctus, from the Claredonian, Pliocene, of Texas. Univ. Kansas Publ., Mus. Nat. Hist., 14:135-138, 2 figs., April 30 (with W. W. Dalquest).
277. A new bat (Myotis) from Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 14:161-164, 1 fig., May 21.
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TAXONOMIC STATUS OF THE WOODRAT, NEOTOMA ALBIGULA, IN SOUTHERN CHIHUAHUA, MEXICO

BY

Sydney Anderson

One of the earliest specimens of mammals known to have been preserved from the state of Chihuahua, Mexico, was a woodrat, *Neotoma.* It was obtained by Lt. D. N. Couch at Santa Rosalía, now known as Ciudad Camargo. The rat was reported by Baird (1859:44), who referred it to *Neotoma micropus,* which he had described in 1855 on the basis of a specimen from Charco Escondido in Tamaulipas. The Chihuahuan specimen consists only of a mounted skin.

When Goldman (1910) revised the genus *Neotoma* he assigned Couch's specimen (USNM 561), along with 50 other Chihuahuan specimens, to *Neotoma albigula albigula* Hartley, 1894. Goldman recognized the species *Neotoma micropus* and mapped its range from Colorado and Kansas in the north to San Luis Potosí in the south and from the Gulf of Mexico west to the Rio Grande Valley in New Mexico and western Texas. He did not record it from Chihuahua. By 1910, *Neotoma albigula* and *N. micropus* each included several subspecies. The range of *N. albigula* lay mostly to the west of that of *N. micropus* but the two overlapped in parts of New Mexico, Texas, and Coahuila. These distributions were summarized by Hall and Kelson (1959). Baker (1956) studied *Neotoma* in Coahuila and there recognized both species; however, he did not examine the 14 specimens from four localities from which Goldman had reported both rats.

I recently wrote a key to include in a faunal report on Chihuahuan mammals. To my surprise specimens from southeastern Chihuahua, presumably of the species *Neotoma albigula,* were identified as *Neotoma micropus* when the key was used by non-mammalogists.

The faunal report has already been delayed by the search for answers to other taxonomic problems and I do not wish to digress again at length, but I will summarize the problem and give some conclusions. The subject would well repay additional study using morphological, distributional, and ecological evidence. Karyological, behavioral, serological, and other types of study in the growing methodological arsenal of taxonomy might also be productively employed.

All specimens from Chihuahua currently assigned to the species *N. albigula,* except four specimens of *Neotoma albigula melanura* from the southwestern part of the state, are from the plateau east of the Sierra Madre. These rats may, on broad ecological grounds, be supposed to have come from a single population or at least a more or less continuously distributed and freely interbreeding series of local populations in similar habitats. Previous workers have assigned most of these rats to a single subspecies. There is no major ecological barrier in this area and the gaps that do occur in the known distribution are in places where little collecting has been done. However, contrary to what might reasonably be supposed, the rats on the plateau are not uniform in their morphological characteristics. After the discovery of *micropus*-like characteristics in two specimens from southeastern Chihuahua, I decided to look more critically at the other rats from that area. I found that many characteristics were involved, not just the one or two used in the key. The rats southeast of the Río Conchos are morphologically intermediate as a population between typical *N. a. albigula* and *N. micropus* and they are, in some ways mentioned below, slightly closer to *micropus.*

Among the previously reported features that distinguish *N. albigula* from *N. micropus* in Chihuahua and adjacent states are: (1) narrower mesopterygoid fossa (about 3.2 mm. or less rather than 4 or more), not broadly excavated near posterior plane of molars (Goldman, 1910:16); (2) relatively larger bullae; (3) color not pale slaty gray but usually darker and with a yellowish, brownish, or buffy hue; (4) smaller overall size, especially hind feet and diameter of tail (Bailey, 1932:171); (5) maxillo-vomerine notch present because medial plate of vomer not posteriorly extended (Finley, 1958:290); and (6) baculum having slender shaft and less massive base (Burt and Barkalow, 1942:290). This is not a complete list and is not documented with all relevant citations, but it does present the major differences. The meaning of these terms and the taxonomic problems posed will be clarified below.

In New Mexico, Goldman (1910) recorded *N. albigula* from 11 of the 17 localities where *N. micropus* was recorded and he wrote nothing suggesting any difficulty of identification. In southeastern Colorado, *N. albigula warreni* and *N. micropus canescens* are sympatric, and some problems of identification were discovered there by Finley (1958), who concluded that certain specimens were probably hybrids. Baily (1932:171) noted that *N. micropus* "is easily distinguished" from *N. albigula* in New Mexico, and James S. Findley informs me that he has had no difficulty distinguishing the two species in his years of work in that state.

In northern Chihuahua three specimens with skins and skulls and two partial skulls from owl pellets seem clearly referrable to *N. micropus.* Four localities are represented and from three of these localities specimens of *N. albigula* were also obtained.

Prior to learning of the problem discussed here, I examined and identified 233 *Neotoma albigula* from the plateau of Chihuahua in various museums. Most of this material has not been restudied and the specimens are not here listed. The specimens were probably correctly distinguished from two other species of *Neotoma* in Chihuahua. These are *N. mexicana,* which inhabits the Sierra Madre (where *N. albigula* is absent) as well as adjacent parts of the range of *N. albigula,* and *N. goldmani,* which is sympatric with *N. albigula* in southeastern Chihuahua. The only other species of *Neotoma* in Chihuahua is *N. micropus,* discussed below. All Chihuahuan records of *N. albigula* and *N. micropus* are mapped in Figure 1. Representative Chihuahuan specimens and some from other areas were selected for study or restudy. These are listed below. In addition to these, a larger number of other specimens were reexamined cursorily in connection with specific questions as they arose at The University of Kansas (KU), The American Museum of Natural History (AMNH), and the United States National Museum (USNM), including the U.S. Biological Survey collection.

LISTS OF SPECIMENS

Not all specimens examined are here listed, but all those from Chihuahua will be listed in a later publication. Three selected groups of specimens are listed below.

Localities of the specimens plotted in Figure 4 and used in the factor analysis are as follows.—*Neotoma albigula albigula* (all Chihuahuan, all KU); Ojo Palomo Viejo, 73911, 73915, 73916; Vado de Fusiles, 79693, 79696, 79699, 79703, 79705; 3.5 mi. N and 1 mi. W San Francisco, 69991; 1 mi. E Samalayuca, 74366; 4 mi. NW Chihuahua City, 69994; 20 mi. N Cuahtemoc, 83369. *Neotoma albigula durangae* (all except the first are Chihuahuan and at KU); San Gabriel (Durango), AMNH 21185 (the holotype of *durangae*); 5 mi. NE Las Cruces, 82799; Sierra Almagre, 9 mi. S Jaco, 56848; 12 mi. S Jaco, 56838, 56840, 56843, 56844; 15 mi. S and 3 mi. E Jaco, 56847; 5 mi. E Parral, 41043,

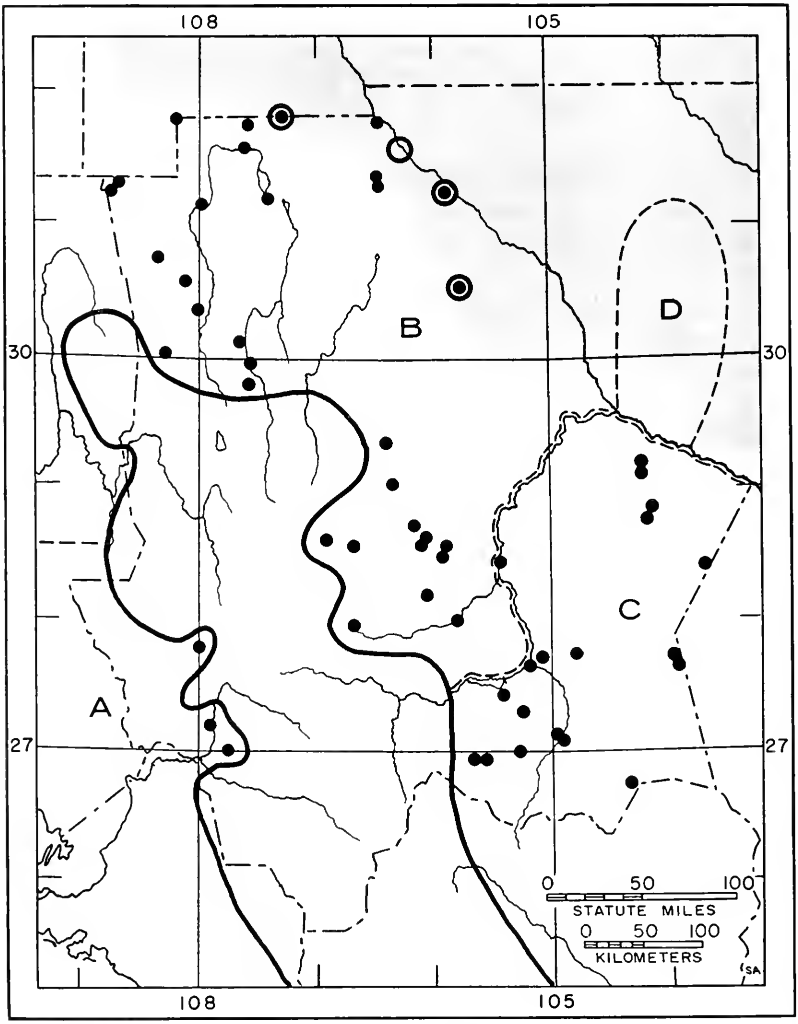

FIG. 1. Map of Chihuahua and vicinity showing the Chihuahuan localities of known occurrence of *Neotoma albigula* (dots) and *N. micropus* (open circles). At three localities both species are known. Specific localities outside of Chihuahua are not plotted. A heavy line encircles an area, largely in the Sierra Madre Occidental, from which *N. albigula* is absent. Subspecies are: *N. a. melanura* (A), *N. a. albigula* (B), *N. a. durangae* (C), and *N. a. robusta* (D). The first and the last of these subspecies are not direct subjects of this report. The range of *N. micropus* is shaded. The shaded area is also inhabited by *N. albigula*.

41045, 41046; Escalón, 83373, 83374. *Neotoma micropus* (all AMNH); Silver City, Grant Co., New Mexico, 127129, 127130; San Antonio, Bexar Co., Texas, 8668, 167865, 167867; 20 mi. S Pecos, Reeves Co., Texas, 56834, 56835;

Burnham Ranch, Brewster Co., Texas, 136589; 2 mi. W Alpine, Brewster Co., Texas; 136583; Fort Clark, Kinney Co., Texas, 12697, 12699.

Specimens numbered 1 through 22 in Figure 5 are: 1, AMNH 2746 (San Fernando de Preso, Tamaulipas); 2, USNM 35551 (Monument 15, Boundary Line, Chihuahua); 3-8, USNM 117170, 117171, 117021, 117018, 117019, and 117017 (Monclova, Coahuila); 9, USNM 117168 (Saltillo, Coahuila); 10, USNM 58072 (Jimulco, Coahuila); 11, KU 54812 (2 mi. N and 6 mi. E Camargo, Chihuahua); 12, KU 83371 (5 km. S Jiménez, Chihuahua); 13, KU 86067 (1 mi. E Julimes, Chihuahua); 14-15, AMNH 68755 and 68572 (Soledad and Alvarez, respectively, San Luis Potosí); 16, KU 89876 (3 mi. NE El Fuerte, Sinaloa); 17, KU 82809 (San Francisco de Borja, Chihuahua); 18-21, KU 73892, 73886, 73872, and 73876 (2 mi. S and 5 mi. W San Francisco, Chihuahua); 22, KU 81487 (8 mi. NE Laguna, Chihuahua).

Specimens for which measurements of bacula are plotted in Figure 6 are as follows.—*Neotoma albigula albigula* (all Chihuahuan, all KU); Vado de Fusiles, 79696; 2 mi. S and 5 mi. W San Francisco, 73878, 73881, 73892, 73895; 1 mi. E Samalayuca, 74366; 11 mi. NNW San Buenaventura, 64269, 64271; 9 mi. WSW San Buenaventura, 79709. *Neotoma albigula durangae* (all Chihuahuan, all KU); 1 mi. E Julimes, 86067; Sierra Almagre, 12 mi. S Jaco, 56843, 56845; 2 mi. W Jiménez, 85397; 5 mi. E Parral, 41046; Escalón, 83373. *Neotoma micropus* (all KU); 1 mi. W Santa Fe Airport, Santa Fe Co., New Mexico, 52353; 24 mi. E Carlsbad, Eddy Co., New Mexico, 100630; La Gloria, Nuevo León, 49594.

Specimens used to derive the statistics in Table 2 are: *Neotoma albigula albigula*, 12 specimens (all KU) from within six miles of the headquarters of the Rancho San Francisco in northwestern Chihuahua; *Neotoma albigula durangae,* seven specimens (all KU) from the Sierra Almagre in southeastern Chihuahua; and *Neotoma micropus,* a composite series including those listed above from at or near Pecos, Burnham Ranch, Alpine, Ft. Clark, and San Antonio, in Texas, Silver City in New Mexico, and Monument 15 in Chihuahua.

METHODS

By means of the craniometric instrument described by Anderson (1968), a number of measurements of skulls (Fig. 2) and bacula (Fig. 3) of *Neotoma* were taken. Cranial measurements were recorded to the nearest twentieth of a millimeter. No greater accuracy should be inferred from the fact that decimal numbers were used. For example, the citation of a measurement of 6.35 means only that the value was nearer to 6.35 than to 6.30 or 6.40.

Positions or coordinates of 36 end points shown in Figure 2 were determined for each skull. These positions were recorded in six sets: (1) from posterior to anterior in ventral view; (2) from midsagittal plane laterally in ventral view; (3) from posterior to anterior in dorsal view; (4) from midsagittal plane laterally in dorsal view; (5) from plane of bullae and incisor tips dorsally; and (6) across the zygomatic plate. The last set consists of only two points, which are on a line oblique to all of the planes used in the other five sets.

When a coordinate was defined by two bilateral points and the points did not lie on a single line perpendicular to the sagittal reference plane the recorded coordinate is that of a line midway between the two different lines. One of the first things concluded when skulls are observed under a grid is that no skull is

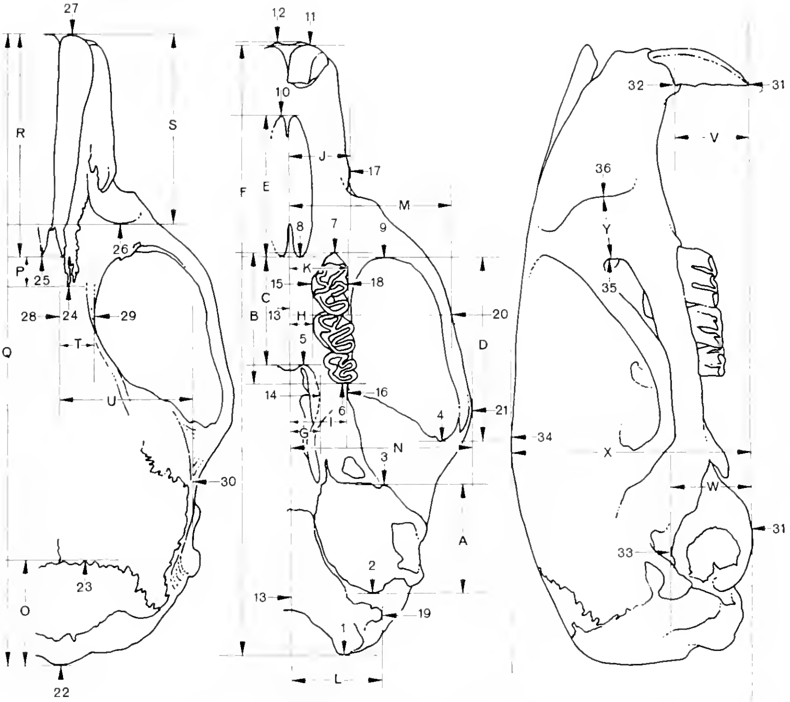

FIG. 2. Skull of *Neotoma albigula durangae* (AMNH 188729) showing measurements described in the text. Coordinates of the numbered end points were recorded and the measurements designated by letters were calculated. Measurements taken laterally from the midsagittal plane were doubled. The craniometer used was described earlier (Anderson, 1968).

exactly symmetrical bilaterally. The average discrepancy varies between different bilateral points. Studies of bilateral variation as such are of interest (see, for example, Van Valen, 1962) but the matter was not pursued farther here. When a bilateral end point was absent on one side, the point on the other side was used alone. This is an advantage of the present system of measurement for in some cases complete sets of measurements are obtainable from rather badly damaged skulls.

Some of the more critical sources of variability in measurements, but certainly not the only sources, are (1) indistinctness of end points in some cases, (2) differences in the alignment of the skull prior to beginning a set of measurements, (3) damage that occurred while the animal was alive and which altered growth in some way, and (4) distortion or damage resulting from treatment or preparation of the skull. The grosser examples of such variation are recognizable to the careful observer and can be excluded or sometimes compensated for, but the lesser examples are not recognizable. For example, the bullae are not fused with the other cranial elements and excessive or even moderate maceration or pressure in cleaning or drying may slightly displace them, or the incisor teeth may loosen enough to be moved in or out.

The reference points or end points from which measurements were derived by subtraction are listed below along with pertinent comments on some. (1) The posterior point of occipital condyle. (2) The posterior point of tympanic bulla. (3) The anterior point of anterolateral bullar process. This process seems to have a greater coefficient of variability than the overall size of the bulla itself, which the reference point was originally selected to help measure. (4) The posterior point of zygomatic aperture. There is considerable bilateral variation in the anteroposterior location of this point. (5) The anterior margin of internal narial opening. (6) The posterior point of alveolar margin of last molar. (7) The anterior point of alveolar margin of first molar. (8) The posterior point of incisive foramen. (9) The anterior point of zygomatic aperture. (10) The anterior point of incisive foramen. (11) The anterior point of incisor at its alveolus. (12) The anterior point of the nasal. This point was not used further in this study but is mentioned here because it is part of the set of measurements used elsewhere. (13) The midsagittal plane, determined visually as the average of a number of discernible midpoints. (14) The lateral point of mesopterygoid fossa. The point is indistinct when the slope of the bone is gradual but it may be quite distinct in other cases. (15) The medialmost point on alveolar margin of any molar, usually the first but sometimes the second. (16) The medial point on constriction of postdental shelf. (17) The lateral point on posterior rostral bulge. (18) The lateral point on crown of first molar. Wear of teeth alters this point. As wear proceeds beyond the widest point of the tooth the tooth becomes narrower. (19) The lateral point of paroccipital process. (20) The lateral point on zygomatic arch in a plane perpendicular to longitudinal reference axis and passing through posterior point of occlusal surface of first molar. The longitudinal reference axis is defined as the line of intersection of the midsagittal plane and a plane through the end points of a standard condylobasilar measurement. These are a posterior point of the condyle and the posterior alveolar margin of the incisor. The axis is not shown in Figure 2. (21) The lateralmost point on zygomatic arch, usually near frontojugal junction. (22) The posterior point of supraoccipital bulge. (23) A point half way between the anterior points of the two anteriormost processes on interparietal margin. This reduces the influence of a single extremely long process, either lateral or medial. (24) The posterior point of premaxillary process. (25) The posterior point of nasal. (26) The posterior point on margin of anterior zygomatic notch. (27) The anterior point of nasal. (28) The midsagittal plane. (29) The medial point on margin of interorbital constriction. (30) The lateral point of bulge, if present, of the braincase. In most *Neotoma* the posterior root of the zygoma arises laterally and obscures the point. The reading is then made to a visually approximated point just dorsal to the posterior flange of the zygomatic process and excluding the flange. (31) A plane through tips of incisors and ventral points of bullae. This plane is not parallel to the longitudinal reference axis mentioned under the twentieth reference point above (see Fig. 2 where this plane but not the reference axis is shown). (32) The dorsalmost visible point on posterior margin of incisor. (33) The dorsalmost visible point of bulla. (34) A plane tangential to dorsal profile of skull and parallel to plane of reference, namely number 31. (35) The posterior margin of zygomatic plate when skull is oriented obliquely so that plate is perpendicular to axis of view. (36) The anterior margin of zygomatic plate as viewed for 35.

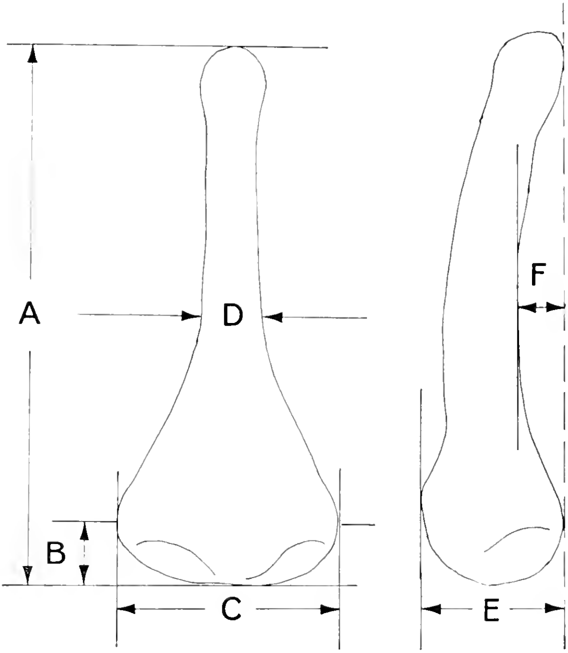

FIG. 3. Baculum showing measurements described in text. The specimen is KU 41046, a relatively old individual from 5 mi. E of Parral, Chihuahua, of the subspecies *Neotoma albigula durangae*. The length of this specimen is 7.65 mm. The dorsal view is at left, the view from the left side is shown at right.

Measurements, which were derived by subtracting the coordinates of various of the above-listed end points (and doubling measurements lateral from the midsagittal plane), are as follows (letters shown in Fig. 2): (A) length of bulla; (B) alveolar length of molar toothrow; (C) length of palate; (D) length of zygomatic aperture; (E) length of incisive foramina; (F) condyloincisive length; (G) breadth of mesopterygoid fossa; (H) breadth of palate; (I) postdental breadth; (J) rostral breadth; (K) breadth of first upper molar; (L) exoccipital breadth; (M) anterior zygomatic breadth; (N) posterior zygomatic breadth; (O) occipitoparietal length; (P) naso-premaxillary difference; (Q) occipitonasal length; (R) nasal length; (S) rostral length; (T) interorbital breadth; (U) breadth of braincase; (V) exposed length of incisor; (W) depth of bullae; (X) depth of skull; (Y) breadth of zygomatic plate.

Measurements of bacula were read on an eyepiece scale with 100 units under a binocular microscope. With the optical system used, 100 units equalled 8.3 mm. If end points were read correctly to the nearest unit of the scale, the measurements are within 0.0415 mm. of the actual values. However, because of the difficulty of aligning a slippery object floating in glycerin and the reduction in resolution resulting from the passage of light from the baculum through cleared tissues and glycerin, measurements are not that accurate. However, more than 90 per cent of the measurements, other than those of dimension B described below, probably are correct to the nearest tenth of a millimeter.

The measurements of bacula are: (A) total length; (B) distance from proximal margin to point of greatest width; (C) greatest width; (D) breadth at midpoint; (E) depth of base, or dorsoventral distance between two parallel planes tangential to the bone as shown in Figure 3; (F) depth of dorsal curvature. The position on an anteroposterior axis of the place of greatest width is in some cases more indefinite than any of the other reference points or planes and the second measurement (B) is consequently less accurate than the other measurements.

COMPARISONS

Samples of *N. albigula albigula* from northern Chihuahua were selected. Other samples, to which the name *N. albigula durangae* will be applied here, are from southeastern Chihuahua and represent the population of questionable taxonomic status. A sample representing *N. micropus* was drawn from a large region extending from central New Mexico to San Antonio, Texas. This sample therefore represents a much larger geographic area than the other samples.

Variation within the Chihuahuan part of the range of *N. a. albigula* and that of *N. a. durangae* was assessed by comparing means of samples from different local areas. Two samples of *N. a. albigula* were compared and three samples of *N. a. durangae* were compared.

Means of 25 cranial and five external measurements of four males and eight females from the vicinity of San Francisco in northwestern Chihuahua were not found to be significantly different ($P<0.05$, Student's *t*-test), therefore the sexes were combined for later calculations. A series of 12 from the vicinity of San Francisco was compared with a series of eight from near Ojo Palomo Viejo in the above 30 measurements. Three measurements were found to be significantly different: breadth of braincase and breadth of mesopterygoid fossa were greater and depth of the bulla was less in the former series.

A comparison of the means for 25 cranial measurements and five external measurements between two series of *N. a. durangae*, one from the vicinity of Parral and one from Escalón, and between the latter series and a series from the Sierra Almagre in extreme eastern Chihuahua, revealed only two statistically significant differences. The alveolar length of the maxillary toothrow in the small series of three from Escalón was larger ($P<0.05$, Student's *t*-test) than in the series of seven from the Sierra Almagre, and the tail was longer in the series from the Sierra Almagre than in the series from Escalón. The latter difference may be the result of measurements by different collectors rather than a real difference in the rats.

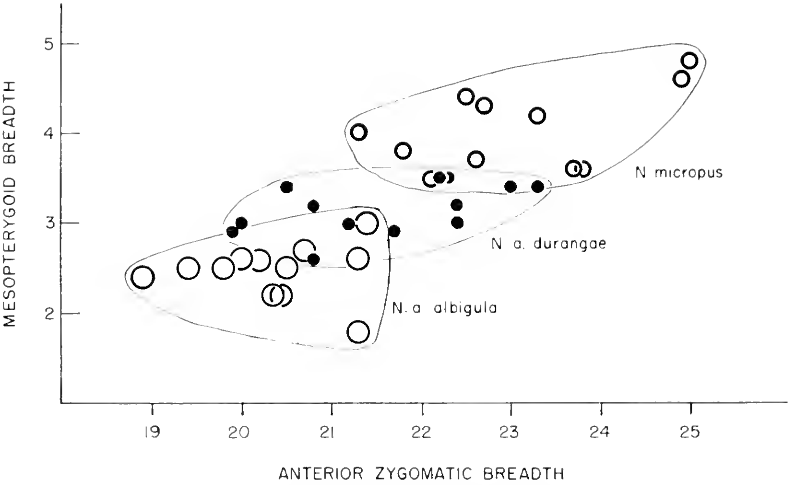

FIG. 4. Graph of two cranial measurements of individuals of three taxa of *Neotoma* as labelled.

When series of *N. a. albigula* (12 from near San Francisco) and *N. a. durangae* (seven from the Sierra Almagre) were compared, using means of 30 measurements, the differences were significant ($P<0.05$, Student's *t*-test) in 11 cranial measurements and in the length of the ear. The means of the former sample were less than those of the latter in all of these measurements except the alveolar length of the maxillary toothrow.

The sample of *N. a. albigula* from the Rancho San Francisco and the sample of *N. a. durangae* from the Sierra Almagre were then compared with a sample of *N. micropus*, again using the 95 per cent confidence level in the Student's *t*-test to compare means. Two or three significant differences among 30 measurements had been detected in the comparisons of samples within each of the two subspecies of *N. albigula,* and 11 significant differences were present between samples of the two subspecies. Further comparisons then revealed eight significant differences between *N. micropus* and *N. a. durangae* and 15 differences between *N. micropus* and *N. a. albigula.*

In terms of these data *N. a. durangae* is nearer to *N. micropus* than to *N. a. albigula,* and the possibility is raised that *durangae* may have been assigned to the wrong species. Other possibilities must also be considered. Could *durangae* be a population of intergrades and there be only one species rather than two? Could the large numbers of significant differences among the 30 measurements reflect nothing more than a general difference in size? Could the 30 measurements be largely irrelevant because diagnostic features were not adequately represented? Testing of these hypotheses and others requires either new evidence or new analysis of existing evidence, or both.

To further compare Chihuahuan samples of *N. albigula,* the method of analysis described by Lidicker (1962:164) was employed. The same samples mentioned above from the vicinity of five localities in Chihuahua were used—San Francisco (A) and Ojo Palomo Viejo (B), both in northern Chihuahua, and Sierra Almagre (C), Parral (D), and Escalón (E) in the southern part of the state. Cranial dimensions and external measurements were used, and the "minimum significant difference" was twice the sum of the calculated standard errors of the means for the two samples, rather than the estimate used by Lidicker. Only measurements significantly different at the 95 per cent level as shown by the Student's *t*-test were considered. Color was not used. Sample A was compared with B, C, and D; B with C; C with D and E; and D with E. The "Total Differentiation" and "Index of Differentiation" taken together as graphically shown by Lidicker (*op. cit.*:165) were low on his scale. The rank on his nine unit scale was in the lower two units in comparisons between the two samples within northern Chihuahua and among the three samples within southern Chihuahua. The rank of the three comparisons between northern and southern samples was in the third unit of Lidicker's scale.

The relatively greater difference, already noted above, between *N. a. albigula* (the northern samples) and *N. a. durangae* (the southern samples) than between samples within either subspecies is again shown. Of the 29 measurements (a thirtieth, length of ear, was not used here) in which differences might have occurred, only 14 were significantly different in at least one pair of samples. As previously noted, only two dimensions differed between samples of *N. a. durangae,* and three between the two samples of *N. a. albigula.* Thirteen measurements were involved in the 25 differences found in inter-subspecies comparisons of samples, which indicates some concordance.

Some of the 30 measurements taken are relevant to three of the six reportedly diagnostic characters. Size in general influences most measurements. Two measurements of the bullae are included, and the breadth of the mesopterygoid fossa is included.

I examined single measurements or pairs of measurements and found that *N. albigula albigula* could be distinguished from *N. micropus* with considerable success. Then I attempted to decide which of these two taxa was phenetically nearest to *N. a. durangae*. This was less successful because *durangae* was intermediate between *N. a. albigula* and *N. micropus* in all characters individually examined. I drew two-dimensional graphs of the most diagnostic measurements. The intermediacy of *N. a. durangae* and its partial overlap with both *N. a. albigula* and *N. micropus* was always evident (see Fig. 4, for example). Further analysis seemed advisable.

FACTOR ANALYSIS

Certain methods of multivariate analysis are useful in attempting to understand situations such as the present one in which a number of more or less correlated variables are involved.

Factor analysis is one such method, in which a large number of correlated variables are reduced to a smaller number of uncorrelated variables. The correlated variables are the measurements. The uncorrelated variables are the "factors." These are abstract hypothetical components, which then need interpretation in biological terms.

For those who want to see some other recent biological uses of factor analysis, the following are of interest: Gould (1967) on the evolution of pelycosaurs; Wallace and Bader (1967) on dentitions of *Mus*; Brown *et al.* (1965) on human cranial proportions; and Lawrence and Bossert (1967) on species of canids

A set of data was subjected to factor analysis by D. Vincent Manson using his Multivariate Statistical (MUST) program (Manson, 1967). Computation required three minutes on an IBM 7094 computer. The data matrix consisted of 25 cranial measurements of each of 36 individuals—12 *N. a. albigula* from several localities in northwestern Chihuahua, 13 *N. a. durangae* from several localities in southeastern Chihuahua and Durango (one specimen only, the holotype of *N. a. durangae*), and 11 *N. micropus* from several localities in New Mexico and Texas.

The first factor, which may be termed the "rat factor," was dominant in all specimens. It shows a clear general homogeneity in the measurements of the mixed sample of skulls but is of no use in discriminating among the subgroups. The second and third factors, however, are useful for this purpose, and, in fact, provide (Fig. 5) a better separation of the three subsamples than any

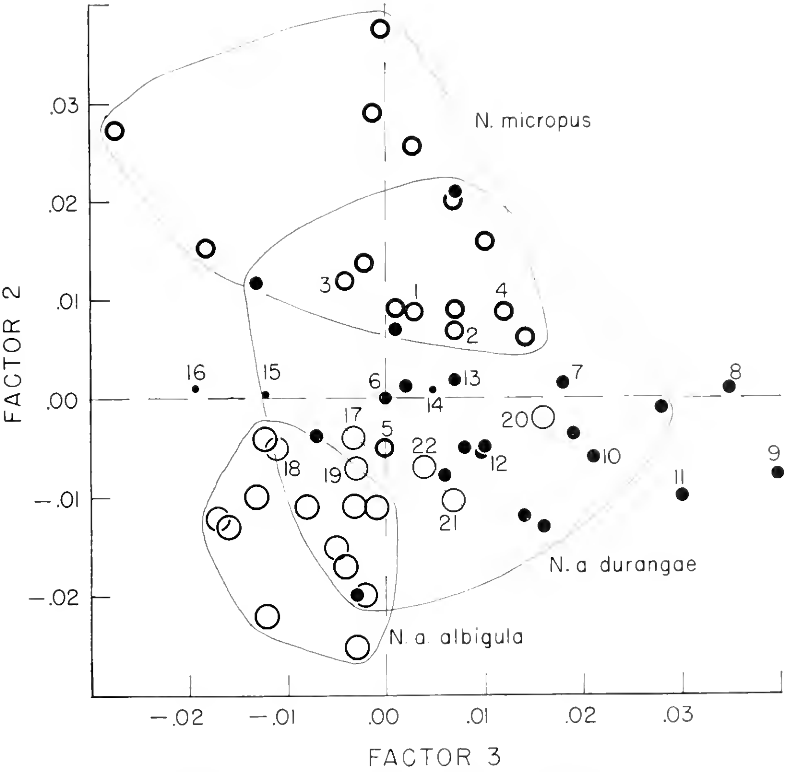

FIG. 5. Graph showing relationships of individuals of *Neotoma* as represented by two factors for each specimen. Unnumbered symbols represent specimens used in the original factor analysis. Numbered symbols are of additional specimens for comparison as described in text. Encircling lines are drawn by eye to make it easier to see the distributions of the original specimens of the three taxa labeled on the graph. Symbols identify all except three specimens. These three are 14 and 15 (*Neotoma albigula leucodon*), and 16 (*Neotoma albigula melanura*).

simpler subset of data such as the graph in Figure 4. The intermediacy of *N. a. durangae* and its overlap with *N. a. albigula* and *N. micropus* were previously surmised and these remain evident. The factor analysis thus extended and refined the earlier results. The interpretation of factors 2 and 3 is facilitated on examination of the matrix of factor components (Table 1 shows the composition of the factors in terms of proportional contribution of each of the 25 cranial measurements). For example, the measurements with greater absolute component values for factor 2 are those that will best serve to distinguish *N. micropus* from *N. a. albigula*, and they thus provide a comparison with diagnostic measurements previously

Table 1.—Factor components for first three factors and 25 measurements (listed by letter as in text).

Measurement	Factor 1 components	Factor 2 components	Factor 3 components
A	0.08722	—0.01964	0.04011
B	0.10493	—0.17303	—0.09230
C	0.09293	—0.34159	0.00964
D	0.15819	0.08160	—0.24123
E	0.11445	0.20428	—0.02983
F	0.51629	—0.06707	—0.13103
G	0.03879	0.35224	0.19642
H	0.03628	0.07745	0.05867
I	0.08381	0.04383	0.00168
J	0.09223	—0.12933	0.06402
K	0.03251	—0.04122	—0.00121
L	0.14823	—0.02236	0.44917
M	0.26318	0.47117	0.12678
N	0.28885	0.38384	0.21413
O	0.08443	—0.02250	0.28622
P	0.03001	—0.14832	0.28972
Q	0.54472	—0.16662	—0.15326
R	0.19234	0.05768	—0.48463
S	0.17175	—0.02826	—0.14695
T	0.07060	—0.12556	0.16935
U	0.21438	—0.40223	0.33691
V	0.06039	0.16584	0.06192
W	0.06960	—0.13902	0.06171
X	0.20122	—0.03247	0.07969
Y	0.05319	—0.00249	—0.04169

ascertained by other methods. Diagnostically, the best five measurements for factor 2 (factor components given in Table 1) are anterior zygomatic breadth, mesopterygoid breadth, posterior zygomatic breadth, breadth of the braincase, and length of the palate. Proportional differences involving these measurements are implied, because absolute size as such was eliminated in the analysis by normalizing the row (or specimen) vectors. There are, of course, mean differences in absolute size between the three subsamples. These differences were readily evaluated by comparing the sums of squares for the normalized data matrix in the computer output or are evident in the data of Table 2. *N. micropus* is largest and *N. a. durangae* is intermediate. There is some overlap between *N. micropus* and *N. a. albigula*. Some of this overlap results from the inclusion of rats of different ages in the samples. All were "adults" but differences in size, toothwear, and amount of fusion between cranial elements all suggest that were larger series available the range of inferred ages or relative ages in the selected sample of "adults" could be justifiably reduced further.

Factor 3 suggests that *N. a. durangae* tends to have some characteristics in which it differs from both *N. a. albigula* and *N. mi-*

cropus, but the tendency is weak. The subsample of *N. a. durangae* has higher factor coefficients on the average for factor 3 than do *N. micropus* or *N. a. albigula.* The most important measurements (those with larger factor components as shown in Table 1) contributing to factor 3 are length of nasal bones, exoccipital breadth, and breadth of braincase, which as already noted also contributes importantly to factor 2. The way in which these three measurements contribute to distinguishing *N. a. durangae* from *N. a. albigula* and *N. micropus* is not visualized simply. The measurements cannot be used singly or in pairs to distinguish individuals of *N. a. durangae* from those of the other two kinds. The tendency for uniqueness in *N. a. durangae* among the three kinds is much less than the tendency for intermediacy shown in many individual measurements and in factor 2.

The two measurements of the auditory bullae have low factor components for all three factors. The alleged usefulness of bullar size is therefore not verified.

Factor analysis in this case contributes the following: it verifies the usefulness of most of the previously suggested diagnostic characters; it discounts the usefulness of bullar size; it indicates that the intermediacy of *N. a. durangae* involves much more than size alone. The measurements that are shown to be most useful by factor analysis are, in general, those regularly used by systematic mammalogists, and the measurements not often used are shown to be less important for diagnostic purposes. This is not an argument for conventionality or against a careful search for useful new characters, but it does indicate that seemingly "subjective" methods are sometimes "objectively" verifiable.

A new specimen may be compared with the results of the present factor analysis, as follows: record the 25 measurements described; obtain the sum of the squares of these measurements and extract its square root; take the first measurement, divide it by the square root noted, and multiply the quotient by the appropriate factor component measurement (for example the first value in the column for factor 2 in Table 1); do the same for each measurement in turn and sum the 25 products. This sum is the value to be plotted (for factor 2) as in Figure 5. The process is repeated using the components for another factor (for example factor 3 if comparison is to be made with factor 2 as in Fig. 5). The process is not overly cumbersome if a desk calculator is available. A program has been written for the

Programma 101 Computer (Olivetti-Underwood) and will be sent upon request.

The information summarized to this point answers certain questions about structural resemblances but does not answer some other interesting questions. For example, are one or two species involved? Three areas where we should look for answers are as follows. Firstly, specimens from localities in Chihuahua between the localities already represented should be studied to learn whether intergradation occurs between *N. a. albigula* and *N. a. durangae,* and whether the zone of such intergradation, if present, is narrow or broad (discussed below). Intergradation is only one possibility (or hypothesis) to be tested. I interpret the available evidence to suggest intergradation between *N. a. albigula* and *N. a. durangae* in Chihuahua. Five specimens especially relevant to this question are numbers 11, 12, 13, 17, and 22 in Figure 5. The first three of these are from south of the Río Conchos and are assigned to *N. a. durangae.* The last two are from north of the Río Conchos and are assigned to *N. a. albigula,* but these specimens are not from localities near the river. No data are at hand for specimens from north of the river and nearer to it than the two mentioned above (and one other included in the original sample of *N. a. albigula*). Study of series from the two banks of the river, if they were available, would be interesting.

Secondly, other characters could be studied. Color and bacular characters have been studied and will be discussed below.

Thirdly, specimens from other parts of the ranges of *N. albigula* and *N. micropus* should be studied. An especially relevant area lies east of Chihuahua. Special attention should be given to what happens distributionally, ecologically, and morphologically in eastern Coahuila where the two species are said to meet. My deliberately limited studies in that direction are as follows.

I examined specimens at The University of Kansas from Coahuila assigned by Baker (1956:281) to *N. a. albigula.* They may better be referred to what I am here calling *N. a. durangae.* Although I have not studied the three specimens from Durango reported by Baker and Greer (1962:126) as *N. a. albigula,* I judge on geographic grounds that they also should be referred to *N. a. durangae.*

Goldman (1910) referred specimens from Saltillo, Coahuila, to *N. albigula leucodon* (USNM 117166, 117167) and *N. micropus micropus* (USNM 117168). The first two are younger than the third but none is in juvenile pelage. Pelages of all are similar in color,

TABLE 2.—MEASUREMENTS IN MILLIMETERS OF SAMPLES OF THREE TAXA OF *Neotoma*. MEASUREMENTS ARE EXPLAINED IN TEXT; SPECIMENS IN EACH SAMPLE ARE ALSO LISTED IN TEXT. MEAN, STANDARD DEVIATION, MINIMUM, MAXIMUM, AND SAMPLE SIZE ARE GIVEN.

	N. albigula albigula	*N. albigula durangae*	*N. micropus*
A (length of bulla)	6.65±0.38 6.15-7.25 n=12	7.20±0.46 6.6-8.0 n=7	7.25±0.32 6.7-7.85 n=12
B (molor toothrow)	8.50±0.29 7.95-8.8 n=12	8.14±0.39 7.7-8.75 n=7	8.76±0.59 7.7-9.3 n=12
C (length of palate)	7.34±0.25 6.8-7.85 n=12	7.81±0.65 7.15-9.1 n=7	7.20±0.65 6.3-8.1 n=12
D (zygomatic aperture)	12.60±0.36 11.95-13.05 n=12	12.62±0.94 11.5-14.0 n=7	13.53±0.76 12.1-14.6 n=12
E (incisive foramen)	9.03±0.46 8.1-9.5 n=12	9.16±0.84 7.6-10.3 n=7	10.05±0.60 9.1-11.0 n=12
F (condyloincisive length)	40.68±0.79 39.4-41.7 n=12	41.96±1.36 40.3-44.35 n=7	43.32±2.30 38.6-45.65 n=12
G (mesopterygoid breadth)	2.75±0.29 2.2-3.2 n=12	3.30±0.26 2.9-3.6 n=7	3.99±0.46 3.4-4.8 n=12
H (breadth of palate)	2.78±0.28 2.2-3.1 n=12	3.06±0.46 2.4-3.7 n=7	3.22±0.32 2.8-3.6 n=12
I (postdental breadth)	6.58±0.18 6.2-6.8 n=12	6.60±0.22 6.2-6.8 n=7	7.33±0.39 6.9-8.2 n=12
J (rostral breadth)	7.24±0.28 6.9-7.9 n=12	7.81±0.39 7.5-8.2 n=7	7.54±0.65 6.6-8.5 n=12
K (breadth of M1)	2.61±0.17 2.25-2.9 n=12	2.60±0.25 2.3-2.8 n=7	2.69±0.17 2.45-3.05 n=12
L (exoccipital breadth)	11.64±0.63 10.4-12.8 n=11	12.54±0.92 11.4-14.2 n=7	12.40±0.73 11.4-13.9 n=12
M (anterior zygomatic breadth)	20.42±0.63 19.2-21.2 n=12	21.41±1.30 19.9-21.7 n=7	22.82±1.41 20.2-24.9 n=12
N (posterior zygomatic breadth)	22.48±0.85 20.4-23.8 n=12	23.34±0.95 22.1-24.7 n=7	24.88±1.44 21.8-27.1 n=12
O (occipitoparietal length)	6.71±0.47 5.65-7.3 n=12	6.93±0.81 6.1-8.3 n=7	7.28±0.80 5.85-8.3 n=12
P (nasopremaxillary difference)	2.32±0.37 1.8-2.9 n=12	2.89±0.30 2.5-3.3 n=7	2.14±0.49 1.4-2.9 n=12

TABLE 2.—CONTINUED.

	N. albigula albigula	*N. albigula durangae*	*N. micropus*
Q (occipitonasal length)	43.32±1.19 41.6-45.0 n=12	43.88±1.72 41.55-46.65 n=7	45.80±2.31 41.1-47.15 n=12
R (length of nasals)	15.02±0.67 13.8-16.05 n=12	15.31±0.69 14.35-16.45 n=7	16.29±1.13 14.6-18.2 n=12
S (rostral length)	13.37±0.57 12.3-14.05 n=12	13.80±0.81 12.85-15.0 n=7	14.51±1.06 12.6-16.3 n=12
T (interorbital breadth)	5.76±0.19 5.4-6.0 n=12	6.06±0.39 5.5-6.7 n=7	5.95±0.46 5.3-7.0 n=12
U (breadth of braincase)	17.76±0.47 17.1-18.6 n=12	17.86±0.61 17.2-18.7 n=7	17.60±0.63 16.7-19.1 n=12
V (incisive projection)	4.39±0.44 3.3-5.1 n=12	5.15±0.34 4.8-5.75 n=7	5.26±0.56 4.7-5.95 n=12
W (depth of bulla)	5.28±0.26 4.9-5.6 n=12	5.96±0.56 5.4-7.0 n=6	5.62±0.24 5.3-6.1 n=12
X (depth of skull)	15.55±0.73 13.85-16.75 n=12	16.37±0.67 15.7-17.25 n=6	16.89±0.79 15.2-18.25 n=12
Y (breadth of zygomatic plate)	4.19±0.20 3.9-4.6 n=12	4.32±0.51 3.9-5.25 n=7	4.53±0.32 4.2-4.95 n=12
Total length	320.5±12.0 305-340 n=10	331.4±7.2 321-341 n=5	332.7±12.8 315-348 n=7
Length of tail	142.8±9.0 131-160 n=10	150.0±3.1 145-153 n=5	139.0±8.8 130-153 n=7
Length of hind foot	32.8±1.9 30-35 n=9	33.4±1.9 30-36 n=7	35.0±2.7 30-39 n=7
Weight	176.6±18.2 155-209 n=10	197.7±30.1 153-245 n=7	245±52.4 191.4-296 n=3

all having a yellowish hue. No. 117168 has a darker dorsal tail stripe than the others, and no. 117167 has larger hind feet (36 mm. as opposed to 33). I judge that a single species is represented. The specimens seem more *albigula*-like than *micropus*-like. Eight specimens from Monclova, Coahuila, include one (USNM 117018) referred by Goldman to *N. albigula albigula* and seven (USNM 117017, 117019-117021, 117169-117171) referred by him to *N. micropus canescens*. Two of the seven are young and their skulls are damaged. Measurements were taken of the other six from Monclova for comparison with the results of the factor analysis already done. On the basis of yellow hue of pelage, smaller size, and narrower mesopterygoid fossa I am inclined to place 117017 and 117019 with 117018. The condition of the vomer posteriorly does not help to separate specimens in the series from Monclova. I also measured a specimen from Jimulco, Coahuila (USNM 58072, a large male referred to *N. albigula albigula* by Goldman), and one from the northern boundary of Chihuahua (USNM 35551, a *N. micropus* of moderate size). I have not examined the three specimens from Jaral, Coahuila, the only other Coahuilan locality of sympatry referred to by Goldman for the species *N. albigula* (two specimens) and *N. micropus* (one specimen).

The coordinates for factors 2 and 3 were calculated for additional specimens measured and are plotted in Figure 5, for comparison with the series used in the original analysis. The additional specimen of *N. micropus* from northern Chihuahua falls with the other *N. micropus* but in the area of overlap with *N. a. durangae.* The rat from Saltillo and the one from Jimulco fall with *N. a. durangae.* The two rats from Monclova, re-identified by me as *N. a. durangae,* fall with other members of that subspecies. Two of the three rats from Monclova identified by both Goldman and me as *N. micropus* fall within the area of overlap of *N. micropus* and *N. a. durangae.* However, the third falls with *N. a. durangae* and outside the area on the graph of *N. micropus.* The uncertainties evident in (1) my own attempts to identify these rats from the alleged locality of sympatry, (2) the differences in assignment of some individuals by Goldman, by me somewhat subjectively, and by the factor analysis of cranial measurements alone, and (3) the lack of clear bimodal clustering in the Monclova sample all suggest, although they do not prove, that only one taxon is present in the sample from Monclova, Coahuila.

In short, to summarize the Coahuilan situation, more work is needed. There is no locality of certain sympatry between two taxa, although the small sample from Monclova is suggestive. As my study has proceeded, my confidence in the existence of a species boundary between *N. albigula* and *N. micropus* as now known, or at least in my ability to define the boundary, has decreased. If they behave as species in eastern Coahuila, the difference between the two species is certainly less than between these two species where they are sympatric in northern Chihuahua and adjacent regions of New Mexico and west Texas.

DISCRIMINANT ANALYSIS

Cranial measurements of the original 36 specimens used in the factor analysis and of 22 additional specimens (the same plotted in Fig. 5 and listed in text) were examined by Discriminant Analysis (five minutes on IBM 7094 computer). The three original groups were used to derive the discriminant functions, except that one specimen of *N. a. durangae* was placed with the *N. micropus* by mistake. The three groups were well separated, including the three specimens of *N. a. durangae* that were not separated by the factor analysis as shown in Figure 5. The mistakenly-placed specimen of *N. a. durangae* appeared with the cluster of *N. micropus* in the analysis, but at the side of the cluster nearest that of *durangae*. The factor analysis uses all measurements and incidentally results in a scatter in which groups may be separated or partly separated. In discriminant analysis only the differences in measurements between specified groups are used. This enhances the separation of groups. Plotting of the additional 22 specimens in terms of discriminant functions places them in scattered positions about or between the three discriminant groups, but their general relative positions are consistent with the relationships otherwise found.

The discriminant analysis tends to separate *N. micropus* more clearly from *N. a. albigula* and *N. a. durangae* than did the factor analysis. Both analyses tend to place additional specimens of *N. micropus* (nos. 1-4 in Fig. 5) with others of that species, and to place additional specimens of *N. albigula* (nos. 13, 15, and 16 in Fig. 5), which are of subspecies other than those already studied, with the specimens of that species already studied.

This technique is still being developed and evaluated, and, therefore, more detailed comments on these results are not included.

COLOR

Color is notoriously more difficult to describe or report on than are measurements to which numerical values easily can be assigned. I have mentioned that *N. micropus canescens,* the widely distributed subspecies that meets *N. albigula* in the Chihuahuan region, differs from *N. albigula albigula* in grayness, paleness, and relative lack of yellowish or buffy hues in dorsal pelage. However, there is considerable variation in color within the wide range of *N. a. albigula* even after its reduction by the present reassignment of specimens south of the Río Conchos of Chihuahua to *N. a. durangae*. There are specimens of *N. a. durangae* that are not distinguishable by color from many *N. a. albigula* from Chihuahua. However, on the average *N. a. durangae* is grayer and paler than *N. a. albigula*. The palest specimens examined of *N. a. durangae* are from Escalón.

The single specimen of *N. a. durangae* that falls in the midst of the *N. a. albigula* in Figure 5 is from Escalón. It therefore resembles *N. a. albigula* cranially and resembles *N. micropus* in color. When only one or two cranial characters and color, which is known to be subject to strong local natural selection, were found to be intermediate in *N. a. durangae*, it seemed reasonable to suggest that selection might have produced a convergence in these few characteristics. However, evidence for intermediacy has accumulated, and a large number of characters are involved. Some of these are not structurally related, are poorly correlated (when individuals in a single series are compared), and are not obviously influenced by local selection. Convergence as a result of selection is less reasonable than the alternative interpretation that these animals have the complex suite of characters because of common ancestry. The interesting question now becomes whether genetic exchange is occurring anywhere in nature between *N. micropus* and *N. albigula*, and, if so, what form the exchange takes. Does free intergradation occur, or occasional hybridization, or do different events occur at different places?

BACULUM

The structure of the male phallus, and of the baculum therein in particular, has been studied for *Neotoma albigula* and *Neotoma micropus* by Burt and Barkalow (1942) and by Hooper (1960). These authors suggested that *N. albigula* differs from *N. micropus* in (1) slenderness of shaft, (2) shallower U-shape of base, (3) larger distal knob, (4) smaller glans, (5) terminal hood relatively larger and not cleft distally, as opposed to slightly cleft, (6) bone longer and its spine shorter relative to both glans and foot lengths. The first three differences were based on study of 15 *albigula* and four *micropus* by Burt and Barkalow. In their table of measurements the range for *micropus* is within that of *albigula* for length and base measurements (both dorsoventral and lateral) but near the middle of the shaft there is little overlap in dorsoventral diameter and none in lateral diameter (0.51 to 0.73 for *albigula*, and 0.80 to 0.91 for *micropus*). Hooper examined three specimens each of *albigula* and *micropus* and one of *Neotoma floridana* and noted that the three species are so similar as to suggest that they are con-

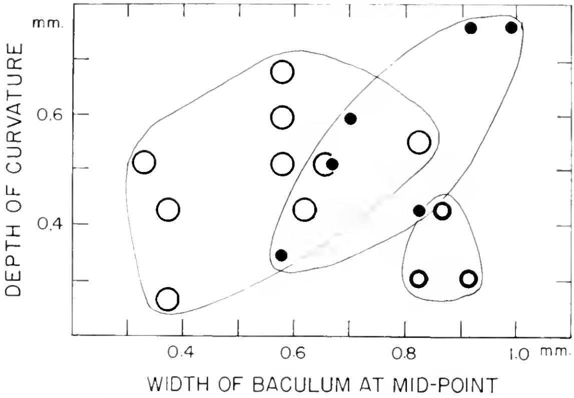

Fig. 6. Graph of two measurements of the bacula of individuals of three taxa of *Neotoma.* Large open circles are *N. albigula albigula*; dots are *N. a. durangae*; small open circles are *N. micropus.* Encircling lines are drawn freehand simply to aid perception of the groups. As in Figures 4 and 5, *durangae* is intermediate to the other two taxa.

specific or are sibling species. Differences 4 through 6 as listed above were said to be slight (Hooper, 1960:5) and I have not attempted to study them in my material.

Series of bacula were selected for study and comparison as follows: *N. albigula albigula* (22), *N. albigula durangae* (16), and *N. micropus* (13). Eighteen were measured, and their values for two measurements are plotted in Figure 6. These are the two measurements of the six taken that best distinguish *N. a. albigula* from *N. micropus* and which therefore are most revealing as to the position of *N. a. durangae.* As in the cranial characters, in color, and in size of entire animal, bacular characters show intermediacy for *N. a. durangae,* and are not clearly nearer either *N. a. albigula* or *N. micropus.*

Structure of Vomer

The degree of development and form of the vomer differ in different taxa of *Neotoma.* Finley (1958) described the differences between the species *N. albigula* (as represented by the subspecies *N. a. warreni*) and *N. micropus* (represented by *N. m. canescens*), and he used these characters in evaluating evidence for species hybridization that he found in southeastern Colorado. Figure 7 illustrates the stages of development. The major variable is the degree of enlargement posteriorly of the medial vomerine plate (shown stippled). In the least developed stage (as in 7B), a distinct

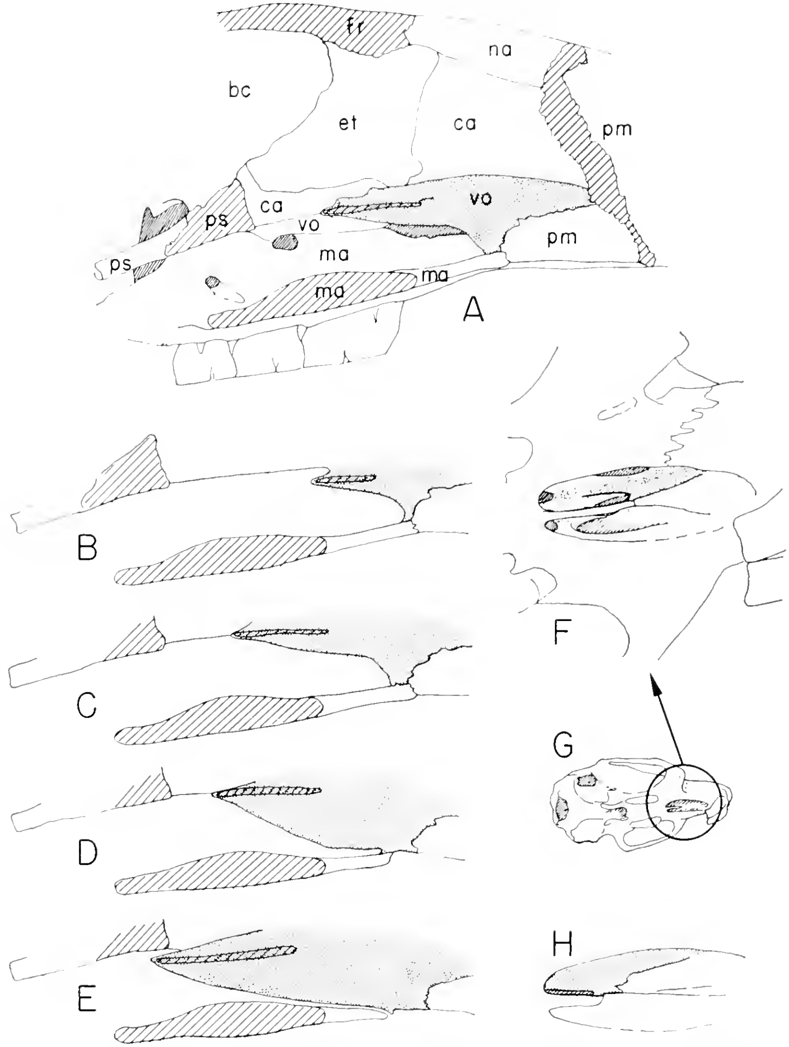

FIG. 7. Drawings of vomer and surrounding elements in skulls of *Neotoma*. A—dissection from the right to a sagittal plane near the middle of skull but leaving the medial partitions of ethmoid, cartilage, and vomer intact. Labelled elements are: *bc*, braincase; *ca*, cartilage; *et*, ethmoid; *fr*, frontal; *ma*, maxillary; *na*, nasal; *pm*, premaxillary; *ps*, presphenoid; and *vo*, vomer. Cut elements are shown by diagonal lines, and the vomerine partition is stippled for ease of comparison with B, C, D, and E. These are diagrams showing four states of vomerine development arranged in morphological sequence from least developed to most developed. States in the range of B and C occur in *N. albigula albigula*, those in the range of C and D occur in *N. albigula durangae*, and those in the range of D and E occur in *N. micropus*. An oblique view looking dorsally and slightly posteriorly into the incisive foramina is shown in F and H, which correspond in state to B and D, respectively. The oblique orientation of skull in F and H is shown by G.

rounded opening is apparent in the medial plane as seen in the incisive foramen (as in 7F). When the plate is larger, conditions such as in 7C, 7D, and 7E are evident. The legend for Figure 7 provides other details.

A condition in *Neotoma palatina* that exceeds that of Figure 7E was kindly pointed out to me by Professor E. R. Hall, who is studying the taxonomic status of this species. In some of the specimens that he has assembled at The University of Kansas the posterior projection of the vomer is so great that it protrudes visibly behind the posterior palatal margin (to the position of the letter E in Fig. 7E).

Certain modifications in adjacent structures are positively correlated with degree of vomerine enlargement: (1) shortness of medial maxillary spine; (2) shortness or loss of articulation of this spine with premaxillary; (3) amount of contact of spine with vomer, at least in stages such as 7C and 7D, although in some specimens a slit may separate these elements (as in 7E); (4) shortening of medial slit between the presphenoid and medial part of vomer and bordered laterally by posterolateral wings of vomer (the opening is reduced in a form such as 7E to a posteriorly directed median opening); and (5) narrowing of maxillo-vomerine gap posteroventral to median part of vomer from a broadly rounded aperture to a narrow slit.

In this complex of related characters, as in all other diagnostic characters studied, *N. a. durangae* is intermediate between *N. albigula albigula* and *N. micropus.*

DISCUSSION

I judge it unwise to synonymize *N. albigula* and *N. micropus* on the basis of available information, although the contrary conclusion is based on tenuous evidence. The basic questions about species limits cannot be resolved without additional information from the field. Nomenclatorially, I think the conservative course is to use the names as presently arranged until better evidence is available. A change at this time would add nothing to our knowledge and would not be especially useful. There is, furthermore, a possibility that not only is *N. albigula* synonymous with *N. micropus*. but that they are both conspecific and hence synonymous at the species level with *N. floridana.* If this be so, the name of the species would become *N. floridana,* for that is the oldest name among these three. The relationships of *N. micropus* and *N. floridana* are currently being studied by Elmer C. Birney at The University of Kansas and perhaps by other students elsewhere. In any case, *N. floridana, N. micropus,* and *N. albigula,* as suggested by previous authors, are certainly closely related.

The following are hypotheses for later consideration. *N. albigula durangae* may be similar to a stock that was ancestral to both *N. albigula* and *N. micropus.* There may or there may not be present day interbreeding between the two species in the region of eastern Coahuila. The original contact, geographically broad though it has become, between the two species in northern Chihuahua, southern New Mexico, and western Texas may have been both secondary to species divergence and later than the contact in northeastern Mexico. The possible hybridization of *N. albigula* and *N. micropus* in southeastern Colorado reported by Finley (1958) needs to be investigated in greater detail.

I have not studied Mexican specimens from south of Chihuahua and Coahuila sufficiently to offer any conclusion about the southern limits of *N. albigula durangae,* or about the relationships of the three most southern subspecies, *N. albigula leucodon, N. a. zacatecae,* and *N. a. subsolanus.*

The discoveries here reported indicate that fascinating scientific problems remain to be discovered and solved, even in the systematics of common and reasonably well known groups. The present results of study of *Neotoma* in northern Mexico add to our knowledge of variation and relationships and also direct attention to further problems warranting study, to the places where they may best be approached, and to some methods likely to be useful.

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I am especially grateful to Professor E. Raymond Hall for his continued support of my studies of Chihuahuan mammals and for his recent willingness to discuss problems of taxonomy in the genus *Neotoma,* including his own current work with *Neotoma palatina.* My work at The University of Kansas was also greatly aided by Dr. J. Knox Jones, Jr., and his curatorial assistants among the graduate students. Various persons at the U.S. National Museum, including especially Dr. Ronald Pine on my most recent visit, were helpful. My colleagues at The American Museum of Natural History, Drs. Richard G. Van Gelder, Karl F. Koopman, and Guy G. Musser, provided valued comments both in the course of my work and upon the completion of the manuscript itself. Our Scientific Assistant, Miss Elizabeth Fryatt helped in various ways, including the computations done on the Programma 101 Computer. Dr. D. Vincent Manson programmed and ran the Factor Analysis and Discriminant Analysis and aided in my statistical interpretation of the results. He should not, however, be held

responsible for the biological interpretations. The preliminary art work and plotting of graphs were done by me and then efficiently completed by graphic artists under the direction of Mr. Joseph Sedacca of The American Museum of Natural History.

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REPRODUCTION AND POPULATION DENSITIES IN A MONTANE SMALL MAMMAL FAUNA

BY

TERRY A. VAUGHAN

Small mammals occupying subalpine environments are adapted in various ways to the severe annual climatic cycle and to the short growing season. In the present study area in Colorado snow covers the ground and little plant growth occurs for approximately seven months of the year, from November through May. During the five-month snow-free period the plants undergo their brief growth and flowering. Reproduction in the small mammals is limited almost completely to this period, and population levels of small mammals in a given year are partly determined by reproductive success and late summer populations of the previous summer. Although faunal studies have yielded information on the geographic distributions and habitat preferences of montane mammals (see Grinnell and Storer, 1924; Grinnell *et al.*, 1930; Bailey, 1932; Hall, 1946; Warren, 1942), and some information is available on their reproduction (see appropriate accounts beyond), population fluctuations and reproductive patterns of montane small mammals remain poorly known. This report contributes information to fill this gap in our knowledge. Because of their abundance in the study area, this report considers primarily the following species: *Sorex vagrans*, vagrant shrew; *Eutamias minimus*, least chipmunk; *Thomomys talpoides*, northern pocket gopher; *Peromyscus maniculatus*, deer mouse; *Microtus montanus*, montane vole.

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STUDY AREA

The study area was three miles southwest of Rabbit Ears Pass, in Grand County, Colorado, at an elevation of 9900 feet. The census quadrats were in rolling, semi-open subalpine "parks" that were nearly devoid of trees except for scattered open stands of spruce, *Picea engelmanii*, and fir, *Abies lasiocarpa*. As indicated by estimates of plant composition, the vegetation was composed of 18 per cent grasses, seven per cent sedges, and 75 per cent forbs (Table 1).

TABLE 1.—RELATIVE FREQUENCIES OF THE COMMON PLANTS IN EIGHT HALF-ACRE QUADRATS IN NORTHERN COLORADO.

Species	Relative frequency
Grasses and sedges	
Stipa lettermani	14.4
Bromus ciliata	1.2
Bromus polyanthus	1.2
Stipa columbiana	.8
Carex sp.	7.4
Forbs	
Collomia linearis	13.4
Achillea lanulosa	11.6
Viola nuttalli	8.6
Taraxicum officinale	6.6
Polygonum douglasii	4.1
Lupinus argenteus	3.8
Agoseris glauca	3.6
Senecio crassulus	2.6
Solidago missouriensis	1.6
All other plants	19.1

Scattered patches of gooseberry *(Ribes montigenum)* occurred locally, and lupine *(Lupinus argenteus)* was often conspicuous late in summer. Logs and stumps were present in most quadrats and were centers of chipmunk activity. In the years from 1964 through 1967, the area was never free of snow until June 5, and most of the plants flowered in August. By early September of each year many forbs had been killed by frost. The earliest snows came in September, but a continuous snow cover usually did not develop until November. Maximum snow depth was usually attained in March, and varied between 6 and 11 feet.

The assemblage of mammals in the study area was typical of subalpine areas in northern Colorado. Table 2 lists the mammals observed or trapped in the study area.

METHODS

An electric fence similar to that developed by Pequegnat and Thompson (1949) was used to study population densities. Around each half-acre quadrat a fine-mesh chicken wire fence 18 inches high was erected, and a copper wire was stretched one inch inside the fence and about three-fourths of an inch above the ground. The copper wire was connected to a Model T Ford spark coil powered by a six volt automobile battery. Any small mammal (less than about 500 grams) that contacted the wire was killed, and from the position of the animal it was clear whether it was entering or leaving the quadrat. Within each quadrat a grid of 169 snap traps was set; the traps were at intervals of 10.5 feet. Macabee gopher traps were set where there were signs of pocket gopher activity. The quadrats were operated for at least four days, and for the first 24 hours the quadrats were checked every four hours. Because small mammals were unable to enter or leave the quadrat on the surface of the ground without being killed, and because even the mammals not attracted to

TABLE 2.—MAMMALS OBSERVED OR TRAPPED IN THE STUDY AREA IN NORTHERN COLORADO.

Scientific name	Vernacular name
Sorex cinereus	Masked shrew
Sorex vagrans	Vagrant shrew
Sorex palustris	Water shrew
Microsorex hoyi	Pygmy shrew
Eutamias minimus	Least chipmunk
Marmota flaviventris	Yellow-bellied marmot
Spermophilus lateralis	Golden-mantled ground squirrel
Thomomys talpoides	Northern pocket gopher
Peromyscus maniculatus	Deer mouse
Clethrionomys gapperi	Red-backed vole
Phenacomys intermedius	Heather vole
Microtus montanus	Montane vole
Microtus longicaudus	Long-tailed vole
Zapus princeps	Meadow jumping mouse
Canis latrans	Coyote
Vulpes vulpes	Red fox
Martes americana	Marten
Mustela erminea	Ermine
Mustela frenata	Long-tailed weasel
Cervus canadensis	American elk
Odocoileus hemionus	Mule deer

the traps, such as shrews, seemed eventually to contact the copper wire, the quadrats seemed at the least to provide reliable indices to the abundance of small mammals.

Pocket gophers were common in the study area, and because these rodents are fossorial it would be expected that they would regularly pass beneath the fence, making accurate estimates of their density impossible. It seemed, however, that pocket gophers were as vulnerable to the wire as were other rodents. When the quadrats were established a strip about six inches wide beneath the wire was completely cleared of vegetation, and usually about one inch of soil was removed with the vegetation. This cleared strip offered a strong attraction to pocket gophers; repeatedly they tunneled to the surface in the strip and were killed by the wire. The direction from which they came could be determined by tracing their burrows. Due to the attraction offered by the cleared strip, a good indication was obtained of pocket gophers moving in or out of the quadrat, and the estimates of their population densities made within the quadrats were, in my judgment, reasonably accurate.

A series of quadrats was established four times in 1965, four times in 1966, and three times in 1967. Each series consisted of four half-acre quadrats. In each of the first two summers, therefore, a total of eight acres was sampled, and in the third summer six acres were studied. Because of adverse weather conditions and late snowmelts in two summers, only in 1966 were quadrats operated in June. In the other two years they were operated in early July. The first set of quadrats each summer was established as soon after snowmelt as possible. At this time most of the plants were just beginning their annual growth and the soil at many sites was still saturated with water. The last set of quadrats each summer was usually operated in early September, after the first late summer frosts, at a time when the annual growth of most plants had been completed. An attempt was made to situate all quadrats in the same plant community. Each set of quadrats was established at a different place in a given summer, but for a given set of quadrats the same sites were used each summer.

A total of 1639 small mammals were taken during this study. Because the quadrats did not always yield adequate samples for reliable information on reproduction, additional trapping was done outside the quadrats and at a considerable distance from them. Animals were frozen in the field soon after capture and were dissected later in the laboratory.

The flora was studied by sampling the frequency of the plants in the census quadrats. One hundred randomly placed plots, each six inches square, were sampled each summer in each quadrat.

POPULATION DENSITIES

In each year of the study the population density of small mammals was low immediately after snowmelt and relatively high in late summer. Although this is probably the basic pattern of change that occurs in most summers, the relative abundance of the species and the monthly changes in population densities of each species seemingly change sharply from year to year.

Summer of 1965

Snowmelt was late in this summer due to an unusually deep winter snowpack and a cold spring. The first set of quadrats was not in operation until July 8, when the soil was still saturated with water and scattered snow drifts persisted in shaded situations; in most places the summer growth of vegetation was barely underway. An occasional dead *M. montanus* or *T. talpoides* was found in places where water had covered the surface of the ground for several weeks during snowmelt.

The density of small mammals was low at this time (Figs. 1-2); the census quadrats indicated a density of 17.5 per acre. The four most abundant species and their densities per acre were: *P. maniculatus*, 7.5; *E. minimus*, 4.0; *M. montanus*, 3.0; *T. talpoides*, 2.5. Because of the difficulty with which pocket gophers are trapped immediately after snowmelt, the figure for *T. talpoides* is probably lower than was the actual density. Although the pattern of changes in density differed between species, by early September the density of small mammals had risen roughly three-fold to 51.0 per acre (Fig. 3). Densities were: *T. talpoides*, 14; *E. minimus*, 14; *P. maniculatus*, 6.5; *S. vagrans*, 6.0. The figures for *E. minimus* seem unreasonably high and should be considered as an index to abundance rather than an expression of actual density. On two occasions chipmunks were observed to leap onto the chicken wire fence enclosing a quad-

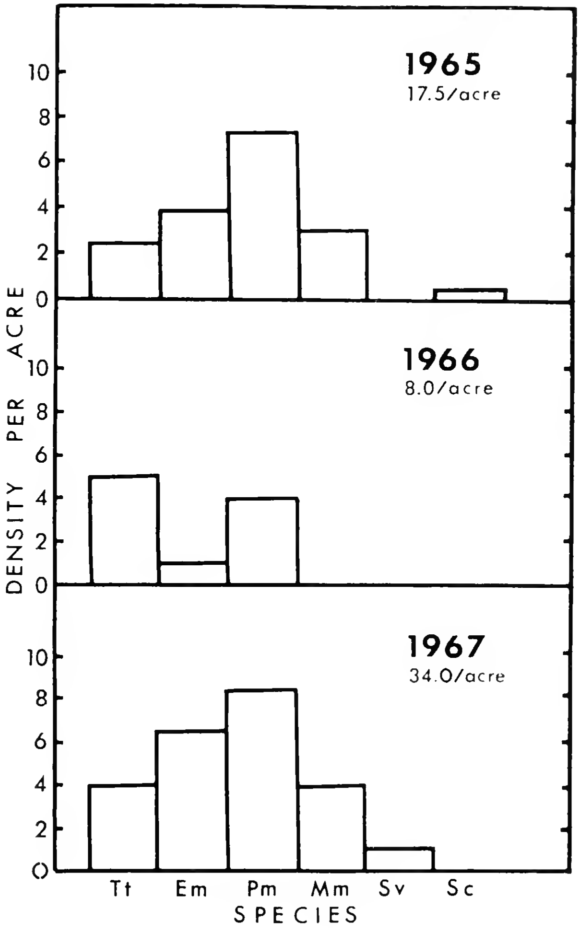

FIG. 1. Early summer densities of six species as determined in four half-acre quadrats each summer. Quadrats were operated soon after snowmelt in June or early July. The following symbols are used: Tt, *Thomomys talpoides*; Em, *Eutamias minimus*; Pm, *Peromyscus maniculatus*; Mm, *Microtus montanus*; Sv, *Sorex vagrans*; Sc, *S. cinereus*.

rat and scramble over the fence without contacting the copper wire; the large number of chipmunks taken in the quadrats may have resulted in part from this type of entry. Usually, however, chipmunks attempted to enter or leave the quadrat by crawling beneath or through the fence; these animals were killed almost instantly when they contacted the copper wire. Additional indication of the abundance of chipmunks in the study area in early September of 1965 is indicated by the fact that the total number of

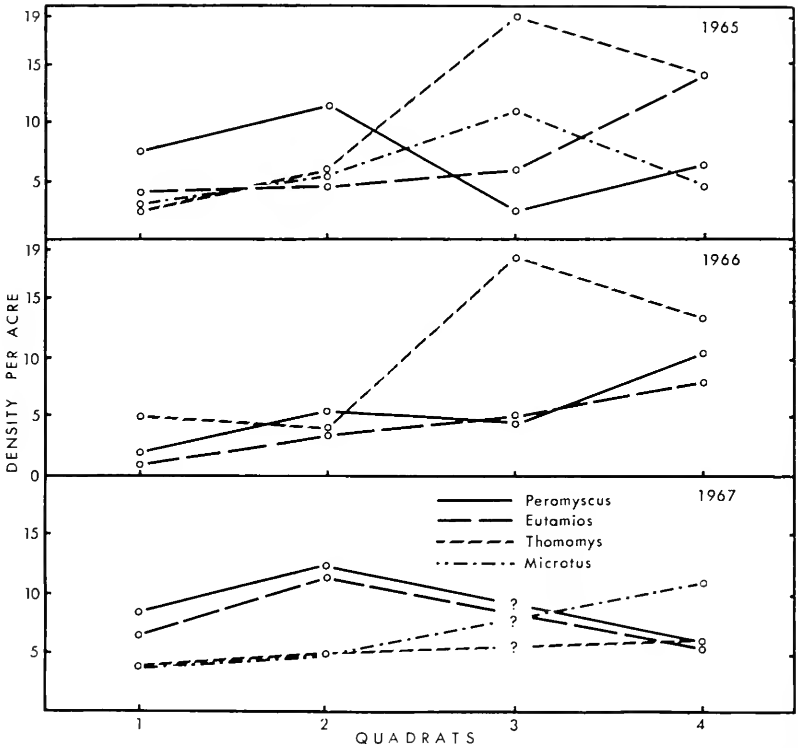

FIG. 2. Changes in densities of some small mammals in summer. Quadrats were operated as follows: series 1, soon after snowmelt, in late June or early July; series 2, in mid- or late July; series 3, in August; series 4, in late August, or early September.

chipmunks taken during operation of the fourth series of quadrats, including individuals killed trying to enter the quadrats, was 51.

The ground remained mostly free of snow until mid-November. Trapping from November 4 to 7 revealed that both *T. talpoides* and *P. maniculatus* were common, but no *M. montanus* were taken. Chipmunks were apparently in hibernation, for none were seen or trapped.

Summer of 1966

Snowmelt was fairly early in this summer and much of the study area was free of snow by about May 25. The first set of quadrats was in operation on June 15 and yielded 8.0 small mammals per acre (*T. talpoides*, 5.0; *P. maniculatus*, 2.0; *E. minimus*, 1.0). The last series of quadrats was established on September 2. The density

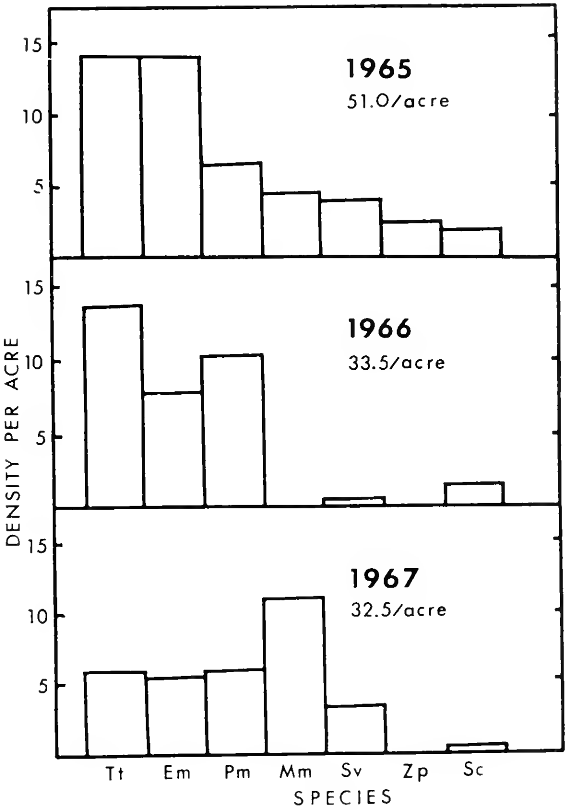

FIG. 3. Late summer densities of six species as determined in four half-acre quadrats each summer. Quadrats were operated in late August or early September, after the first late-summer frosts. Symbols for species are the same as in Fig. 1, but Zp, for *Zapus princeps*, is also used.

of small mammals was four times as great at this time (33.5 per acre) as it was in June (Figs. 1-3). The most abundant species and their densities were *T. talpoides* (13.5), *P. maniculatus* (10.5), and *E. minimus* (8.0).

Summer of 1967

Snowmelt persisted through the first half of June and occasional snow fell through mid-June. Although the first set of quadrats were not studied in 1967, it was clear that the pattern of change in the density of small mammals that typified the previous two summers was at least partly reversed in 1967 (Figs. 1-3). The set of quadrats started on July 1 indicated a fairly dense population of 34 small mammals per acre (*P. maniculatus,* 12.5; *E. minimus,* 11.5; *T. talpoides,* 5.0; *M. montanus,* 5.0). In 1967, rather than a steady rise in density through late summer, as occurred in the other years, there was a decline by late August to 32.5 per acre. This was due largely to drops from July to late August in the densities of both *P. maniculatus* (from 12.5 to 6.0) and *E. minimus* (from 11.5 to 5.5). Populations were lower in late summer of 1967 than they were at comparable times in either of the other years.

Population Dynamics

Sharp fluctuations in small mammal populations were seemingly the rule throughout the study. As shown in Figures 1 to 3, the relative densities and the absolute densities of the different species shifted markedly from summer to summer as well as from month to month within a summer. Early in the summer of 1965, for example, the most abundant species was *P. maniculatus; T. talpoides* was fourth in terms of abundance. This relationship was altered two months later, when *T. talpoides* was the most abundant mammal. Whereas the density of *Thomomys* rose steadily during the summer, that of *P. maniculatus* was lower early in September than it was just after snowmelt. The summer of 1965 was unusually cool and rainy; perhaps this weather resulted in poor survival of young *Peromyscus.* In any case, the summer of 1966 presented a different picture. In early summer *T. talpoides* was the most abundant species with *P. maniculatus* second. Although the rate of increase was different in each species (Fig. 2), this order was maintained through early September. As a further difference between these two summers, *M. montanus* was taken commonly and consistently throughout the summer of 1965, but only one individual was taken in the quadrats in 1966. Densities of small mammals were generally low in 1967, but *M. montanus* was commoner late in that summer than at any other time in the study. The density of the entire community of small mammals in late summer also fluctuated, being highest in 1965 (51 per acre), and roughly the same in 1966 and 1967 (33.5 per acre and 32.5 per acre, respectively).

The period of dispersal of young of the year was signalled by the occasional capture at the quadrats, usually as the animals tried to enter, of species that did not regularly occur there and that probably found optimal conditions in nearby moist situations. Species of this type were *Microsorex hoyi, Phenacomys intermedius,* and

Zapus princeps. *Sorex cinereus*, a species that was taken occasionally throughout the summer, was taken much more frequently in late summer. In nearby areas in Wyoming this species is known to favor moist habitats (Brown, 1967). Probably largely as a result of the dispersal of young animals, the greatest diversity of species was usually encountered in late summer.

In the study area the population levels of small mammals were influenced strongly by the survival of young. In southern Colorado, Hansen (1962) found that high survival of young was associated with high densities of pocket gophers and low survival of young was associated with a declining population. Age ratios at the end of the breeding season, then, can be a partial basis for predictions of future densities. Limited data on age ratios of pocket gophers in the study area are relevant to a consideration of population fluctuations. Density of pocket gophers was high in late summer of 1965 (14 per acre) and survival of young, as indicated by the fact that 87 per cent of the 38 animals taken were young, was high. The density was about the same in late summer of 1966, but survival of young was probably low (50 per cent of 22 animals were young). Pocket gopher density declined in 1967 to but six per acre in late summer. This drop was perhaps due both to low survival of young the previous summer and to continued low survival in the summer of 1967. At that time, 48 per cent (10 of 21) of the animals taken were young.

Apparently there were changes in the density of the long-tailed weasel *(Mustela frenata)* in the period of this study. Evidence for these changes consists of sight records, made during roughly 40 days spent in the field each summer, and on the number of weasels killed at the quadrats. (A total of approximately 2400 linear feet of electric fence was in operation each time a series of quadrats was studied.) No weasels were taken at the quadrats in 1965, and only two weasels were seen. In 1966 six weasels were killed by the electric fences and weasels were observed regularly; in 1967 four weasels were taken by the electric fences and many were seen. Although the data give only a general idea of abundance, weasels were clearly far more abundant in 1966 and 1967 than they were in 1965.

REPRODUCTIVE CYCLES

The reproductive cycles of only those species taken with regularity in the quadrats are discussed. Reproductive data are presented in Tables 3-4 and in Figs. 4-8.

TABLE 3.—LITTER SIZES, AS INDICATED BY NUMBERS OF FETUSES AND PLACENTAL SCARS, IN SEVEN SPECIES. THE MEAN NUMBER IS GIVEN, FOLLOWED BY THE STANDARD ERROR, THE SIZE OF THE SAMPLE (IN PARENTHESES), AND THE RANGE.

Species	Fetuses	Placental scars
Sorex vagrans	5.6 ± .43 (7), 4-7	
Eutamias minimus	5.7 ± .15 (52), 3-8	5.7 ± .15 (97), 2-10
Thomomys talpoides	4.0 ± .53 (12), 2-7	5.0 ± .16 (66), 2-8
Peromyscus maniculatus	5.6 ± .12 (111), 2-9	5.9 ± .31 (34), 2-10
Clethrionomys gapperi	6.1 ± .50 (10), 4-8	
Phenacomys intermedius	4.8 ± .75 (4), 3-6	5.3 ± .52 (11), 2-9
Microtus montanus	5.8 ± .25 (46), 2-10	

Sorex cinereus

This species was uncommon in the quadrats, but was more abundant in nearby moist areas. Of the 19 individuals taken in the quadrats, four (21 per cent) were adults. Breeding apparently extends at least into September, for a pregnant yearling female with six fetuses was taken on September 3, and males with spermatozoa in their testes were taken on September 2. Young animals were recorded as early as July 14.

Sorex vagrans

Because of the small sample of this shrew (N=73) only a general picture of its reproductive cycle was gained. Clothier (1955) recorded pregnant *S. vagrans* from April 1 until August 8 in Montana. The seven pregnant shrews from the present study area were taken from June 15 to August 15. There was no evidence that breeding females (yearlings) had more than one litter in their second summer, and no young of either sex were recorded in breeding condition in their first summer. Fertile males (all yearlings) were taken from June through early September. Whereas but 11 per cent of the 31 females taken in August and September were yearlings, 56 per cent of the 18 males from this period were yearlings. Doubtless few females survive their second summer. The cessation of breeding in the late summer, therefore, may be due primarily to the loss of yearling females from the population. The mean number of fetuses for seven females was 5.6 (Table 3). Clothier determined a mean litter size of 6.4, based on 33 pregnant females from Montana.

Eutamias minimus

This species hibernates from October or November, depending on snow conditions, to the time of snowmelt in spring. In each year of the study, chipmunks were seen as soon as any snowfree ground appeared. Individuals were first noted in the study area as follows: June 13, 1965; May 15, 1966; June 7, 1967.

Seemingly not all female chipmunks breed as yearlings. Of 93 females taken in June and July of 1966, for example, 17 (18 per cent) had threadlike uteri and gave no morphological indication of approaching estrous. These animals (hereinafter termed non-breeding females) averaged appreciably lighter in weight than did breeding females. Twenty-six breeding females in a sample from June, 1966, averaged 45.5 grams (range 37.2 to 58.7), whereas nine non-breeding females averaged 38.2 (33.6 to 42.1). Perhaps females that do not attain a certain critical weight in their first summer do not undergo

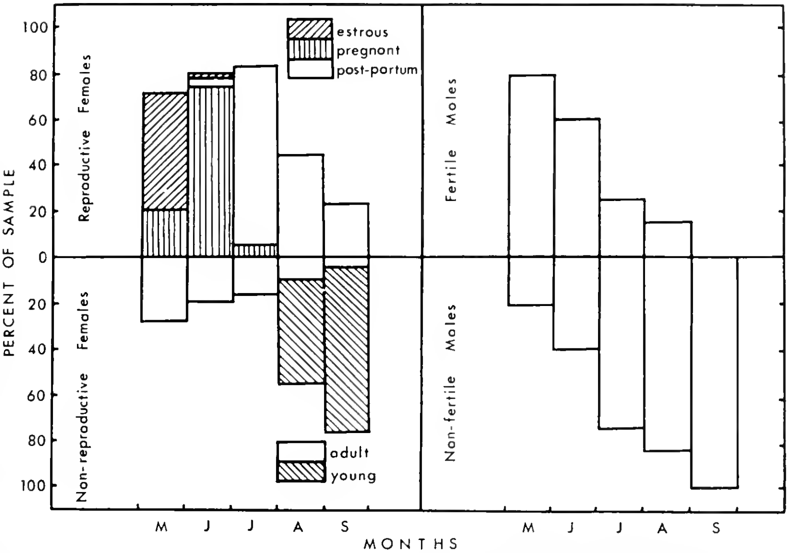

FIG. 4. Summary of the reproductive cycle of *Eutamias minimus* based on samples of 177 males and 247 females.

estrous in their second summer. If this be true, large numbers of non-breeding females would be expected in a year following a summer made unusually short by a late snowmelt and by early autumn snows. Reproduction in such a summer would be unusually low and the population density would be strongly affected.

The female reproductive organs undergo development in preparation for breeding before the animals emerge from hibernation, because females are in estrous soon, within roughly a week, after emergence from hibernation. A sample of 18 females was taken at the height of snowmelt (May 18, 1966) at sites probably free of snow for one to two weeks. Four of these animals had embryos, nine had swollen, flaccid, highly vascular uteri and were judged to be in or near estrous, and five were non-breeding females. In some cases pregnant females were taken on soil saturated with water and adjacent to snowbanks up to five feet deep. Much chasing of one animal by another occurred during snowmelt, an activity that I assumed to be associated with breeding. Virtually all except the non-breeding females were pregnant by mid-June. Of 31 reproductively active females taken at this time, one had placental scars and the rest were pregnant. For these females the mean size of the fetuses was 12 mm. (crown-rump length, full-term fetuses measured about 25 mm.). Parturition was largely completed by mid-July, for of 59 reproductive females taken in July only four had fetuses; the rest had placental scars and enlarged mammae (see Fig. 4). The mean number of fetuses was 5.7; the mean number of placental scars also was 5.7 (Table 3). Litter size as indicated by this type of data did not differ appreciably from year to year.

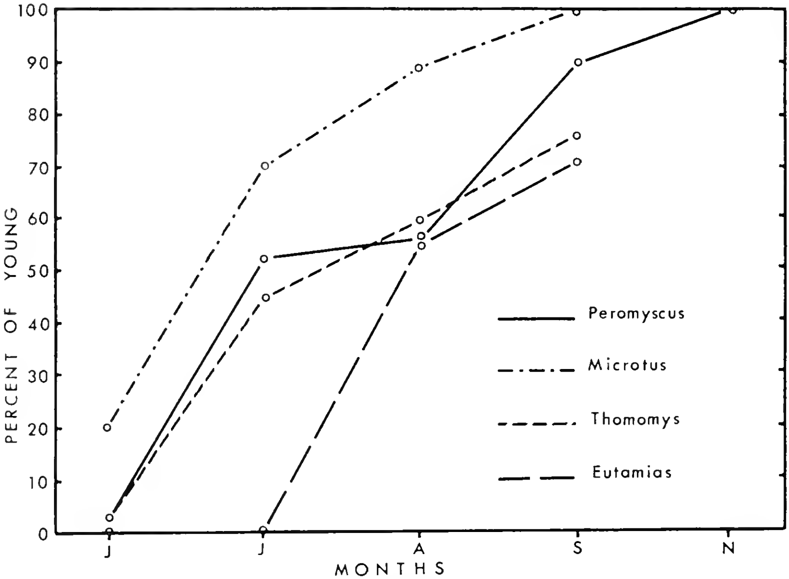

FIG. 5. Percentages of young in the total monthly samples (representing 1965, 1966 and 1967) of four species. Sample sizes are as follows: *Eutamias minimus*, 424; *Thomomys talpoides*, 353; *Peromyscus maniculatus*, 480; *Microtus montanus*, 195.

Young chipmunks apparently stay in the nest roughly 30 days and begin appearing above ground in early August. From this time onward, they form a progressively larger proportion of the population. As shown in Figure 5, 54 per cent of the chipmunks taken in August (N=162) were young; for September the corresponding figure was 70 per cent (N=61). There was no indication that any females enter estrous in their first summer.

Records from 1966 illustrate best the reproductive cycle of the male. Snowmelt was at its height on May 18, when roughly half of the surface of the ground was still under snow. Of a sample of 30 males taken on this date, 80 per cent were in breeding condition. In these animals, the testes and the caudal epididymides contained spermatozoa and the seminal vesicles were enlarged and turgid. The non-breeding males taken at this time were not individuals that had yet to reach breeding condition and would breed later, but rather were males that would not reach breeding condition during the summer. Each monthly sample contained such reproductively inactive yearling males. Probably all males that would have bred in 1966 were in breeding condition at the time of snowmelt. The reproductive organs of males doubtless enlarge before the animals emerge from hibernation, for the testes and seminal vesicles averaged largest in recently-emerged males; both testes and seminal vesicles regressed rapidly in size from mid-July until August (Table 4). Spermatogenesis was occurring in all of the reproductive males taken in May and mid-June, whereas of the 12 reproductive males taken in July only four had spermatozoa in the testes. A continued reduction in spermatogenesis in August probably occurs, but I lack sufficient data to illustrate this trend.

Thomomys talpoides

This species is active throughout the winter beneath the snowpack. In February, 1966, burrows were found extending at least one foot above the ground into the snowpack, which was roughly 50 inches deep. This species is a sharply seasonal breeder, and its reproductive cycle in my study area was similar to the cycles described for this species elsewhere in Colorado by Hansen (1960) and Vaughan (1967).

In summer young of this species (animals that have not been through a breeding season) can be distinguished easily from adults (animals that are in breeding condition or have been through a reproductive cycle). In addition to differences in total weights, adult females have pubic gaps whereas young do not (Hisaw, 1924; Miller, 1946; Hansen, 1960). Adult males in breeding condition have much larger bacula and testes than do young. In adult males with regressed testes, these organs are flaccid, reddish, and often partially wrinkled, whereas those of young males are turgid, yellowish or whitish, and have a smooth surface.

Females had a single litter a year and bred early, in May or June. More than half (69 per cent) of the June-taken females already had borne young, and only 10 per cent had not entered estrous (Fig. 6). In August only seven per cent of the adult females (N=31) were pregnant; the remainder had placental scars. No evidence was found of females breeding in their first

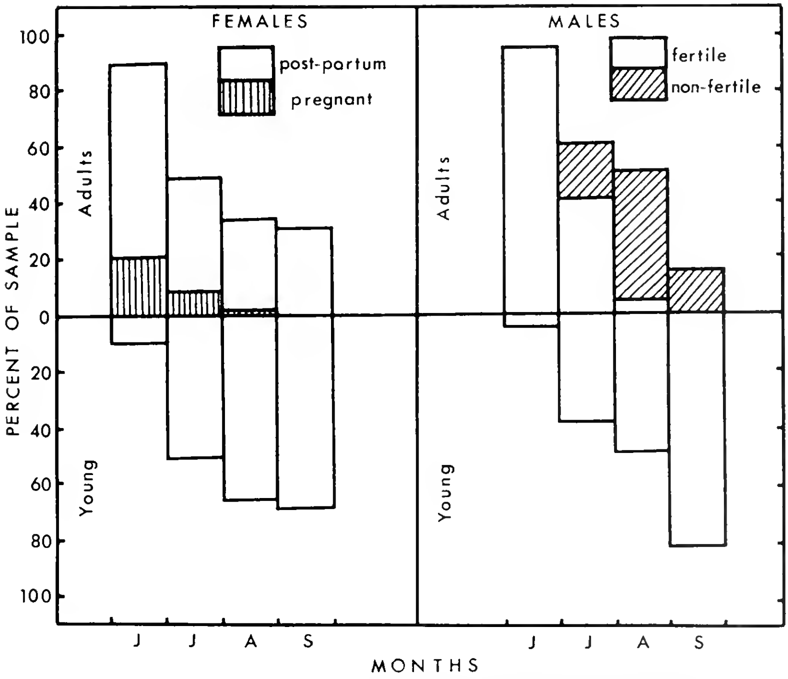

FIG. 6. Summary of the reproductive cycle of *Thomomys talpoides* based on samples of 191 males and 162 females.

TABLE 4.—LENGTHS OF THE TESTES AND SEMINAL VESICLES IN THE SUMMER MONTHS IN FOUR SPECIES. THE MEAN LENGTH IS GIVEN, FOLLOWED BY THE STANDARD ERROR AND THE SIZE OF THE SAMPLE (IN PARENTHESES).

Species	Month	Testes	Seminal vesicles
Eutamias minimus	May	10.1 ± .38 (30)	6.81 ± .32 (30)
	June	8.9 ± .26 (64)	6.2 ± .19 (61)
	July	6.5 ± .26 (49)	4.2 ± .24 (47)
	August	5.2 ± .20 (28)	3.6 ± .22 (28)
	September	6.3 ± .38 (6)	
Thomomys talpoides	May	19.0 ± .53 (4)	14.8 ± .07 (4)
	June	16.8 ± .33 (33)	13.8 ± .75 (33)
	July	14.5 ± .45 (21)	10.8 ± .70 (21)
	August	11.3 ± .42 (31)	8.8 ± .57 (31)
	September	9.7 ± .95 (2)	
Peromyscus maniculatus	May	8.4 ± .19 (8)	8.4 ± .28 (8)
	June	8.7 ± .10 (98)	9.9 ± .17 (99)
	July	9.2 ± .18 (36)	10.8 ± .36 (36)
	August	8.9 ± .39 (16)	10.0 ± .52 (16)
	September	5.1 ± .11 (4)	
Microtus montanus	June	10.8 ± .17 (7)	13.4 ± .43 (7)
	July	11.0 ± .46 (3)	10.5 ± 1.4 (3)
	August	9.9 ± .40 (27)	12.6 ± .60 (27)
	September	11.8 ± .67 (2)	12.4 ± .14 (2)

summer or of females bearing two litters per year. The mean number of fetuses and placental scars per female was 5.0 and 4.0, respectively (Table 3).

The reproductive organs of males undergo marked seasonal changes in size and probably reach maximum development at about the time of snowmelt (late May or early June), after which the testes and seminal vesicles of adults become progressively smaller through the rest of the summer (Table 4). In August only 30 per cent of the adult males examined (N=30) were fertile. Young males do not become fertile in their first summer.

Young pocket gophers were first recorded in June, and formed an ever increasing part of the population during the rest of the summer (Figs. 5-6). Seventy six per cent of the pocket gophers taken in September (N=58) were young.

Peromyscus maniculatus

Little information bearing on the winter activity of this species is available from the study area. Several specimens have been taken in the winter in partially snow-free areas, and during snowmelt in the spring some of the runways and nests beneath log piles and matted vegetation were probably those used by *Peromyscus* in the winter. Such evidence suggests that in the study area this species remained active at least part of the winter beneath the deep snowpack. Tracks, judged to be those of *Peromyscus*, were occasionally seen on the surface of the snow in midwinter, but this animal probably was active mostly in the depth hoar beneath the snowpack.

Females breed soon after snowmelt. About 33 per cent of the females in a small sample taken during snowmelt in May of 1966 were pregnant (Fig. 7). Because no young animals were encountered at this time it seems unlikely that breeding began before snowmelt. The percentage of pregnant females in monthly samples declined from a high of 89 per cent in June to 38 per cent in

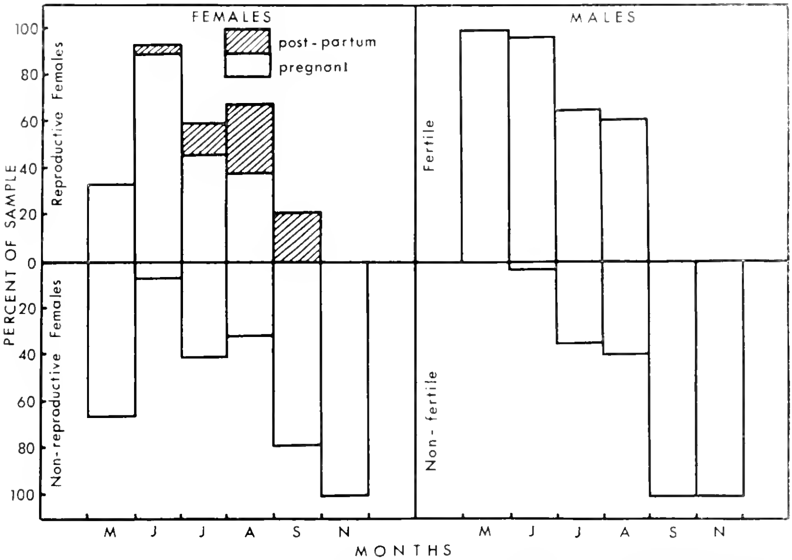

Fig. 7. Summary of the reproductive cycle of *Peromyscus maniculatus* based on samples of 260 males and 220 females.

August (Fig. 7), and no pregnant females were taken after August. Some yearling females that bred in May or early June had a second litter before September as females that had obviously suckled young and were carrying fetuses were noted regularly. In addition, some, but seemingly not all, young females bred during their first summer; a few small, partially gray-pelaged females with fetuses were taken in August of 1965 and 1966. The late summer decline in the percentage of pregnant females in the population seems due to a cessation of breeding by yearling or older females (and to their death) and to a low percentage of young females that breed in their first summer. The reproductive burden for the population, then, seems to be borne primarily by the overwintering yearling females.

Litter sizes were large in the study area. The mean number of fetuses and placental scars was 5.6 and 5.9, respectively (Table 3). These averages did not differ significantly from year to year. Large litters were judged by Spencer and Steinhoff (1968) to be typical of populations of *P. maniculatus* occupying areas with short growing seasons, where the animals must make the most of a short period of food abundance. Mean litter size in the present study was considerably larger than the 4.6 determined by Jameson (1953) for *P. maniculatus* occurring at elevations between 3500 and 5000 feet on the western slope of the Sierra Nevada Mountains in California, where the breeding season in one year of his study extended from April through November.

Considering both sexes, the age structure of the population of *P. maniculatus* in the present study area underwent striking and similar changes each summer of the study. June samples contained almost entirely yearling (or older) breeding animals. Reflecting the sudden onset of breeding in early summer, young appeared suddenly and in large numbers in July, when they averaged 40.5 per cent of the female population and 61.0 per cent of the male population. Young animals formed a progressively higher percentage of the population through the rest of the summer and autumn (Figs. 5 and 7). A small sample (N=21) from November consisted entirely of young of the year, indicating that individuals of either sex rarely survived a second autumn. The breeding population of May and June, therefore, probably consisted entirely of animals born the previous summer.

All adult males taken in May and nearly all (97 per cent) taken in June were fertile, but the percentage of fertile males in the population became progressively lower from July (65 per cent) and August (61 per cent) to September, when none was taken. The testes and seminal vesicles of yearling males do not regress appreciably in size through the summer (Table 4). Such males probably remain continuously in breeding condition through the summer, but by September the reproductive organs of the few surviving yearlings are regressed and the animals are not fertile. Young males born early in the summer begin producing sperm when the animals weight but 15 grams, less than 75 per cent of the weight of fully grown males, whereas young that are born later in the summer do not become fertile until the following summer. None of the young individuals taken in September and November, even those weighing more than 15 grams, was fertile.

Clethrionomys gapperi

This was one of the least common rodents on the study area. Breeding extended at least from May through November, because juvenile mice were taken at irregular intervals from May through late December. Ten pregnant individuals were captured in July and August, and the mean number of fetuses was 6.1 (Table 3). Adult females have more than one litter per summer, and young animals breed in their first summer. Several small August-taken females with nearly unworn teeth carried fetuses or had placental scars and were judged to have been born earlier in the summer. In several small males of roughly the same age as these females, spermatozoa were abundant in the testes and the caudal epididymides.

Phenacomys intermedius

This rodent was never common in the quadrats and most individuals were taken in late summer or in autumn. The occurrence of fertile males from the time of snowmelt in May in one year (1966) until late August, and the occurrence of pregnant females from June through September, indicates that breeding takes place through most of the summer. Females are polyestrous in Colorado according to Warren (1942). An August-taken female weighing only 16 grams (roughly half the weight of a fully grown female), and having nearly unworn teeth, was pregnant, and males of similar size from mid-summer had sperm in their caudal epididymides. This evidence indicates that young animals born early in the summer breed in their first summer. Young animals born later in the year seemingly do not reach breeding condition their first autumn, however, for none of four November-taken males, weighing from 17 to 23 grams, was fertile, and three young females (18 to 29 grams) taken at the same time had transparent, threadlike uteri. The mean number of embryos and placental scars was 4.8 and 5.3, respectively (Table 3).

Microtus montanus

This species is not known to hibernate. In the study area abundant evidence, in the form of runways and nests made in winter and uncovered during snowmelt, indicated that montane voles were active through the winter beneath the snow. Because no specimens were taken in the winter, and because few were caught until July, it is not known if breeding occurred in the winter.

Compared to other rodents of the area, these voles have an unusually long breeding period. The females taken earliest in the year were caught during snowmelt on May 17, 1966; these two individuals had placental scars, had recently suckled young, and were taken at a site that had been free of snow for but a few days. These animals unquestionably had their litters beneath the snowpack. Breeding continued from snowmelt at least through August, when 54 per cent of the females taken carried embryos (Fig. 8). Hall (1946) found that in Nevada this species breeds through November, and this may well be true for the present study area. Young of the year were distinguished from yearlings primarily on the basis of weight (individuals of more than 35 grams were classed as yearlings), and it seemed that most of the pregnant individuals

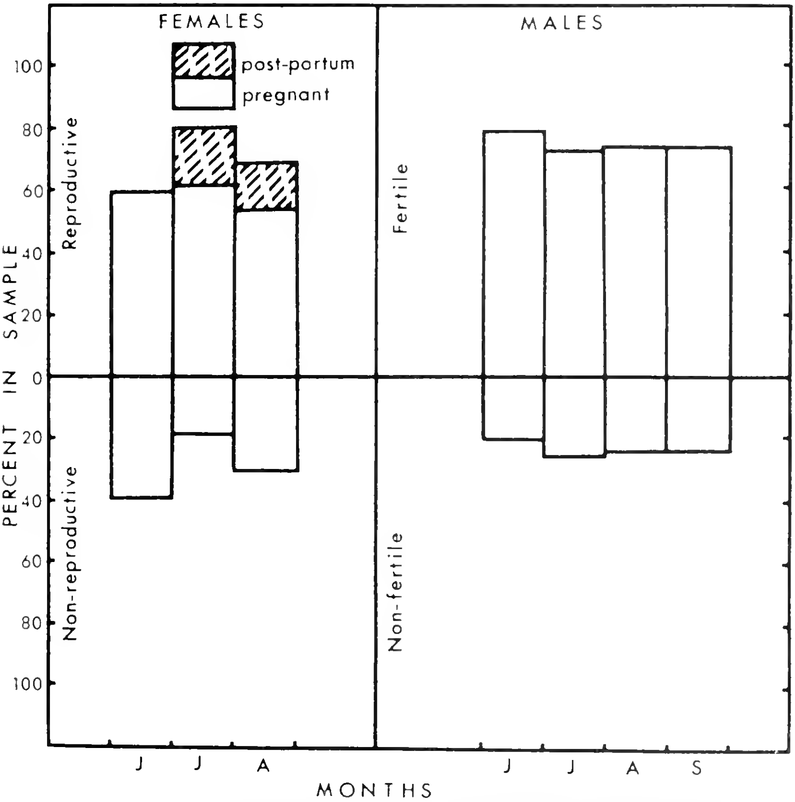

FIG. 8. Summary of the reproductive cycle of *Microtus montanus* based on samples of 111 males and 84 females.

taken in August were animals born earlier in the summer. Small females weighing but 17 grams had embryos, and some individuals weighing less than 20 grams had placental scars. Of 33 pregnant females taken in August, only five (15 per cent) were judged to be yearlings. Seemingly, then, as yearling females that bred early in the summer are increasingly outnumbered by young females, a progressively greater share of the reproductive burden shifts to young females. The sharp rise observed in August in two years in the population density of *M. montanus* indicates that the young breeding females that form a major part of the relatively high August population probably contribute considerably more young to the population than do the few yearling females that survive the winter and participate in early summer breeding. It would be expected, therefore, that the size of the population in the autumn would be determined primarily by the survival rates of early summer litters.

The mean number of fetuses for 46 pregnant females was 5.8, and did not differ significantly between summers. This is similar to the litter size recorded by Hall (1946) in Nevada.

Most of the males trapped each summer from June through August were fertile (Fig. 8). Males began producing sperm when they were roughly 20 to 25 grams in weight, and only three of the 37 males (eight per cent) that weighed more than 25 grams were not fertile. In the months from which specimens are available, no important changes in the mean sizes of the seminal vesicles and testes of males heavier than 25 grams were noted (Table 4), indicating that males stay in breeding condition through the summer. Young males far outnumber yearling males in July and August, and probably most of the breeding from mid July or August until winter is done by young males. Young males first appeared in the population in June and formed an increasing segment of the population through the remainder of the summer (Fig. 5). Of 75 males taken in August, 65 (88 per cent) were judged to be young.

DISCUSSION

The yearly cycle of breeding and of changes in the densities of the small mammals of the study area has been influenced by several demanding environmental features: (1) a short annual growing season, averaging about thee months, and a snow-free period of about five months; (2) low temperatures through most of the year and a frost-free period of only about 60 days; (3) annual "catastrophes," first in the form of snowmelt, attended typically by flooding of much of the surface of the ground, and second, in the form of periodic "open" autumns, when temperatures approach zero but no snow cover that protects small mammals from the cold has developed. Some characteristic aspects of the life cycles of subalpine small mammals probably have developed in response to restrictions imposed by these environmental features.

The reproductive cycles of the small mammals considered here seem adapted to the short growing season. Adaptations include large litters and few litters per year. In addition, reproductive organs enlarge and mature while snow still covers the ground, and breeding occurs during or immediately after snowmelt. Of the five most common species, three—*T. talpoides, E. minimus* and *S. vagrans*—have but one litter per year. Another, *P. maniculatus,* is polyestrous, but breeding is confined to the summer months and ceases in September. Only *M. montanus* has a long breeding period; this season coincides roughly with the snow-free part of the year. Even this species, however, has large litters relative to those of other voles in less boreal areas. Corthum (1967) found that in Indiana *M. ochrogaster* and *M. pennsylvanicus* had litter sizes of 3.9 and 4.5, respectively, and that breeding occurred throughout the year. In the present study area, by contrast, *M. montanus* had a litter size of 5.8 and roughly a five-month breeding period, giving this species a substantially lower reproductive potential than that of either species studied by Corthum. The presence of a fairly high percentage of non-reproductive yearling *E. minimus* in the population is noteworthy. Perhaps the time from birth to first hibernation is so short at high elevations that some individuals born unusually late do not reach a critical stage of development (size?) before hibernation and therefore do not become sexually active in the usual breeding season during and immediately after snowmelt. All of the small mammals in the present study area, despite large litter sizes, have fairly low reproductive potentials because few litters are produced annually. It may be, however, that the partial protection against predation afforded by a continuous, deep snow cover for seven months of the year compensates for a low reproductive rate.

The timing, length and severity of snowmelt probably has a strong influence on small mammal populations. Most of these mammals are forced to abandon low-lying or poorly-drained sites during the height of snowmelt, and local, temporary shifts to drier sites occur (see Ingles, 1949; Hansen, 1962). Local concentrations of chipmunks were observed during the snowmelt periods of 1965 and 1966. From June 14 to 18 of 1965, for example, continuous deep snow covered roughly 75 per cent of the surface of the ground. Strips of bare but saturated soil occured along the southern borders of stands of conifers and on certain south- or west-facing slopes. Chipmunks had emerged from hibernation in these areas and were concentrated around logs, stumps, and rock piles, sites where the animals could mostly avoid the saturated soil and running water. Although these shifts occur when population densities are lowest, if the occupancy of these refuges is maintained locally into the time of natality by a prolonged snowmelt or by an unusually heavy runoff, the resultant crowding and heightening of interspecific competition would be expected to decrease markedly the survival of young.

In the early summer of 1965 dead montane voles and pocket gophers were found occasionally at low-lying sites; Hansen (1962) also found dead pocket gophers during snowmelt in southern Colorado. This limited evidence, supported by our lack of success in trapping small mammals in areas saturated with water from snowmelt, suggests that animals that are not able to move to dry refuges during snowmelt are drowned or die of exposure. Jenkins (1948) thought that periodic flooding of meadows in the Sierra Nevadas of California affected population levels of *M. montanus.* One of the difficulties small mammals face at such times was made apparent when a tent that I pitched on frozen ground in the morning on May 15, 1966, was awash with flowing water when I returned in late afternoon of the same day. At this time of the year *Zapus princeps* and *Sorex palustris* were taken occasionally on open slopes where they were never recorded later in the summer.

Another transition period, that from summer to winter, may be a time of stress for small mammals. As pointed out by Formozov (1946) and Pruitt (1957, 1960) certain small mammals (for example, shrews and voles) retreat beneath the snow when it reaches a depth of six inches or more. These animals spend the winter in a moist subnivean environment where the temperature remains fairly constant at close to freezing and where they are insulated by snow from the violent climatic fluctuations frequently occurring above them. If a snowpack does not develop before extreme cold descends, however, small mammals (such as *M. montanus*) that seek plant material for food on the surface of the ground are forced to forage for frozen, low quality food without protection from extreme cold that imposes considerable metabolic demands. Appreciable mortality may occur at such times. Such snowless conditions persisted into early November of 1965, and at this time no *M. montanus* were taken on the surface of the ground despite intensive trapping. At this time the soil was frozen to a depth of several inches, and temperatures of –4° F were recorded on two nights. The unusually low populations of *M. montanus* in the summer of 1966 may have been due, in part, to this late development of a snow cover in the autumn of 1965. When snow does not cover the ground, voles may avoid difficult conditions on the surface by confining much of their activity to beneath the ground. In early summer of 1966 the few *M. montanus* taken were trapped in abandoned burrows of pocket gophers; no voles were taken at this time on the surface of the ground.

Finally, what are the most important factors controlling fluctuations of population densities of small mammals in the study area? Natality seems fairly constant for each species from year to year. A consideration of sources of mortality, consequently, seems most germane. Under some conditions abundance or quality (or both) of food are thought to influence mortality (Keith *et al.*, 1959; Schultz, 1964). Food is seemingly not a limiting factor in the study area, however, for I considered the vegetation and the food habits of the mammals (unpublished data) and found ample food to be available each year. In my judgment, the most important factors controlling populations are the length, timing, and severity of snowmelt in the spring, the time at which a continuous snowpack first develops in the autumn, and the intensity of predation. Only predation needs further comment.

The most abundant and seemingly most important mammalian predator of small mammals in the study area seemed to be the long-tailed weasel. Elsewhere in Colorado I have observed weasels chasing chipmunks and have found *Microtus* in weasel stomachs, and weasels have frequently been taken in pocket gopher burrows in Colorado (Vaughan, 1961). It seems reasonable, therefore, that weasels in the study area were preying mostly on terrestrial rodents. As mentioned earlier, weasel density fluctuated in the period of this study, but was high during the summer of 1967, a time when density of small mammals was low. As pointed out by Pearson (1966), the most important predator-prey interactions, in terms of effects on rodent populations, are those that occur when rodent density is low. It may be that in montane situations the patterns of rodent cycles are modified by periodically intense predation when weasels are abundant and populations of preferred prey, such as pocket gophers, are low.

SUMMARY

A series of electric fences, each fence enclosing a half-acre quadrat, was used to study population densities of small mammals in a subalpine area in northern Colorado, and information on reproductive cycles, based on dissections of 1639 animals, was obtained for the eight most common species.

The climate of the study area is sharply seasonal, with snow on the ground for about seven months of the year. Reproduction and population cycles of small mammals seem dominated by this demanding climatic pattern; in most species the period of natality is short relative to the long period of mortality and population decline. Following are some basic features of the life cycles of the small mammals of the study area:

1. Population densities fluctuated widely, but an annual cycle involving low populations immediately after snowmelt in early summer and high populations in late summer seemed characteristic.

2. Yearly and month-to-month changes in the relative and absolute densities of the different species in the summer were the rule. Population densities of *Microtus montanus* seemed most variable.

3. Because nearly 100 per cent mortality occurred each summer among yearling animals of three species *(Peromyscus maniculatus, Sorex vagrans,* and *M. montanus),* and young of the year comprised most of the autumn populations of the other two of the five most common species *(Thomomys talpoides* and *Eutamias minimus),* survival rates of young animals was a primary factor influencing population levels.

4. Large litters are characteristic of all species, and most species have short seasons of natality. Of the five most common species, three *(T. talpoides, E. minimus,* and *S. vagrans)* have one litter a year and two *(P. maniculatus* and *M. montanus)* are polyestrous. In *E. minimus* a substantial segment of the yearling population each year does not breed, a unique situation perhaps associated with short growing seasons.

5. The striking fluctuations in the densities of small mammals seem most strongly influenced by the duration, severity, and timing of snowmelt, by the time at which the ground is first continuously covered by snow in the autumn, and by predation, particularly when, as occurred in 1967, high populations of weasels and low populations of rodents occur concurrently.

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THE SPECIES PROBLEM IN THE THOMOMYS BOTTAE—THOMOMYS UMBRINUS COMPLEX OF POCKET GOPHERS IN ARIZONA

BY

Donald F. Hoffmeister

In southwestern United States and northern Mexico, there are two common, small pocket gophers, *Thomomys bottae* and *Thomomys umbrinus.* These are allopatric nearly everywhere (Fig. 1). Where the two occur together or adjacent, there has always been considerable doubt as to which "species" any population should be referred. This has been true in southwestern Texas (Davis Mountains), southern Arizona, eastern Coahuila, and eastern Sinaloa. The two "species" have been regarded as conspecific on some occasions and as distinct species on other occasions. In 1959, Hall and Kelson regarded the two as conspecific basing this on the remarks of Hoffmeister and Goodpaster (1954:95).

Gophers in the Huachuca Mountains, Arizona

Hoffmeister and Goodpaster, working in southern Arizona (1954), regarded *Thomomys bottae* and *T. umbrinus* as conspecific for a variety of reasons. Mearns (1897:719) described a pocket gopher "from the aspen and spruce zone at the summit of the Huachuca Mountains" that had the characters of *Thomomys umbrinus.* Our collecting on the summit of these mountains in a clearing in the aspens and fir revealed an isolated population of gophers that had the features of *T. bottae*, and since two characters supposedly valuable in distinguishing *bottae* and *umbrinus* were variable—namely color and number of pectoral mammae—we concluded that in the Huachuca Mountains, Arizona, it is "advisable to refer all material to one species, for which the earliest name is *T. bottae* [but] by this we do not mean to imply that *T. umbrinus* is necessarily a synonym of *T. bottae*" (Hoffmeister and Goodpaster, 1954:95). Further collecting in the Huachuca Mountains indicated that at intermediate elevations, between the summit and the bahada, a distinct kind of gopher exists and these are referable to *Thomomys umbrinus.* Re-examination of the 87 gophers that Hoffmeister and Goodpaster studied in the Huachucas indicates that seven are referable to *T. umbrinus*, and these seven are from the oak-belt on the

Fig. 1. Distribution of *Thomomys bottae* and *Thomomys umbrinus* in western North America. Specimens from parts of the range marked with a question mark have been regarded as more *bottae*-like than *umbrinus*-like by some authors.

Mountains. The type of Mearns' gopher indeed is *umbrinus*-like. We doubt that it came from the summit of the higher peaks of the Huachucas. In any event, it is clear that in the Huachuca Mountains, Arizona, there are two kinds of pocket gophers—*T. bottae* and *T. umbrinus*.

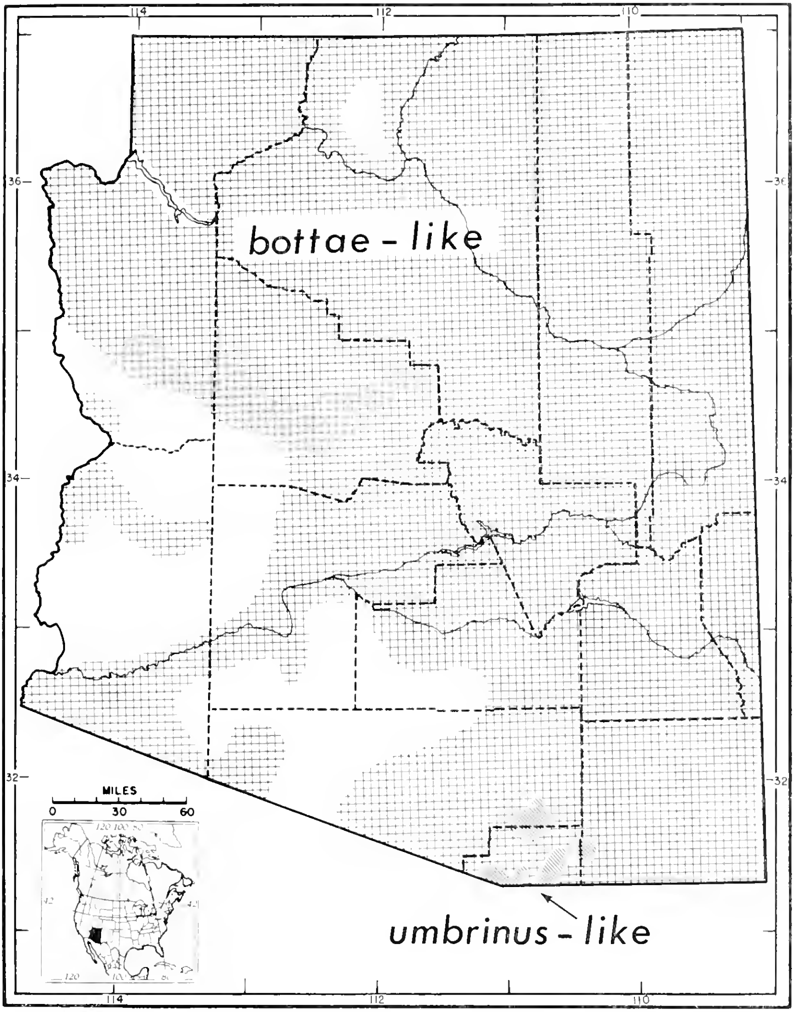


FIG. 2. Range of *Thomomys bottae* and *Thomomys umbrinus* in Arizona. Sycamore Canyon, Patagonia Mountains, the area of study, is immediately above the tip of the arrow.

GOPHERS IN THE PATAGONIA MOUNTAINS, ARIZONA

In Arizona, *Thomomys bottae* and *Thomomys umbrinus* are allopatric in three counties, Cochise, Santa Cruz, and Pima (Fig. 2), and are to be found within a half-mile or less of each other at more than 10 localities. One of the most interesting of these is Sycamore

Canyon on the west side of the Patagonia Mountains, Santa Cruz County. In the higher parts of the Patagonias, *umbrinus*-like gophers are found; in the Santa Cruz River Valley, to the west of these mountains, the gophers are *bottae*-like. *T. bottae* is found up the Canyon as far as 4400 feet elevation; *T. umbrinus* down the canyon to 4100 feet elevation (Fig. 3). In some places along this canyon, the two kinds of gophers are to be found "together" and in other places seem to be intermediate, as if intergrading or hybridizing. In southern Arizona where the two kinds occur so close together, there is no character displacement and it is difficult to select characters useful in differentiating the two kinds.

Previous Methods for Distinguishing the Two Kinds

Bailey (1915), in his revision of the pocket gophers of the genus *Thomomys*, recognized a *Thomomys umbrinus* group but did not formally characterize it. However, features of one pair of pectoral mammae, dichromatic color, and short skull were mentioned. Nelson and Goldman (1934) more clearly defined *T. umbrinus*, pointing out that the species is "normally recognizable by the differing num-

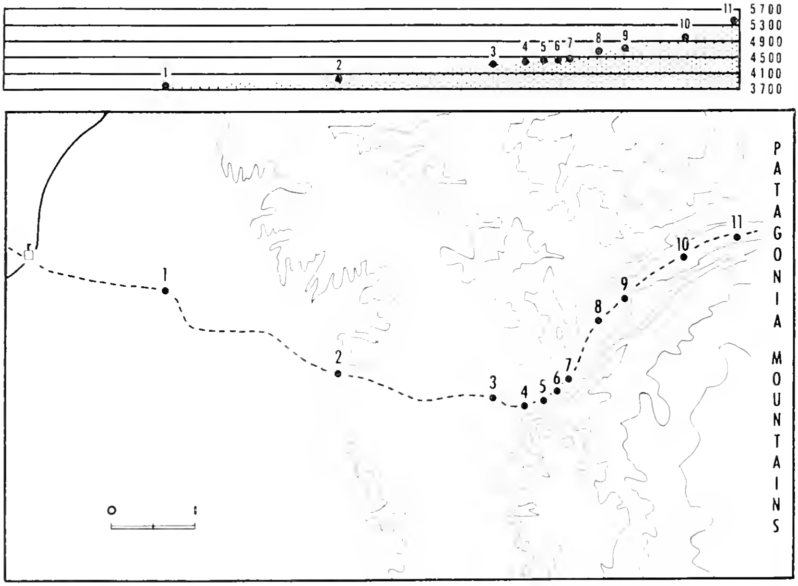


Fig. 3. Collecting sites in Sycamore Canyon. Elevation in feet is indicated in the upper transect. The dotted line indicates the road up the Canyon. The scale is for one mile. The Santa Cruz River Valley is to the left, west of Arizona Highway 89. The crest of the Patagonia Mountains it to the right.

ber of pectoral mammae (one pair in *umbrinus,* two pairs in *bottae*) and in the summation of cranial details, none of which is very trenchant" (p. 105). Blair (1939) characterized *T. umbrinus* by "small, rounded skull, small size, and weak forefeet." Davis (1946: 266) in characterizing *T. umbrinus* employed the variation in "the margin of the anterior base of the zygoma where it meets the frontal." This character is shown in Figs. 8-9. Goldman (1947:6) characterized the *Thomomys umbrinus* group by certain color and cranial features, but not by the number of pectoral mammae. Baker (1953), in studying the pocket gophers in Coahuila, used the character of the maxillo-frontal suture, the position of the lacrimal, and the procumbency of the incisors in separating *umbrinus* and *bottae.* Anderson (1966:196) noted that 17 characters are seemingly useful in distinguishing the two species in Chihuahua, but specifically mentioned only seven of the 17 characters, and these only in a casual way. Dunnigan (1967:142-144) pointed out several characteristics useful in separating Sinaloan specimens of the two species.

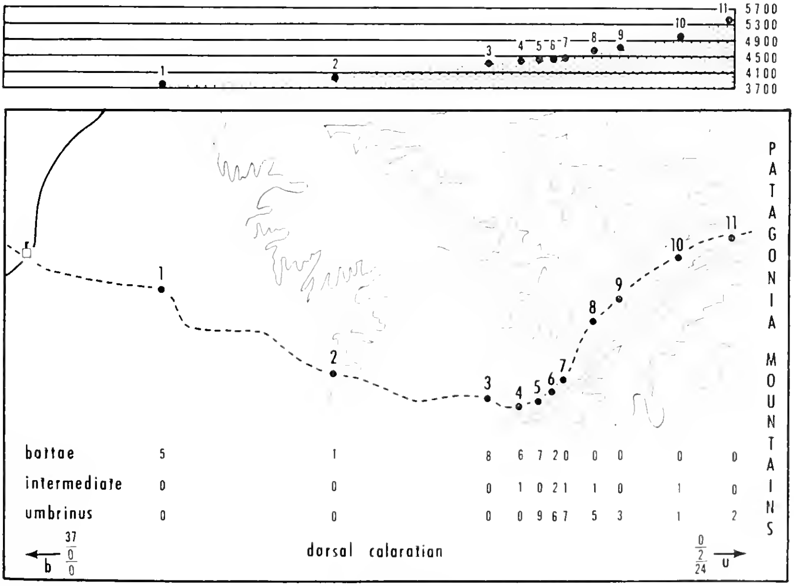


Fig. 4. Distribution of gophers with *bottae* color (1 and 2 of Fig. 6), intermediate, or *umbrinus*-color (5 and 6 of Fig. 6). The 37 gophers from below Sycamore Canyon (lower left corner) all are *bottae*-like in color; two of the *umbrinus* (lower right corner) are intermediate in color. On the map at locality 6, for example, two specimens were like *bottae* in color, two were intermediate, and six resembled *umbrinus.*

The characters employed by these various workers are not useful individually in separating the two kinds in Arizona nor is a combination of their characters highly reliable either. Coloration, including the presence or absence of a broad, dark dorsal stripe, is variable, although often useful. Most specimens regarded as *T. umbrinus* have one pair of pectoral mammae and most *T. bottae* have two pair, although there is variation in this character as well. Among approximately 200 specimens of *T. bottae* from Arizona, on which field examination for number of mammae was made, five have only one pair, not two. Nelson and Goldman (1934:117) recorded at least one, possibly three, other *T. bottae* with a single pair of pectoral mammae. Variation in the shape of the maxillo-frontal suture and in the position of the lacrimal at one locality in Arizona is summarized in Figs. 8-9. Some of the variation in cranial and external measurements in the population in Sycamore Canyon, Arizona, is shown in Table 1. The variation from throughout the range of *T. bottae* or *T. umbrinus* would show the overlap in measurements to be even greater.

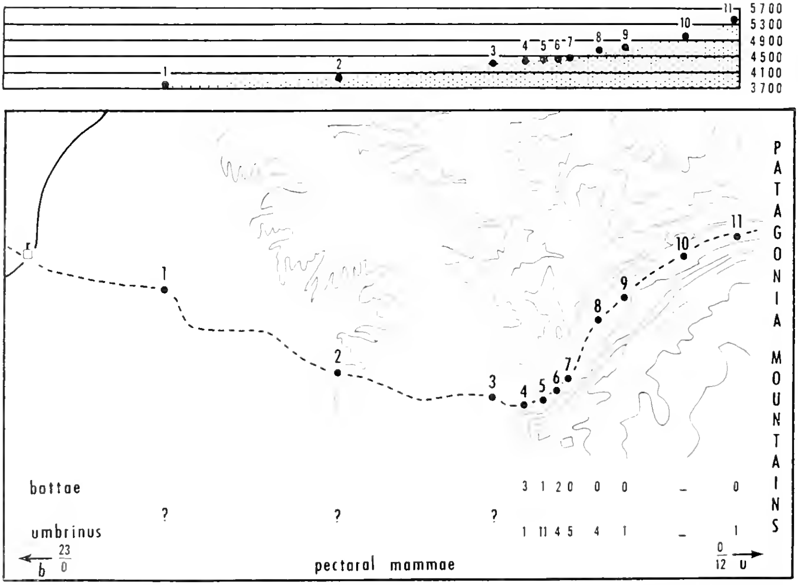


Fig. 5. Distribution of gophers with two pair of pectoral mammae *(bottae)* or one pair *(umbrinus)*. Of the females from the Santa Cruz River Valley, 23 had the mammae-count of *bottae*, none the count of *umbrinus* (see arrow at lower left). All 12 in the Patagonia Mountains had the count of *umbrinus*. Counts for localities 1 to 3 are not available; for localities 7 to 11, the counts are all *umbrinus*-like. Note the variation at localities 4, 5, and 6.

SPECIAL PROBLEM IN SYCAMORE CANYON, PATAGONIA MOUNTAINS

At the mouth of Sycamore Canyon, the dorsal coloration of specimens is typically like that of *T. bottae* (1 and 2 in Fig. 6). Part way up Sycamore Canyon, some have the color of *T. bottae*, some of *T. umbrinus*, and some are clearly intermediate. This is true at localities 4, 5, 6, 7, and 8, as shown in Fig. 4. All 23 specimens of *Thomomys* examined for mammae from below Sycamore Canyon had the number typical of *T. bottae*. All 12 specimens examined from the Patagonia Mountains had the number typical of *T. umbrinus*. Proceeding up the Canyon, at localities 4, 5, and 6, some specimens have one pair, others two pair of pectoral mammae (Fig. 5). Field work in 1968 produced an additional two females from locality 5, not listed on the map (Fig. 5), one of which had two pair of pectoral mammae, the other one pair. The coloration of the dorsum did not always correlate with the number of mammae, nor did the size of the baculum or the skull. Within Sycamore Canyon, some pocket gophers are typical *T. bottae* or typical *T. umbrinus*, but some have characteristics of both, especially at intermediate elevations, as between localities 3 to 8.

The ecological differences of the two species, if any, must be subtle. At the lower end of the Canyon *T. bottae* lives in the loose, mostly rock-free soils without heavy stands of oak. *T. umbrinus* at the upper end of the Canyon lives in rocky, shallow soil and in subterranean runways that by necessity are of such small diameter that it is nearly impossible to place a trap within the burrow. Often they are within stands of oak. There is no clear break between these two ecological situations at intermediate localities within Sycamore Canyon. Rocky soil and friable soil does occur very close together, and within openings in oak forests, within the Canyon.

MATERIALS AND METHODS

Since Sycamore Canyon appeared to be an area of hybridization or secondary intergradation, 11 collecting stations were established between elevations of 4100 and 5400 feet (Fig. 3). In 1968, substations were established below locality 3, at 0.85 mi. (one specimen), 0.4 mi. (one), and 0.2 mi. (two). These are included with locality 3. Some stations (4 to 7) were only 1/10 of a mile apart. A total of 84 specimens was collected between 1959 and 1968 from the stations in Sycamore Canyon together with 44 specimens from the adjacent Santa Cruz River Valley (listed as *bottae* in subsequent discussions) and 33 specimens from the higher parts of the Patagonia Mountains (listed as *umbrinus*). Twenty-five additional specimens from Sycamore Canyon were borrowed from the University of Arizona. These specimens were assigned to one of the 11 collecting sites, although in some cases they probably do not

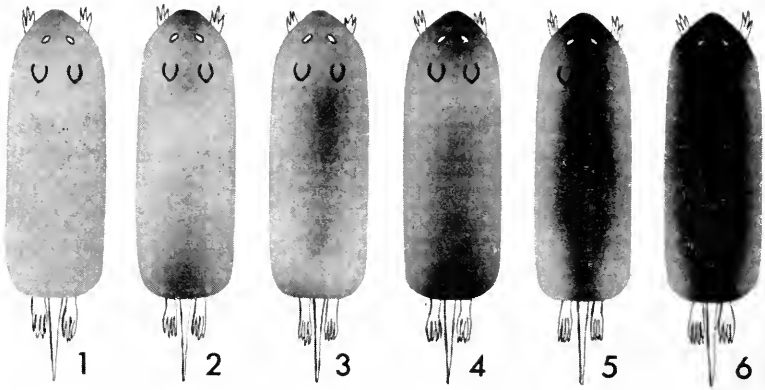


FIG. 6. Dorsal coloration in "typical" *bottae* (1 and 2) and "typical" *umbrinus* (5 and 6). Intermediate banding is indicated by 3 and 4.

precisely correspond. This probably is true for those listed as locality 6, which appear out of place in Table 2.

Most females were checked for number of mammary glands before skinning, although some of the earliest collections and borrowed specimens lack this information. Bacula were cleared in KOH, stained with alazarin red, and the height of the head was measured with an ocular micrometer.

Color was valued from light to dark as one to six. Specimens without a dark dorsal stripe were coded as one, those with a pronounced black stripe as six, and intermediates were coded between (see Fig. 6). In *bottae*-like animals,

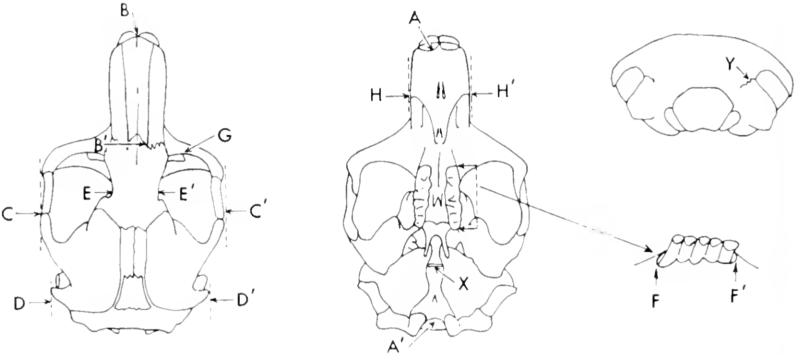


FIG. 7. Method of taking cranial measurements. AA′, basilar length; BB′, greatest length of nasal; CC′, greatest zygomatic breadth; DD′, mastoid breadth; EE′, least interorbital breadth; FF′, maxillary toothrow; BG′, length of rostrum; HH′, breadth of rostrum. Features for aging are X, basioccipital-basisphenoid suture; Y, supraoccipital-exoccipital suture.

without a prominent dorsal stripe, the sides have an ochraceous color; in *umbrinus*-like animals, and nearly all those color-coded 4, 5, and 6, have a somewhat purplish cast overlying the ochraceous on the sides.

Cranial measurements were taken as indicated in Figure 7. Only animals judged to be adult were used. Specimens were placed in four age-groups. In the oldest group, the basioccipital-basisphenoid suture is closed, the supraoccipital-exoccipital suture closed, and the temporal ridges prominent in both sexes, but less so in females. In the next younger group, the basioccipital-basisphenoid suture is not closed (X in Fig. 7), the supraoccipital-exoccipital suture mostly closed (Y in Fig. 7), and the temporal ridges present but only moderately prominent. The two younger groups were not used. Males and females were treated separately because of the secondary sexual variation (Table 1).

The position where the maxillo-frontal suture comes in contact with the lacrimal varies (Fig. 8), and this variation is given a value of 1 for *bottae*-like, 2 for intermediate, and 3 or 3.5 for *umbrinus*-like. The shape of the maxillo-frontal suture, from concave (Fig. 9) to convex, is given a similar value of 1, 2, and 3 or 3.5 from *bottae*-like to *umbrinus*-like.

CHARACTERS USEFUL IN DISTINGUISHING GOPHERS IN SOUTHERN ARIZONA

In separating *bottae*-like and *umbrinus*-like gophers in southern Arizona, the following color and morphological features were most useful. They are probably of decreasing value in the order given except for the analysis of chromosomes.

Dorsal coloration.—*T. umbrinus* has a dark band running from the tip of the nose to the base of the tail. The width of the band varies. Usually it is broadest in the middle of the back and also extends completely between the eyes and ears. Immediately below the black band, the lateral coloration is ochraceous, usually with an overlay of color, hard to describe, that gives an iridescent or purplish cast. *T. bottae* has the lateral coloration extending over the back, with a slight sprinkling of dark hairs in the middorsal area. Rarely is there an indication of a dark band (see Fig. 6).

Number of pectoral mammae.—*T. umbrinus* has only one pair of pectoral mammae; *T. bottae* two pairs. Variation from this arrangement is discussed above.

Length of baculum.—In eastern Santa Cruz County, the greatest length of the baculum in *T. bottae* is usually more than 11.0 mm.; in *T. umbrinus,* usually less than 10.2 mm.

External measurements.—For eastern Santa Cruz County, body length in adult male *T. bottae* is usually more than 152 mm.; in *T. umbrinus*, less than 149; in females, there is overlap, with *T. bottae* more than 138, *T. umbrinus* less than 143. The hind foot is usually longer than 29.5 mm. in male *T. bottae*, less than 29.2 in male *T. umbrinus*; more than 27.0, rather than less, in female *T. bottae*. There is overlap in length of tail, but in male *T. bottae* it is usually more than 60 mm., in *T. umbrinus,* less.

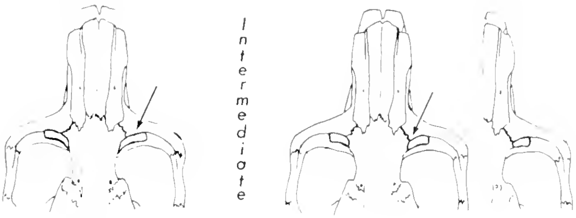
Cranial measurements.—The most useful cranial measurements were basilar length, zygomatic breadth, mastoid breadth, and length of nasals. There is less overlap in these measurements between males of the two species than in

Table 1.—Measurements (in millimeters), values (position and shape of maxillo-frontal suture), and numbers (mammae) for various features of male and female *Thomomys bottae* and *T. umbrinus* from the Santa Cruz River Valley near Nogales and the Patagonia Mountains, respectively. The mean is followed by plus or minus one standard deviation.

Measurement	Males		Females	
	bottae (N=11)	*umbrinus* (N=9)	*bottae* (N=26)	*umbrinus* (N=17)
Length of body	163.6 ±5.57	137.8 ±5.59	152.7 ±7.30	130.5 ±12.52
Length of tail	70.1 ±5.17	55.1 ±3.41	63.8 ±4.08	52.1 ± 4.78
Length of hind foot	31.0 ±0.77	27.1 ±1.05	29.7 ±1.38	25.2 ± 0.97
Basilar length	35.86±0.68	31.04±0.91	32.89±1.06	29.40± 1.11
Length of nasals	14.39±0.63	12.69±0.45	12.76±0.65	11.45± 0.62
Zygomatic breadth	25.87±1.00	22.31±0.81	23.50±0.66	21.02± 0.84
Mastoid breadth	21.31±0.51	18.38±0.52	19.87±0.64	17.36± 0.55
Interorbital breadth	6.76±0.08	6.73±0.29	6.85±0.26	6.69± 0.18
Length max. toothrow	8.22±0.30	7.63±0.41	8.30±0.43	7.62± 0.25
Length of rostrum	17.52±0.42	15.07±0.39	15.72±0.63	14.04± 0.71
Breadth of rostrum	8.68±0.35	7.91±0.32	7.95±0.29	7.34± 0.26
Suture position (1-3.5)	1.18±0.40	2.33±0.50	1.58±0.50	2.71± 0.47
Suture shape (1-3.5)	1.18±0.40	2.22±0.45	1.23±0.38	2.71± 0.56
Dorsal color (1-6)	1.27±0.47	4.67±1.87	2.04±0.82	5.41± 0.79
Length of baculum	11.97±0.51	9.19±0.52	....	....
Height of baculum (base)	2.08±0.25	1.90±0.19	....	....
Pairs pectoral mammae	....	....	2	1

females. In males in eastern Santa Cruz County, basilar length is usually more than 34.4 mm. in *T. bottae*, less than 32.9 in *T. umbrinus*; zygomatic breadth more than 23.9 mm. rather than less than 23.9; mastoid breadth more than 20.2 mm. rather than less than 19.4; nasals usually longer than 13.4 mm. rather than shorter. In females the overlap is indicated by the fact that basilar length is usually more than 30.8 mm. in *T. bottae*, less than 31.6 in *T. umbrinus*; zygomatic breadth is more than 22.2 mm. in *T. bottae*, less than 22.7 in *T. umbrinus*; mastoid breadth is more than 18.5 mm. in *T. bottae* rather than less; nasals are longer than 11.5 mm. in *T. bottae*, shorter than 12.6 in *T. umbrinus*.

Position and shape of the maxillo-frontal suture.—The position and shape of the maxillo-frontal suture are discussed above and in Figures 8-9. The position-values given in these figures indicate the variability of each character. Further-



			bottae-like	Intermediate	umbrinus-like	
umbrinus		42	7	5	25	5
bottae		49	22	16	10	1
Sycamore Canyon Patagonia Mts	1	5	4	0	1	0
	2	1	1	0	0	0
	3	8	5	2	1	0
	4	7	1	2	2	2
	5	16	2	1	12	1
	6	9	1	2	5	1
	7	9	1	2	6	0
	8	6	0	0	3	3
	9	2	0	0	2	0
	10	2	0	1	1	0
	11	2	0	0	1	1

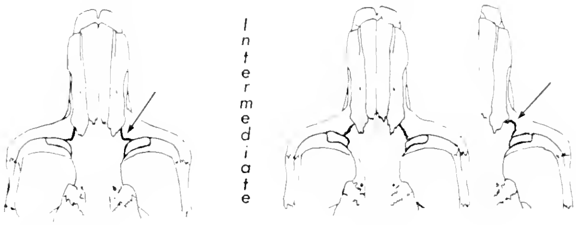
FIG. 8. Position of the maxillo-frontal suture relative to the lacrimal (see arrow). In *bottae*-like gophers, the suture reaches the lacrimal near the center of that bone, but in *umbrinus*-like gophers the suture reaches the lacrimal near the medial side. The 42 specimens of *umbrinus,* 49 of *bottae*, and those from each of the 11 localities in Sycamore Canyon (left column) are scored as to whether they are *bottae*-like, *umbrinus*-like, or intermediate.

more, it is frequently difficult to ascertain if the maxillo-frontal suture is straight or convex, or its precise position relative to the lacrimal.

Length and breadth of rostrum.—In males of *T. bottae*, the length and breadth of the rostrum, respectively, is usually more than 16.3 mm. and 8.3 mm. rather than less; in females, usually more than 14.9 and 7.6 rather than less.

Chromosomes.—Analysis of the chromosome number and karyotypes in the Patagonia Mountains has been made by Patton and Dingman (1968), and the following summary is from their report. "Typical" specimens of *T. bottae* have 2n=76, no acrocentrics or minute chromosomes, with all being metacentrics, submetacentrics, or subtelocentrics. "Typical" specimens of *T. umbrinus* have 2n=78, 62 acrocentrics and minute chromosomes, with the remainder being biarmed. However, populations of *T. bottae* from within 100 miles of the Patagonias display considerable variation in the number of acrocentrics—one population from less than 50 miles away has 18 acrocentrics. One wonders how great the variation in number of acrocentrics might be throughout the range of *T. bottae,* judging from the amount of morphological variation. Only three populations of one subspecies of *T. umbrinus* was studied and the variation was minor.

Employment of characters.—Each character listed above displays overlap between the two species. In dorsal coloration, number of pectoral mammae, and



			bottae-like	Intermediate	umbrinus-like	
umbrinus		42	5	1	33	3
bottae		48	27	8	13	0
Sycamore Canyon Patagonia Mts	1	5	4	1	0	0
	2	2	0	1	0	0
	3	8	4	3	1	0
	4	7	2	2	2	1
	5	16	0	2	12	2
	6	9	1	2	5	1
	7	9	1	2	3	3
	8	6	0	1	5	0
	9	3	0	0	3	0
	10	2	0	1	0	1
	11	2	0	1	1	0

FIG. 9. Shape of the maxillo-frontal suture (arrow). It is concave in *bottae*, straight or convex in *umbrinus*, or intermediate. The specimens are scored as in Fig. 8.

length of baculum, there is least overlap. Scatter diagrams were prepared for nearly all combinations of characters, including color as coded, but there was no obvious means of separating *T. bottae* and *T. umbrinus* in the area of this study by use of these diagrams. The use of all characters in combination is necessary if the two are to be distinguished.

Using a computer program BIMD 05 as modified by Charles Thaeler (1968), employing discriminant coefficients, 16 characters were used in the analysis for males (including length and height of head of baculum) and 15 for females. The discriminant function coefficient was determined for each character and these summed for each specimen. The values for male *T. bottae* range from 5.822 to 6.450 and for male *T. umbrinus* from 4.102 to 5.018. The values for the male pocket gophers from Sycamore Canyon localities 1 to 11 (Fig. 10) range from 3.514 to 6.581. Some are well within the range of one or the other species and some fall between the two. The values for female *T. bottae* range from 4.452 to 5.444 and for female *T. umbrinus* from 2.064 to 2.870. The values for the female pocket gophers from localities 1 through 11 range from 1.614 to 5.373. The values for the males and females are corrected to correspond and both are plotted on one graph (Fig. 10). Twenty-nine specimens in Sycamore Canyon fall between the range of the samples of the two species and this suggests that these specimens are hybrids or intergrades (see Fig. 10 and Table 2).

Independently of the above procedure, another approach was undertaken. The relationships of the specimens were determined by taxonomic distance coefficients (Sokal and Sneath, 1963:147, 300). The same characters were employed as in the analysis by the discriminant function coefficients. In using these taxonomic distance coefficients, the lesser the distance between two, the greater their phenetic relationship. Each specimen was judged to be a *T. bottae*, aberrant *bottae*, hybrid, aberrant *umbrinus*, or *T. umbrinus*. The results of this analysis, listed by locality, are shown in Table 2. Note that the results from this analysis do not differ greatly from those of the analysis by the discriminant function coefficients or the next analysis made. It should be noted that the sample sizes may differ in the different analyses.

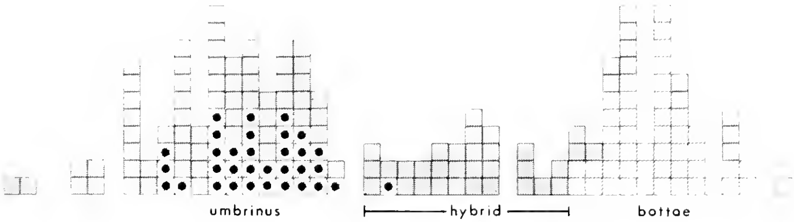


FIG. 10. Distribution of pocket gophers from Sycamore Canyon, Patagonia Mts., as determined by discriminant function coefficients. Light diagonal lines are *T. bottae*, dots are *T. umbrinus*, and heavy diagonal lines represent various localities within the Canyon. Each square represents one individual. The hybrids are indicated.

Still another procedure was employed to segregate *T. bottae* or *T. umbrinus*. A lower or upper limit of the range of variation was set at two standard deviations. For males, 11 characters were used—color, length of baculum, three external, four cranial, and position and shape of the maxillo-frontal suture. For females, 10 characters were used, with the one for length of baculum omitted. Each character for each specimen was scored, as *bottae* if it fell within two standard deviations of the known sample of *T. bottae*, or *T. umbrinus*, or intermediate. The result was that a male specimen might be scored as 10/11 *bottae* (=10 characters *bottae*-like) and 1/11 intermediate, and regarded as *T. bottae*; or 4/11 *bottae*, 5/11 *umbrinus*, 2/11 intermediate, and regarded as a hybrid. The results of this analysis are given in Table 2. Although the concordance of this system with the others is not so great as between the first two, and one would not expect it to be, there still is considerable similarity.

DISCUSSION

A large number of the specimens from Sycamore Canyon are intermediate between *T. bottae* and *T. umbrinus* (Table 2). These are from "intermediate" localities also. It seems apparent that there is hybridization or intergradation between the two species. From localities 1 through 11 within the Canyon, 29 specimens are "intermediate" as determined by the discriminant function analysis. Using the taxonomic distance coefficients, 21 specimens are "inter-

TABLE 2.—PLACEMENT OF POCKET GOPHERS FROM THE 11 LOCALITIES IN SYCAMORE CANYON (NOS. 1 THROUGH 11) AS TO ONE OR THE OTHER SPECIES OR AS "INTERMEDIATE" USING THREE DIFFERENT METHODS OF ANALYSIS.

	T. bottae	1	2	3	4	5	6	7	8	9	10	11	*T. umbrinus*
Discriminant Function Analysis													
bottae	44	5	2	6			3*						
hybrid			2	9	8	5	4	1					1
umbrinus				2	1	10	13	9	7	12	4	3	32
Taxonomic Distance Coefficient													
bottae	37	5		2			1*						
"aberrant"			2	2			3*						
hybrid			2	9	5	4	1						
"aberrant"				2	3	2	2	3		3			
umbrinus				1	1	11	13	10	7	8	5	2	26
Two Standard Deviations													
bottae	36	5	1	6			1*						
"aberrant"	1		1	1			2*						
hybrid			2	5	6	4	4						
"aberrant"				1	1	1		1		1			
umbrinus				3	2	12	13	10	7	10	5	2	26

* These may not be from locality 6, and perhaps should be identified with a lower locality.

mediate" and an additional 22 are regarded as aberrant (possibly hybrids, or possibly referable to a species). Using the 2 SD method, 21 specimens are regarded as "intermediate" and an additional nine as aberrant.

In parts of the Patagonia Mountains, *Thomomys bottae* and *T. umbrinus*, which are usually allopatric, have not evolved effective genetic isolation. Where the two groups of populations make secondary contact, either sympatrically or in allopatric zones, introgressive hybridization occurs. In Sycamore Canyon, at locality 1 and below, all specimens are *T. bottae*; at locality 8 and above, all are *T. umbrinus*. From localities 2 through 7, a distance of less than three miles, there are to be found *T. bottae,* hybrids, and *T. umbrinus.* Most of the hybridization occurs between locality 6 and a place one-half mile below locality 3, a distance of about one and a half miles. This is approximately the same area where Patton and Dingman (1968) found four hybrids in Sycamore Canyon. The zone of hybridization seems well marked but narrow.

On the basis of karyology, nine specimens from Sycamore Canyon are hybrids or backcross hybrids. These are from a narrow zone also—localities 2 through 7. Four of these hybrids have been reported upon and discussed by Patton and Dingman (1968). One is regarded as a F_1 hybrid, three as backcrosses. Five specimens that were karyotyped by M. R. Lee and E. Zimmerman indicate that three are F_1 hybrids and two are probably backcrosses. Of these five, three are from locality 3 and two from two tenths of a mile below locality 3.

A basic consideration is whether, in southern Arizona, *T. bottae* and *T. umbrinus* are distinct species. Samples of gophers taken from the Santa Cruz River Valley and from the upper parts of Sycamore Canyon, a distance of only eight miles, would leave little doubt but that the samples were from distinct species if collections were not available from the intervening area. But such questions arise as these: (1) Are all gophers that live on poor, rocky soil of small size (*umbrinus*-like)? Often they are small, but do not have the other characteristics of *umbrinus*. (2) Do small-sized gophers frequently have but one pair of pectoral mammae (*umbrinus*-like)? There is no evidence that such is the case. (3) Do gophers that live at higher elevations have a darker dorsal coloration? Frequently at higher elevations the soils are darker and so are the gophers, but the dark color is not necessarily restricted to a middorsal band as in *umbrinus*. *T. bottae* and *T. umbrinus* are judged on chromosomal distinctiveness as two species in Arizona (Patton and Dingman, 1968). Yet, in view of the survey of the variation in the karyology of only a few *T. bottae* in Arizona, are the differences great enough to regard these as distinct species? Probably, but further evidence will be needed.

With all of the evidence here marshalled, it still is a matter of interpretation as to whether the populations of *bottae* and *umbrinus* in southern Arizona are subspecifically or specifically distinct. I would interpret the evidence as indicating that they are distinct species, with introgressive or allopatric hybridization occurring in a narrow zone in one place in southern Arizona, and possibly in several other areas where the range of the two species come together, and especially where it has been difficult to assign specimens to one or the other species. The narrowness of the zone of hybridization, in spite of the extensive interchange of genetical material within this zone, would suggest specific differentiation. Admittedly, the suggested presence of backcross hybrids, based on karyology, and the seeming vigor of these and other hybrids, may argue against specific status.

Does this hybridization that occurs at one place, and perhaps several places, represent the incipient formation of two species or rather the infrequent intermingling of genetical material of two established species? Although difficult to decide, I would guess the latter. The allopatric distribution of *umbrinus*-like gophers and *bottae*-like gophers over large areas (Fig. 1) suggests that these two evolved independently. In at least one place where the two species come together, allopatric hybridization occurs with nearly complete genetic interchange and backcrossing, yet the parental populations maintain their identities.

The situation in Sycamore Canyon, Arizona, seemingly fits the definition of Remington's suture-zone hybridization, judging from the summary of Yang and Selander (1968:139). There is extensive hybridization in a narrow zone between morphologically dissimilar, allopatric populations. There is backcrossing with no reproductive isolation or hybrid inferiority. Despite interbreeding and backcrossing, introgression of genes into the parental population is limited. Where the species *Thomomys bottae* and *T. umbrinus* live sympatrically, be it Sycamore Canyon or the few other places throughout their ranges, even though there may be only partial ecological and reproductive isolation between the two, the area of contact is so small that swamping does not occur.

SUMMARY

In places in southeastern Arizona, *Thomomys bottae*-like gophers and *Thomomys umbrinus*-like gophers ocur together or within a few yards of each other. Characters useful in distinguishing these two species elsewhere will not serve here for some animals have some characters of both species. Three analyses of the population in Sycamore Canyon, west side of the Patagonia Mountains, were made using discriminant function analysis, taxonomic distance coefficients, and two standard deviations of each side of the mean. Characters employed were dorsal coloration, number of pectoral mammae, length of baculum, various external and cranial measurements, and position and shape of the maxillo-frontal suture relative to the lacrimal. These analyses indicate that somewhere between 21 and 29 specimens, out of 109, are intermediates or hybrids. Within a 3 mile area of contact, at intermediate elevations within Sycamore Canyon, extensive hybridization, not intergradation, occurs between the two species, *T. bottae* and *T. umbrinus*.

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RESTOS FOSILES DE MAMIFEROS DE TLAPACOYA, ESTADO DE MEXICO (PLEISTOCENO-RECIENTE)

POR

TICUL ALVAREZ

Las excavaciones realizadas por el personal del Departamento de Prehistoria, Instituto Nacional de Antropología e Historia, en el cerro de Tlapacoya, México, durante los años de 1966 y 1967, han proporcionado una gran cantidad de huesos de vertebrados, siendo por ello hasta el momento, una de las más importantes localidades para el conocimiento de la Fauna Pleistocénica de la parte central de México, conocida como Valle de México. Estas excavaciones son también muy valiosas porque por primera vez se tienen de esta región de México, fechas de C^{14}, que nos dan una idea de cuándo dichas faunas existieron y harán posible futuras correlaciones, tanto con descubrimientos del pasado, como con los descubrimientos venideros.

La fauna estudiada y que dió origen a este trabajo se limita a los mamíferos encontrados en las excavaciones del año de 1966, realizadas por los Arqueólogos Elizabeth y Mickael Goodlife, quienes laboraron para el Departamento de Prehistoria. Además de los fósiles de mamíferos, se rescataron gran cantidad de huesos de aves, que son objeto de minucioso estudio por parte del Dr. Allan R. Phillips del Instituto de Biología de la Universidad Nacional Autonoma de México, y del Dr. Pierce Brodkorb de la Universidad de Florida.

Las excavaciones se realizaron en la falda sureste del cerro de Tlapacoya, a 1.5 kilómetros al sur del pueblo del mismo nombre (113° 02′ 40″ long. E y 19° 17′ 49″ lat. N), estado de México y que a su vez se encuentra a 26 kilómetros al Sureste del centro de la Ciudad de México (Fig. 1). Los hallazgos se llevaron acabo en dos calas o trincheras denominadas respectivamente alfa y beta, situadas a 37 metros una de la otra.

La cala alfa tenía 30 metros de extensión y anchura entre dos y tres metros. La capa principal donde se encontraron los huesos fue denominada con los números XLI a XLII. La trinchera beta midió 53 metros de largo y de dos a cuatro metros de ancho. La capa en la que se encontró mayor número de restos óseos fue de cenizas volcánicas, que se encontraba en contacto con la roca madre. La capa de ceniza se denominó con el número XLVI.

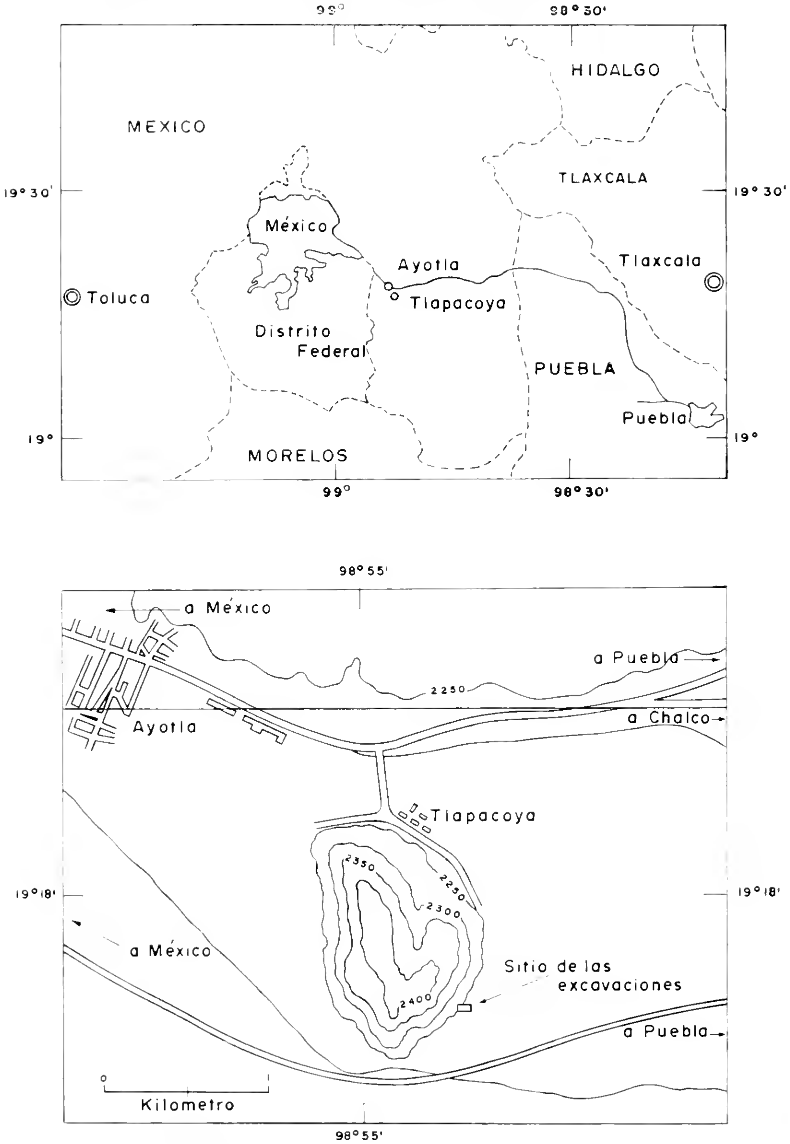

Fig. 1. Mapa del área y sitio exacto de las excavaciones.

La estratificación de las trincheras es muy complicada, habiéndose dividido hasta en 54 diferentes estratos (Goodlife y Goodlife, 1969); sin embargo, sólo dos son importantes desde el punto de vista paleontológico, porque en ellos se encontraron la mayor parte de los restos óseos (Fig. 2).

El más moderno se encontró en la trinchera alfa y se supone haya sido un hogar del hombre prehistórico por la gran acumulación de huesos, principalmente de mamíferos grandes, así como por haberse encontrado un área limpia, con carbón y grandes piedras alrededor (Goodlife y Goodlife, 1966). Los restos de carbón de este lugar han sido fechados por C^{14} en 24,000 ± 4000 años antes del presente (Haynes, 1967).

El otro estrato en que se encontraron gran número de huesos, es ceniza volcánica en contacto con la roca del cerro. No existe fecha de material de esta capa, pero suponemos que sea alrededor de los 30,000 años, ya que la muestra de una capa superior a la de cenizas data de hace 24,200 ± 500.

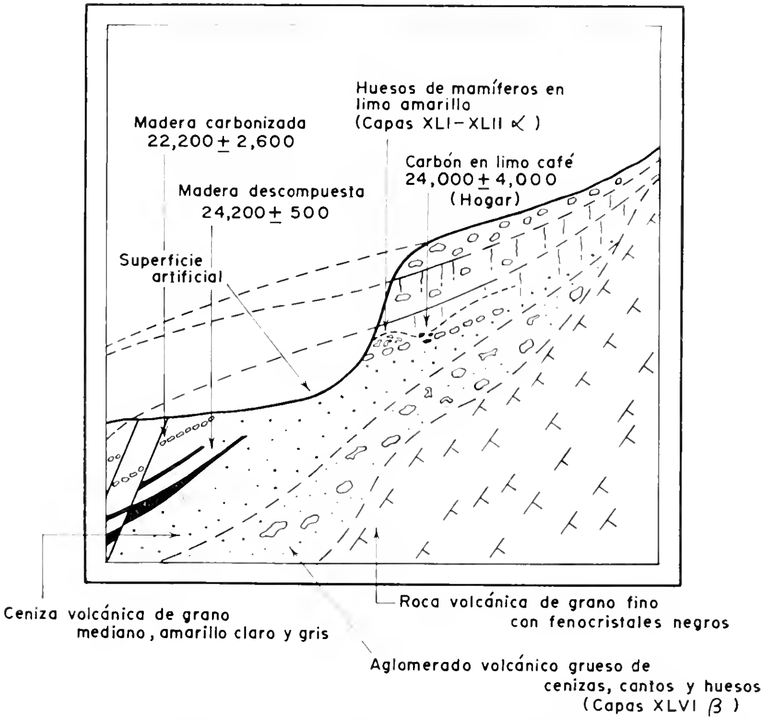

FIG. 2. Estratigrafía generalizada de los calas alfa y beta de Tlapacoya (66-1), basada en la de Haynes (1967), con modificaciónes.

Los restos de esta capa están constituídos principalmente por aves y pequeños mamíferos, aunque también existen algunos restos de animales de mayor tamaño.

Los ejemplares que forman la base de este estudio se encuentran catálogados en el Laboratorio de Paleozoología, del Departamento de Prehistoria, Instituto Nacional de Antropología e Historia (DP). Dos mandíbulas de la nueva especie de *Odocoileus* aquí descrita, se encuentran en la colección de Paleontología de Vertebrados de la Smithsonian Institution. Si no se especifica de otra manera, todas las medidas están en milímetros.

Agradezco al Prof. José Luis Lorenzo, Jefe del Departamento de Prehistoria su sugerenica y ayuda para realizar este trabajo. A la arqueóloga Lorena Mirambell, encargada del proyecto de Tlapacoya, por su valiosa cooperación para aclarar diferentes problemas estratigráficos y de otra índole. A los arqueólogos Elizabeth y Mickael Goodlife por ser ellos quiénes realizaron las excavaciones y pusieron todo su empeño por rescatar los materiales óseos en el mejor estado posible.

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LISTA DE ESPECIES

CHIROPTERA

Phyllostomatidae

Mormoops megalophylla (Peters, 1864)

Material.—Húmero (928 DP).

El hueso fósil encontrado en Tlapacoya, no difiere en nada de los usados para su comparación, por lo cual se identifica como *Mormoops megalophylla,* murciélago muy abundante en las zonas bajas de México, pero que no se ha registrado del Valle de México en épocas recientes.

La capa de donde proviene tiene antiguedad mayor a los 24,000 años antes del presente y se encuentra justamente arriba de las capas formadas por cenizas de la erupción volcánica.

LAGOMORPHA

Leporidae

Sylvilagus cunicularius (Waterhouse, 1848)

Material.—Calcáneo (929 DP).

El calcáneo se ha identificado como perteneciente a la especie *S. cunicularius,* con base en su tamaño, que es realmente mayor que el de *S. floridanus* o que *Romerolagus*, los otros dos Leporidae que existen en el valle de México. *S. cunicularius* es todavía un conejo muy abundante en todo el sur del altiplano mexicano, extendiendo su distribución hasta las costas de Sinaloa. Medidas: longitud del hueso 26.4; ancho máximo del mismo, 11.3.

Como fósil se ha registrado de Veracruz (Dalquest, 1961). El calcáneo de Tlapacoya tiene antiguedad aproximada de 12,000 años ye se encontró, formando parte de él un conjunto de huesos de un hogar, en la cala alfa.

Sylvilagus floridanus (J. A. Allen, 1890)

Material.—Fragmento de mandíbula con pm2-m2 (930 DP).

Al contrario del calcáneo anterior, este material se identificó como *S. floridanus* por se menor tamaño. Al compararlo con mandíbulas de *floridanus* no encontramos diferencias palpables en cuento a forma y tamaño, no siendo así con *S. cunicularius* que si bien la forma no difiere, el tamaño de *cunicularius* es notablemente más grande.

S. floridanus es un animal que ha sobrevivido a la presión demográfica del Valle de México y todavía es posible encontrarlo con cierta facilidad.

La mandíbula de *S. floridanus* fue encontrada en la capa de ceniza de la erupción volcánica, que se calcula de una antiguedad mayor a 24,000 años.

RODENTIA

Geomyidae

Pappogeomys sp.

Material.—Fragmento de mandíbula, con i-m2, sin procesos; *ibid.*, sin incisivo; fragmento maxilar y premaxilar con incisivo (936-938 DP).

Debido a lo fragmentado y escaso del material, nos ha sido imposible poder determinar la especie de los restos de tuzas encontrados en Tlapacoya, con antiguedad mayor a los 24,000 años; sin embargo, si creemos que el género esté bien determinado ya que los incisivos superiores presentan el surco medio tan característico de este género.

A juzgar por el tamaño, los fósiles de Tlapacoya no pertenecen a ninguna de las especies que actualmente viven en el Valle de México, de los cuales *Pappogeomys merriami* es la más grande y la que habita actualmente en el área de donde se rescataran los fósiles, la otra especie *P. tylorhinus* es más pequeña y habita al noroeste del Valle de México. En la Figura 3 se compara el ancho de los incisivos inferiores y la longitud del premolar del fósil, con ejemplares de *P. merriami* y *P. tylorhinus* viéndose que el fósil queda por abajo, de las medidas de los adultos de *merriami* y *tylorhinus* y sólo es igual que algunos ejemplares muy jóvenes de las especies citadas.

Cualitativamente, el carácter que mayor significado tiene y por el cual no hemos querido asignar los ejemplares de Tlapacoya a una de las especies vivientes, principalmente de las del Valle de México, es que el surco medio de la cara frontal del incisivo está más afuera de la mitad de la cara del incisivo, de tal manera que la porción interna (1.4) es el 127.2 por ciento de la porción externa (1.1) (Fig. 4A). En 20 ejemplares de *P. merriami* tomadas al azar (en cuanto a edad y sexo) la media es 96.3 por ciento, con 111.1 a 80.0 de variación y en 18 ejemplares de *P. tylorhinus* es de 97.6 (102.0-85.2) por ciento.

Otro carácter se presenta en el premolar inferior, en el cual el ángulo entrante externo que separa a los dos lóbulos que forman el diente, presenta una proyección interna y hacia adelante (Fig. 4B). Esta proyección no la hemos encontrado tan bien marcada en ninguno de los 50 ejemplares de *P. merriami* y *P. tylorhinus* que hemos examinado, aunque si se encuentra en muchos de ellos una indicación de dicha proyección. Sin embargo, consideramos que la variación en este respecto puede ser mayor, por lo que su significado taxonómico se desvanece.

Merriam (1895) coloca dentro de los géneros que poseen el surco medio del incisivo en la parte externa a *Geomys* y *Zygogeomys*, dos géneros que presentan dos surcos en vez de uno como sucede entre otros *Pappogeomys*. El autor antes citado no menciona nada al respecto de la variación de los ángulos en el premolar inferior.

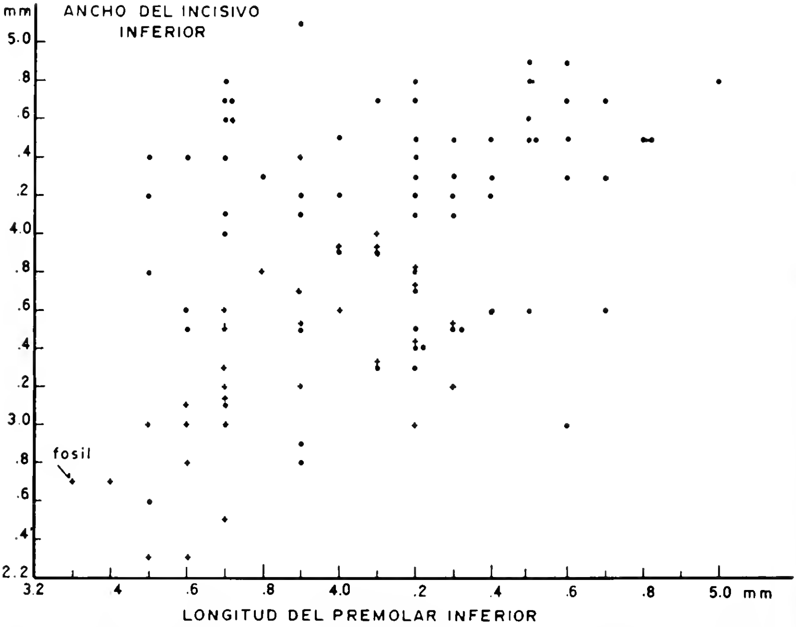

FIG. 3. Gráfica de la relación entre el ancho del incisivo inferior y la longitud del premolar inferior en *Pappogeomys*. Los puntos representan medidas de *P. merriami* y cruces de *P. tylorhinus*.

Considerando que el material fósil de Tlapacoya no coincidió en elgunas características con las especies del Valle de México, preferimos asignar este material sólo al género *Pappogeomys*, esperando que exista más material, tanto fósil como viviente, para poder determinar si se trata de una especie no descrita o bien, solo un extremo de la variación de alguna de las especies actuales.

Cricetidae

Peromyscus maldonadoi Alvarez, 1967

Material.—Fragmento de mandíbula derecha, sin procesos ni borde inferior de la rama, ni la mitad posterior de m3 (1153 DP).

Tomando en consideración el tamaño de la mandíbula, así como los pocos caracteres que se puden apreciar en la mandíbula procedente de Tlapacoya, ésta es muy semejante tipo de *Peromyscus maldonadoi* especie descrita del Pleistoceno de Tequesquinahua, México.

En la estructura y tamaño de los molares encontramos también mucha similitud. La serie de molares inferiores mide en el tipo de *P. maldonadoi* 5.8, igual que en el ejemplar de Tlapacoya. Aunque la estructura de los molares en el tipo de *P. maldonadoi* no se puede apreciar en detalle, debido al desgaste de los mismos, si es posible apreciar que existe una similitud en la forma general entre este ejemplar y la del de Tlapacoya que es más joven; así, el segundo molar es relativamente grande y cuadrado en ambos ejemplares. La única diferencia aparente es la ausencia de ectostilidio en el tipo de *P. mal-*

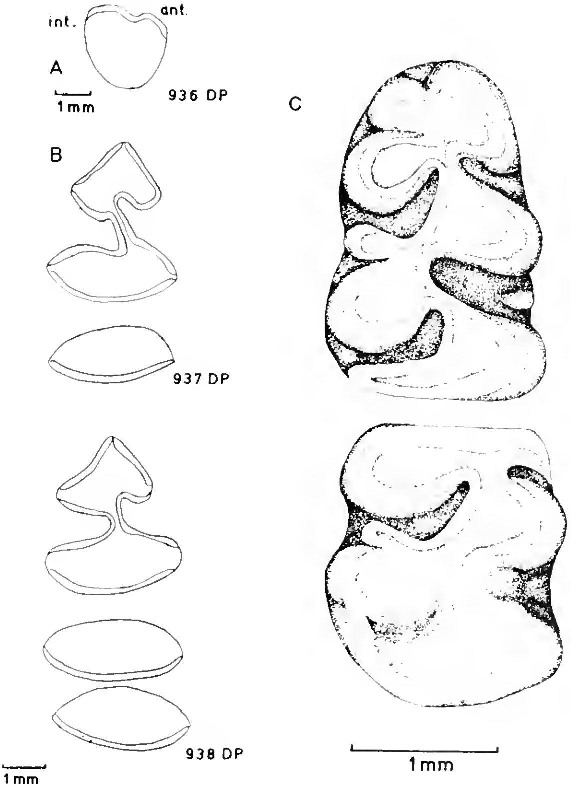

FIG. 4. A, corte transversal del incisivo superior del *Pappogeomys* fósil; B, premolares y molares del *Pappogeomys* fósil; C, primero y segundo molares de *Peromyscus maldonadoi.*

donadoi y que si está bien desarrollado en el ejemplar de Tlapacoya, especialmente en el primer molar, ya que en el segundo dicha estructura no está bien marcada (Fig. 4C). Sin embargo, esta diferencia no es de tomarse mucho en cuenta ya que según Hooper (1957) la presencia de stilos y lofos es muy variable en las especies de *Peromyscus.*

Debido a la semejanza de estructura de la mandíbula procedente de Tlapacoya, con el tipo de *P. maldonadoi,* así como que ambas proceden de localidades muy cercanas y de depósitos Pleistocénicos, consideramos que sean de la misma especie. Tlapacoya se encuentra a 42 kilómetros al sureste de Tequesquinahua, México y el estrato en que se encuentra la mandíbula de Tlapacoya fue fechado en más de 24,000 años; aunque del tipo de *P. maldonadoi* no tenemos la edad, suponemos que proviene del Pleistoceno por el tipo de fauna con que se encontró asociado (Alvarez, 1967).

Para completar más la diagnosis de la especie *P. maldonadoi,* describiremos a continuación la estructura de los molares del ejemplar de Tlapacoya, siguiendo la terminología dada por Hooper (1957). El primer molar presenta protoconidio dividido en la parte anterior y con el doblez menor bien marcado; el mesostilidio unido por medio del mesolofidio a la cara anterior del entoconidio; cíngulo posterior sin llegar al borde interno del molar; con ectostilidio, pero sin ectolofidio.

El segundo molar presenta el cíngulo anterior extendido hasta el borde externo del molar, ectostilidio poco desarrollado, sin ectolofidio; mesolofidio unido al ectoconidio en su parte anterior, sin mesolofidio; cíngulo posterior extendido hasta el borde lingual del molar y continuándose en cierta forma con el borde del ectoconidio.

La estructura de los molares, así como el tamaño de los mismos es muy parecido a *P. zarhinchus,* del cual difiere en que el primer pliegue primario tiene dirección oblicua al eje longitudinal del molar, además de ser más profunda.

Medidas del ejemplar de Tlapacoya: longitud de la serie de molares, 5.8; longitud de m1, 2.23, ancho, 1.43; longitud de m2, 1.82, ancho, 1.50.

Neotoma mexicana Baird, 1855

Material.—Primer molar inferior izquierdo (939 DP).

El molar difiere en algunos detalles de los 10 ejemplares usados para comparación, pero la variación entre ellos es muy grande, de tal manera que consideramos que las diferencias entre el molar de Tlapacoya, que además no son constantes, y todos los otros molares, sean más bien de caracter individual que específico.

Freudenberg (1922: 104) enlistó restos de *Neotoma* del Valle de México, sin mencionar las especies ni dar ninguna medida o figura que nos pudiera dar una idea de qué especie se trata. Alvarez (1967) describió *N. magnodonta* del Pleistoceno del Valle de México, que difiere de *N. mexicana* en varios caracteres morfológicos y sobre todo en su mayor tamaño.

Los restos aquí registrados como *N. mexicana,* se encontraron formando parte de la concentración mayor de huesos de la cala beta, que se supone fueron depositados por el hombre hace unos 24,000 años. Existe la posibilidad de que el molar de *Neotoma* haya llegado hasta el hogar por acarreo a través de los tuneles de tuza.

Microtus mexicanus (Saussure, 1861)

Material.—Mandíbula con incisivo, m1-2. Sin proceso angular y coronoide (940 DP).

La única diferencia con las mandíbulas que se usaron para comparación, estriba en que el fósil es ligeramente mayor. Procede del área del hogar y presenta la misma posibilidad que el molar de *Neotoma.*

Neochoerus pinckneyi Hay, 1926

Material.—Primer molar izquierdo inferior (941 DP).

El molar de carpincho encontrado en Tlapacoya, tentativamente se asigna a *N. pinckneyi,* especie que se ha registrado en América del Norte. Actualmente se está realizando un estudio del Material de Carpinchos que proviene de Chapala y Zacualco, Jalisco y en el que se ha encontrado una variación tan grande en la forma y medida del premolar inferior, que nos hace pensar que los diferentes géneros de la familia Hydrochoeridae son variación de un mismo taxon y que por lo tanto, muchas especies deberán ser puestas en sinonimía.

La corona del molar de Tlapacoya mide de largo 9.8 y de ancho, 6.9 y procede de la capa más profunda que se excavó o sea la de cenizas volcánicas.

CARNIVORA

Canidae

Canis sp.

Material.—Un fragmento de mandíbula, sin ningún diente (942 DP).

Aunque la falta de dientes hace más díficil la identificación de este fragmento, la consideramos como *Canis* por la forma del borde inferior de la mandíbula; posición de la fosa coroidea del alveolo de m3, caracteres que no difieren de las mandíbulas de *Canis lupus, C. latrans, C. familiaris* con que fue comparado.

Se encontró este fragmento en la capa de ceniza volcánica, que data de más de 24,000 años.

Ursidae

Ursus americanus Pallas, 1780

Material.—Cráneo fragmentado, dos mandíbulas; dos fémures; tibias izquierda y derecha; pélvis fragmentada; fragmentos de escápula izquierda; calcáneo, uno completo y otro roto; astrágalo; ocho vértebras; 12 falanges; dos ulnas fragmentadas y dos radios (950-976 DP).

Todos los materiales identificados como de oso se encontraron en una misma capa y muy juntos entre sí, por lo que suponemos que se trate de un solo individuo.

La comparación de las medidas de los molares del ejemplar de Tlapacoya con los dados por Kurtén (1963:5) para 25 ejemplares de *Ursus americanus* del Reciente, nos muestra que nuestro ejemplar se aparta ligeramente de la amplitud dada por dicho autor. P4, M2, m2, y m3 son menores, en cambio M2 y p4 son mayores que el máximo de la variación dada por Kurtén *(op. cit.).*

Tomando en cuenta las medidas de Stock (1950) para una mandíbula de *U. americanus* de la cueva de San Josecito, Nuevo León, la mandíbula de Tlapacoya, es un poco mayor, pero los dientes son notablemente más pequeños. Stock *(op. cit.)* identifica como *U. americanus* el oso de San Josecito, aunque señala su parecido en la dentición con *U. optimus*, especie del Pleistoceno de California caracterizado por su robusta dentadura. El ejemplar de Tlapacoya creo que sea típico *U. americanus*, aunque posiblemente una subespecie más pequeña que los actualmente conocidos.

Los huesos del oso se encontraron formando la mayor parte del grupo designado como hogar en la cala alfa y como ya se indicó, data de 24,000 años aproximadamente.

Procyonidae

Procyon lotor (Linnaeus, 1758)

Material.—Mitad anterior de mandíbula, desde el borde posterior de m1, con pm4 y m1. Fragmento maxilar con alveolo de M1 y con el M2; mitad inferior del húmero; mitad inferior de tibia; un astrágalo; tercio superior de ulna (943-948 DP).

La mandíbula perteneció a un individuo joven, sin embargo, tanto ésta como los restos postcraneales son ligeramente de mayor tamaño que los usados para comparación. Esta diferencia probablemente se deba a distinto desarrollo o sexo del material comparado.

Los restos de *Procyon* fueron encontrados en tres capas diferentes. La más antigua corresponde a las cenizas volcánicas de la cala beta, que como ya se ha indicado, data de más de 24,000 años; otros restos se hallaron en la aglomeración de huesos y piedras denominada como hogar y que tiene una edad de 24,000 años y por último, se localizaron algunos restos en capas más superficiales que las del hogar, que corresponden a una aproximada de 8000 a 9000 años.

Mustelidae

Lutra canadensis (Schreber, 1776)

Material.—Fragmentos de un cráneo: región basal; frontales; pterigoides, maxila izquierda con la carnacia "*in situ*" y alvéolos de premolares y molares (949 DP).

Se comparó con cuatro cráneos de ejemplares recientes y se encontró que difiere sólo en pequeños detalles, como presentar el talonoide de la carnacia más angosto; el borde posterior del mismo es ligeramente cóncavo en contra de convexo en los actuales. El tamaño del carnacia es más pequeño que en los ejemplares de comparación que presentan el mismo desgaste en el diente. Medidas del carnacia del fósil, seguidas de las de dos ejemplares recientes: largo, 12.2, 14.1, 12.2; ancho 10.0, 11.9, 10.2.

Este género no se había registrado anteriormente en el Pleistoceno mexicano, ni tampoco se conoce del Reciente en el Valle de México. Los restos de *Lutra* de Tlapacoya fueron rescatados en el mismo nivel que los de *Neochoerus* o sea el estrato más profundo, formado por los depósitos de una erupción volcánica.

ARCTIODACTYLA

Cervidae

Odocoileus virginianus (Zimmermann, 1780)

Material.—Rama mandibular derecha con dientes; mitad posterior de la mandíbula derecha desde el primer premolar; astragalo; región parietal muy fragmentada, con la base de las astas; tres falanges segundas; dos falanges primeras completas y dos mitades; fragmento de calcáneo; articulación inferior de la escápula; fragmento basal de asta con una punta; dos fémures completos; metatarso, dos mitades superiores de metatarso; atlas (977-1000, 1151-1152 DP).

Todo el material que se refiere a *Odocoileus virginianus* se identificó como tal, con base principalmente en el tamaño, ya que cualitativamente no difiere del material asignado a la especie de *Odocoileus* aquí descrita y que es de mucho mayor tamaño.

Los restos de *O. virginianus* se encontraron en diferentes capas; sin embargo, la mayor frecuencia está en la capa más profunda, tanto en la cala alfa, como la beta que pertenece a la erupción volcánica. Existen restos en una capa de la cala beta, situada por arriba de la playa, que se ha fechado en 22,200 años, pero por abajo de la otra capa fechada en 14,000 años de antiguedad. Por último, encontramos también algunos restos de venado cola blanca en el hogar y otros pocos en la capa más superficial.

Odocoileus halli, especie nueva

Holotypo.—Mandíbula izquierda y derecha del mismo ejemplar procedente de la capa XLII de la trinchera alfa de Tlapacoya, México, y catalogada con los números 1082 y 1083. Departamento de Prehistoria, Instituto Nacional de Antropología e Historia. Mandíbula derecho completa, sin incisivos, ni tercer molar, sin proceso coronoide; mandíbula izquierda con los premolares y molares, sin incisivos, le falta la región desde el último molar hacia atrás (Fig. 5).

Paratipos.—Ocho mandíbulas sin incisivos pero con premolares y molares; una rama mandibular sin dientes; cuatro series de dientes superiores con fragmento del maxilar, 15 premolares y molares sueltos; región posterior del cráneo, con la base de las astas; parietales de ambos lados con la base de las astas; región parietal; tres fragmentos de asta; numerosos elementos post-craneales (1001-1150, 1177-1180, 1191 DP).

Edad.—Pleistoceno-Reciente, fecha de C 14 de 22,000 ± 2600 años.

Diagnosis.—Tamaño grande para el género, longitud alveolar de la mandíbula de 104 a 115; máxilar, 117.3. Forma de los premolares y molares igual a *Odocoileus virginianus*, crestas de la cara lingual de los premolares y molares bien desarrollada; segunda mitad de pm4 menos de la mitad de la anterior; la mayoría de los molares con un estilo entre los dos lóbulos externos.

Description de los Molares

La descripción de las estructuras molares está basada en tres ejemplares que presentan desde el que no tiene desgaste alguno hasta el ejemplar viejo, con los molares muy desgastados (Fig. 5).

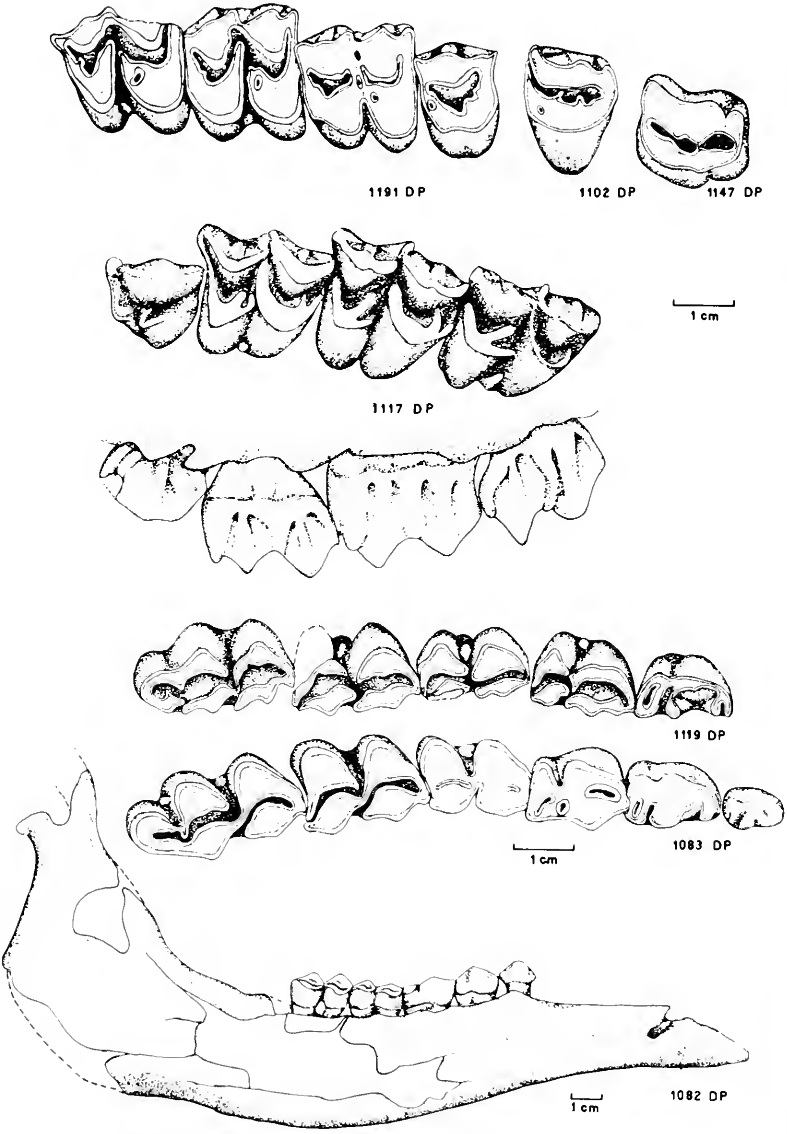

FIG. 5. Molares y mandíbula de *Odocoileus halli*. De arriba hacia abajo, primero una serie compuesta de premolares y molares superiores (1147, 1102, 1191 DP); serie de dientes superiores con menos desgaste (1117 DP); vista lingual de los dientes (1117 D.P.); vista oclusal de una serie de molares inferiores (1119 DP); vista de los molares inferiores izquierdos del tipo (1083 DP) y de la mandíbula derecha del tipo (1082 DP).

Molares inferiores.—El pm2 es sencillo y consta de una sola cúspide central y dos crestas oblicuas posteriores, las cuales con el desgaste van despareciendo, el tamaño del diente es como la mitad del premolar siguiente, el cual ya presenta varias complicaciones en su estructura. La cara externa está dividida en dos lóbulos por una escotadura poco profunda, el lóbulo posterior es aproximadamente un tercio del lóbulo anterior. La cara lingual presenta una entrada en forma de U que separa de cara oclusal en dos lóbulos, el anterior es muy pequeño y está a su vez dividio en dos pequeños lóbulos los cuales con el desgaste se van uniendo hasta verse en los animales muy viejos sólo una pequeña entrante. El lóbulo posterior, está a su vez dividido por dos ángulos entrantes muy profundos. La combinación de estos dos ángulos y el ángulo externo, dan a la parte posterior del premolar forma de E con sus tres salientes hacia el lado lingual.

El pm4, es ya muy parecido a los molares, está constituido por dos lóbulos, el posterior es más pequeño que el anterior. Cada lóbulo tiene dos crestas longitudinales, la lingual es casi recta; en cambio, la externa es en forma de V o de U según el desgaste.

En el ejemplar con poco desgaste solamente en la parte anterior de las crestas, la dentina se une; en cambio, en todos los otros la dentina se encuentra rodeada de esmalte; conforme el desgaste se continúa, las crestas se van uniendo hasta formar una sola placa con dos islas ovales de dentina, situada más o menos en el centro de los lóbulos. En la cara externa entre los dos lóbulos y en la base de la cara, existe un pequeño estilo.

Los molares 1 y 2 son iguales al premolar 4, pero el segundo lóbulo tiende a ser más grande, hasta alcanzar un tamaño igual al primer lóbulo en el tercer molar. El m1 presenta mayor desgaste que m2. Los estilos entre los lóbulos están mejor desarrollados que en pm4.

El m3 presenta tres lóbulos, los dos primeros más o menos del mismo tamaño y el tercero muy reducido.

La parte anterior de las crestas del primer lóbulo presentan la dentina continua, así como la parte posterior interna del primer lóbulo y la parte anterior de la cresta externa. El borde posterior interno de la cresta lingual del segundo lóbulo y la parte anterior de la cresta lingual del tercer lóbulo, también se continúa, así como las partes, posteriores de las crestas del tercer lóbulo. Conforme avanza el desgaste, la dentina se va uniendo, sin embargo la parte posterior de la cresta lingual del lóbulo primario no se une con los del segundo lóbulo.

En la cara interna tanto de los dos últimos premolares como de los tres molares, hay unas pequeñas crestas que van de la parte más alta de la corona a la base de la misma.

Dientes superiores.—Los tres premolares están formados por un solo lóbulo, en cambio los molares están formados por dos. El PM2 es el más largo de los premolares. La cara labial está dividida por un ángulo entrante muy cerrado, situado en el primer quinto anterior del diente, después tiene otra entrante más abierta, en la base de la cual no existe ningún estilo. La cara oclusal se encuentra dividida en la mitad por una isla de esmalte que se extiende longitudinalmente, con entrantes y salientes irregulares. La cara lingual también tiene una entrante muy tenue, situada en el primer tercio anterior.

El PM3 es más corto que el PM2, y su estructura más sencilla, consta de dos crestas con dentina enmedio, la labial es recta y la lingual en forma de U. La parte anterior y la posterior de las crestas, se continuan. En la cara interna de la cresta lingual existen dos proyecciones hacia la cara interna de la cresta labial, sin llegar a unirse con ella. En la cara externa existen tres bordes bien marcados que van de la parte más alta del molar a la base de la corona, en donde se juntan formando un borde horizontal en la base. Las crestas bajan de los extremos anterior y posterior de la corona y de la parte media de la misma. El PM4 es igual al anterior, pero ligeramente más corto.

Los tres molares son semejantes entre sí y están formados de dos lóbulos, cada uno de igual magnitud y separados por una entrante lingual en cuya base, en algunos ejemplares existe un estilo más o menos bien desarrollado.

Las crestas labiales de los dos lóbulos de cada molar se continuan entre sí, lo mismo que con la parte anterior y posterior de las crestas labiales, no así los bordes posterior interno de las crestas linguales del primer y segundo lóbulo respectivamente, los cuales están separados entre sí y de la cresta labial.

En la cara externa de los molares existen cinco crestas bien marcadas que bajan de la parte alta de la corona a la base de la misma, en donde se unen. Las crestas se encuentran en la parte anterior del molar, otra en la posterior, una en donde se unen los dos lóbulos y dos más en la parte media de cada lóbulo. Entre cresta y cresta existe una depresión en forma de V ó de U con la parte más profunda hacia la base.

Descripcion de las Astas

De las astas de *Odocoileus halli* sólo se recobraron cinco fragmentos, de los cuales dos están muy destruidos y son muy pequeños para poder sacar alguna conclusión, de los otros tres, el mejor de ellos es el no. 1137 D.P., y forma parte de un cráneo fragmentado de donde se recobraron los occipitales, región basal y fragmentos de los frontales con una parte de asta de 15 cm de longitud y la región basal de otra asta unida al frontal. El corte transversal (Fig. 6) de la base del asta de mayor tamaño es ligeramente ovalado, con el diámetro mayor transversal de 37.3 y el anteroposterior de 29.5. El corte del asta por arriba de la primera punta es más circular, con el diámetro transversal de 35.84 y el anteroposterior de 33.5. Toda la superficie del asta es rugosa; falta el anillo basal por lo que no podemos decir qué forma y tamaño pudo haber tenido. La superficie anterior del asta se abre aproximadamente a 165° con respecto a la superficie del frontal (Fig. 6).

Otro fragmento de asta forma parte de una región frontal (1095 DP) con la base de ambas astas, las cuales se elevan en ángulo de más o menos 170° con respecto a la superficie del frontal. El corte transversal de la misma es de forma circular en sus caras anteriores y laterales pero completamente plana en la cara posterior (Fig. 6). Los diámetros transversal y anteroposterior son respectivamente de 31.8 y 22.8.

Por último, existe un fragmento de asta (1085 DP) que consta de unos 18 cm de la rama principal con la región basal de una punta. El corte transversal de la rama principal antes de la punta (Fig. 6) es ovalado, su diámetro mayor es de 37.3, en cambio el anteroposterior es de 24.0. El corte después de la punta conserva la misma forma ovalada aunque ya no tan marcada, principalmente porque presenta un abultamiento anterointerno; el diámetro transversal es de 26.5 y anteroposterior de 18.1

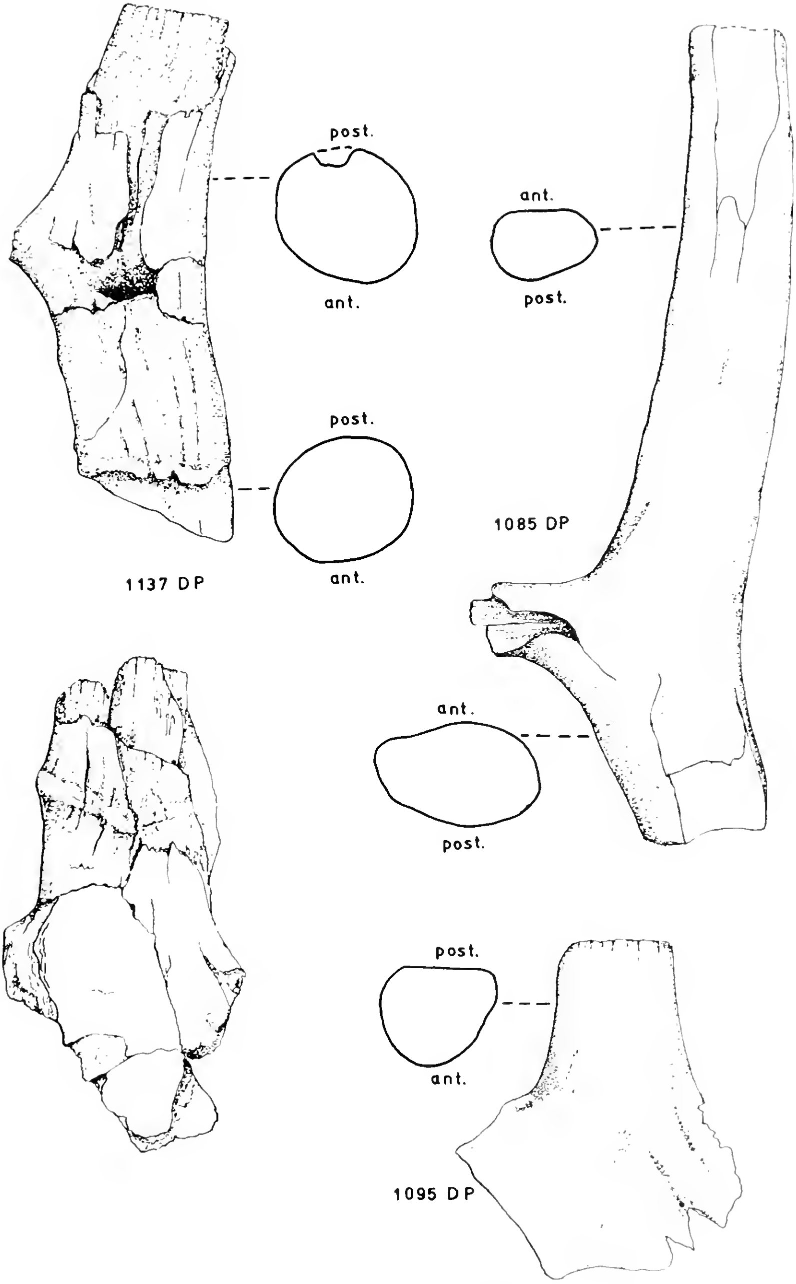

Fig. 6. Diferentes fragmentos de asta de *O. halli* con cortes transversales de los mismos.

Comparación

De todas las especies conocidas, tanto fósiles como vivientes *Odocoileus halli* difiere por su mayor tamaño, que es casi igual al de un pequeño *Cervus*. La única especie que se le parece en tamaño es *Odocoileus brachyodontus* Oelrich, 1953, pero difiere en que las crestas anterointerna y posterointerna están unidas a la cresta transversal, en cambio en *O. brachyodontus* dichas crestas se encuentran separadas. Además, existe diferencia en épocas, ya que *O. brachyodontus* es del Plioceno y *O. halli* es del fin del Pleistoceno.

Notas

Desde el momento en que el material de Tlapacoya fue visto por el Dr. Clayton E. Ray de la Smithsonian Institution, me sugirió la idea de que pudiera corresponder nuestro material a *Sangamona fugitiva*, sin embargo al examinar la descripción de este género y ver el molde del tipo que nos fue enviado por el Dr. Ray, encontramos que difiere mucho. De acuerdo con la descripción original *Sangamona* difiere de los otros venados por carecer de las costillas en las caras externas de los lóbulos de los molares. Dichas costillas están bien marcadas en todos los molares de Tlapacoya; comparando el tipo de *Sangamona* con material de *Odocoileus halli*, encontramos que efectivamente las costillas

CUADRO 1.—MEDIDAS MANDIBULARES Y DE LOS DIENTES MAXILARES DE *Odocoileus halli*.

Medidas mandibulares		No. 1001	No. 1002	No. 1082	No. 1083	No. 1116	No. 1119	No. 1177
pm2	largo	......	......	9.8	10.0	......	10.6	11.8
	ancho	......	......	7.0	6.9	......	6.8	7.0
pm3	largo	......	......	16.3	15.7	......	15.9	15.6
	ancho	......	......	10.1	10.9	......	10.0	9.8
pm4	largo	17.9	18.2	17.6	16.3	17.8	17.8	16.7
	ancho	12.7	12.6	12.7	12.4	12.5	12.6	11.3
m1	largo	18.4	19.4	16.3	16.5	17.1	15.5	17.8
	ancho	13.8	14.0	12.9	12.3	12.9	11.5	13.2
m2	largo	20.4	20.7	20.5	20.4	19.7	20.4	21.0
	ancho	14.5	14.4	14.0	14.7	13.7	13.4	15.1
m3	largo	27.8	28.0	......	27.0	30.0	25.9	24.6
	ancho	13.2	13.2	......	14.4	13.7	13.2	13.9
longitud alveolar		115.3	115.2	105.2	104.5	115.0	111.2	......
mínima altura de la rama mand.		21.9	20.2	20.4	18.5	20.8	......	......
Altura rama bajo m1-2		43.6	44.5	39.8	39.0	38.4	38.1	......

Medidas de los dientes maxilares		No. 1060	No. 1092	No. 1117	No. 1145	No. 1180	Sueltos	
PM2	largo	......	......	......	......	16.2	18.3	17.7
	ancho	......	......	......	......	12.9	15.9	15.5
PM3	largo	16.0	......	......	......	16.4	14.9	16.4
	ancho	16.8	......	......	......	14.3	16.9	19.9
PM4	largo	17.1	......	17.2	......	15.4	......	......
	ancho	17.5	......	......	......	18.7	......	......
M1	largo	22.4	19.7	22.4	......	......	......	......
	ancho	18.3	20.9	20.9	19.5	......	......	......
M2	largo	23.6	21.3	23.7	18.9	......	......	......
	ancho	20.5	23.0	22.7	21.2	......	......	......
M3	largo	23.3	21.8	23.1	20.0	......	......	......
	ancho	18.2	21.4	20.6	21.1	......	......	......

son muy poco marcadas y que la cara externa bajo el paracono y metacono no presenta ninguna costilla, en cambio en este mismo lugar *Odocoileus halli* al igual que todas las otras especies de *Odocoileus*, presentan una costilla que desciende del metacono y paracono.

Sangamona presenta también un estilo entre los dos lóbulos internos, dicho estilo se presenta en la mayoría de los molares de *Odocoileus halli*, así como en otras especies que se pudieron ver, *O. hemionus* y *O. virginianus* en ejemplares y *O. salinae, O. cascensis, O. brachyodontus* en las figuras publicadas en su descripción; otra forma que nos fue sugerida con posibilidad de ser igual a nuestro material fue *Rangifer fricki* Schultz y Howard 1935. Al comparar el material de Tlapacoya con la figura publicada en la descripción original de *R. fricki*, encontramos una semejanza muy estrecha en la forma de los dientes, así como en sus dimenciones. Las únicas diferencias estriban en la longitud de algunos dientes: el segundo premolar inferior es ligeramente más largo en *R. fricki*; en cambio, el tercer molar inferior es más corto que en *O. halli*. Los molares superiores en general son más largos y sobre todo más anchos en *O. halli* que en *R. fricki*. A pesar de que la semejanza en forma es muy estrecha entre *Odocoileus halli* y *R. fricki* y que se asignan a diferentes géneros, preferimos poner la especie *halli* dentro de el género *Odocoileus*, porque como ya se indica, la estructura de los molares no difiere más que en su tamaño mayor, pero no en la estructura esencial de los dientes, creemos que más bien *Rangifer fricki* puede ser un forma de *Odocoileus*.

Odocoileus halli ha sido nombrado en honor al Dr. E. Raymond Hall, como un estimonio de gratitud por todas las enseñanzas y atenciones que siempre he recibido de él.

DISCUSION

Las excavaciones realizadas en el cerro de Tlapacoya, México, durante el año de 1966, nos dan por primera vez dentro del llamado Valle de México, algunas fechas relacionadas con la fauna existente en dicha área. Los restos de animales fueron encontrados al realizar dos calas perpendículares a la línea de la falda del cerro. Dentro de los muchos estratos que se identificaron, dos de ellos proporcionaron la mayoría de los huesos estudiados.

El estrato más antiguo en que se encontraron huesos, está formado por cenizas volcánicas que en este punto se hallan en contacto con la roca basal y que tienen un espesor de un metro aproximadamente. La edad de esta capa no se determinó directamente, pero se infiere que sea mayor a los 24,000 años, ya que los restos procedentes de una capa superior dieron la fecha antes indicada.

La fauna de este estrato está formada por numerosos restos de aves acuáticas y de mamíferos como *Pappogeomys* sp., *Sylvilagus floridanus, Neochoerus pinckneyi, Lutra canadensis, Peromyscus maldonadoi, Odocoileus virginianus,* y *Mormoops megalophylla.*

La asociación de las aves acuáticas con mamíferos como *Neochoerus* y *Lutra*, nos hacen pensar que hace 24,000 años la región de Tlapacoya era mucho más húmeda y que debió de existir un lago, en cuyas márgenes la vegetación era exuberante. Por los restos encontrados en esta capa, es difícil dicernir el tipo de clima existente en esa época con respecto a la temperatura, ya que la asociación faunística no es exclusiva de tierras calientes, aunque sí se le encuentra con preferencia en tal tipo de climas; además, la presencia de *Mormoops*, género de murciélago que muy raramente se encuentra en climas frios y que vive más bién en lugares cálidos, nos inclina a pensar que el clima de esa época ero más cálido y húmedo que el actual.

El otro estrato en que fueron abundantes los restos óseos, se encontró principalmente en la trinchera alfa y data de 22,000 años aproximadamente.

Los restos encontrados en este sitio, fueron principalmente huesos de mamíferos grandes y formaban una aglomeración muy marcada alrededor de unas grandes piedras que rodeaban un claro, en donde se encontró carbón, así como restos de utensilios humanos, ha sido interpretado como un hogar del hombre prehistórico.

Aunque existen restos de pequeños mamíferos, la gran mayoría corresponden a *Odocoileus halli*, especie de venado muy grande y que sin duda alguna proporcionó al hombre buena cantidad de carne. También se encontró en la trinchera beta, pero no se hallaron restos de este animal en los más antiguos de 24,000 años, lo que nos hace suponer que dicho venado fue un inmigrante reciente, exterminado por la acción del hombre; en cambio *Odocoileus virginianus*, cuya talla es mucho menor que *O. halli*, ya existía en el Valle de México desde hace más de 24,000 años y ha logrado resistir desde entonces el impacto de la acción humana, ya que este venado es uno de los pocos mamíferos de tamaño regular que todavía se encuentran en los bosques de coníferas alrededor del Valle de México.

Summary

The Departamento de Prehistoria of the Instituto Nacional de Antropologia e Historia has been working for several years at Tlapacoya in the Valley of Mexico, looking for remains of prehistoric man. In 1966, two trenches were dug on the south side of Cerro Tlapacoya. Only two of the many strata found in the trenches furnished good quantities of bones. The oldest is a volcanic ash, which at this point is on bed rock. The exact age of this stratum is unknown, but the one above it was aged by C^{14} analysis as 24,000 years old.

Bones in this ash belong mainly to birds. Among the mammals it was possible to identify *Pappogeomys* sp., *Sylvilagus floridanus*, *Neochoerus pinckneyi*, *Lutra canadensis*, *Peromyscus maldonadoi*, *Odocoileus virginianus*, and *Mormoops megalophylla*.

The association of aquatic birds principally (cormorants, herons, grebes, etc.) and mammals like *Lutra* and *Neochoerus* indicates that 24,000 years ago the region of Tlapacoya was more humid than now; probably the vegetation was more luxuriant than in Recent times. It is possible also that the average temperature was higher than it now is, as indicated by the presence of *Mormoops*, a bat which is abundant in warm regions. On the other hand, the rest of the mammalian fauna is found today in both warm and cool climates. Thus the fauna does not clearly indicate a particular climate.

The other stratum with bones was found in the trench alpha and was dated as 22,000 years old. Bones from this level were of large mammals and it is believed that they were brought in by man, because they were grouped around several big stones and associated with charcoal. Most of the bones belong to a big deer, *Odocoileus halli*, here described on the basis of its large size—larger than any other known *Odocoileus*. Comparison of *O. halli* with *Sangamona* reveals that they differ in the construction of the lingual ridges of the molars.

Other remains found associated with *O. halli* were identified as follows: *Urusus americanus*, an almost complete skeleton; *Sylvilagus cunicularius*, *Pappogeomys* sp., *Neotoma mexicana*, *Microtus mexicanus*, *Canis* sp., *Procyon lotor* and *Odocoileus virginianus*. All these mammals except the two first named still live today in the Valley of Mexico.

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BIOGEOGRAPHY OF SOUTHWESTERN BOREAL AND DESERT MAMMALS

BY

JAMES S. FINDLEY

The southwestern part of the United States is a funnel-shaped region, consisting ecologically of an eastern and a western desert bisected by forested highlands through which only one or two lowland gaps permit the interchange of desert organisms. During later Pleistocene time the two deserts have been sundered and reunited, and the biota of the forested highlands has alternately spread and been fragmented into island-like refugia. It is my thesis that these historical events have been the principal agents in the remarkable diversification of mammals in the Southwest. This conclusion is reached primarily on the basis of the observation of contemporary distribution and variation patterns and secondarily on the basis of deductions from known facts of southwestern climatic history.

If the patterns of distribution and variation of mammals appeared non-correlated, one might conclude that a diversity of factors had shaped the patterns. If on the other hand certain patterns reappear commonly, one might suppose that only a few factors were involved, and it might be possible to identify these. It seems to me that the kinds of patterns displayed by southwestern mammals are indeed limited and often similar. The most frequent of these patterns are described in the following section. I have not attempted to be exhaustive, hoping that the selected examples are typical and point the way to the overall picture.

THE BOREAL PATTERN

Boreal mammals are those that occupy montane coniferous forest zones where soil moisture is available and aridity is not an important limiting factor. The major features of the boreal pattern are:

1. Reduction of number of kinds of strictly boreal species with decreasing latitude, even given seemingly comparable habitats.
2. Gradual replacement of northern boreal species with others at successively lower latitudes.
3. Altitudinal zonation of northern and southern boreal species in areas of sympatry.
4. Increase in lower altitudinal limits of northern kinds at successively more southerly latitudes.

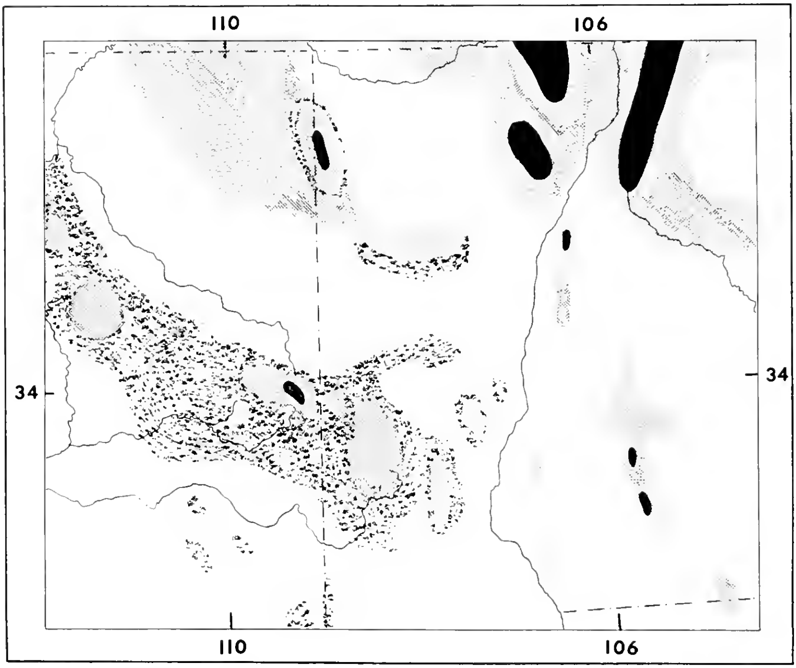

FIG. 1. Geographic distribution of three species of *Eutamias:* black, *E. minimus;* blotched pattern, *E. dorsalis;* stipple, *E. quadrivittatus* group.

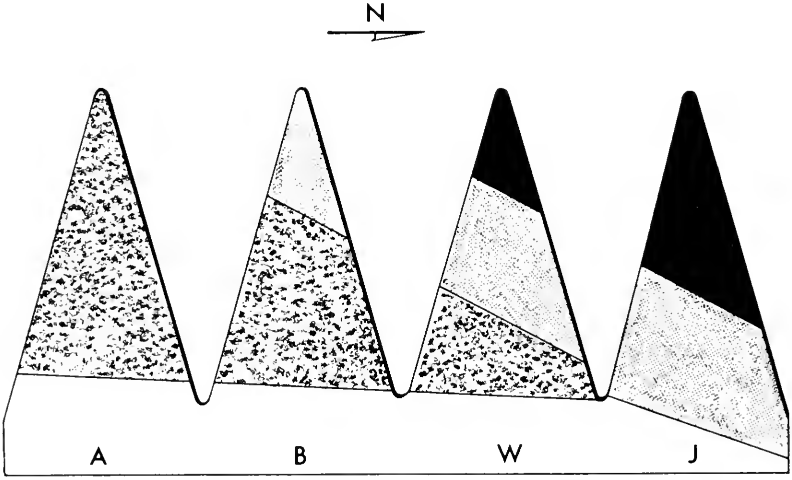

FIG. 2. Altitudinal relationships of three species of *Eutamias* on southwestern mountain ranges: black, *E. minimus;* stipple, *E. quadrivittatus* group; blotched pattern, *E. dorsalis;* A, Animas Mountains; B, Black Range; W, White Mountains; J, Jemez Mountains.

Selected examples of southwestern boreal mammals displaying various aspects of this pattern follow.

Chipmunks of the Genus *Eutamias*

Figures 1 and 2 show geographic and ecologic distribution of chipmunks in a part of the Southwest. Using the White Mountains of Arizona as a focal point for discussion, it can be seen that in the higher parts of this range the least chipmunk, *Eutamias minimus*, occurs in a rich, mesic, mixed coniferous forest along with the gray-necked chipmunk, *E. cinereicollis*, which is found to the lower limit of the ponderosa forest and there overlaps, and is replaced by, the cliff chipmunk, *E. dorsalis*. The latter may, under suitable circumstances, occur nearly to sea level in the Sonoran desert. *Eutamias dorsalis* is widespread around the margins of the Sonoran desert, occurring in chaparral, encinal, pinyon-juniper woodland, and similar xeric habitats. However in the absence of other chipmunks, this species may occur in pine or mixed coniferous forest. The gray-necked chipmunk, together with its close relatives and

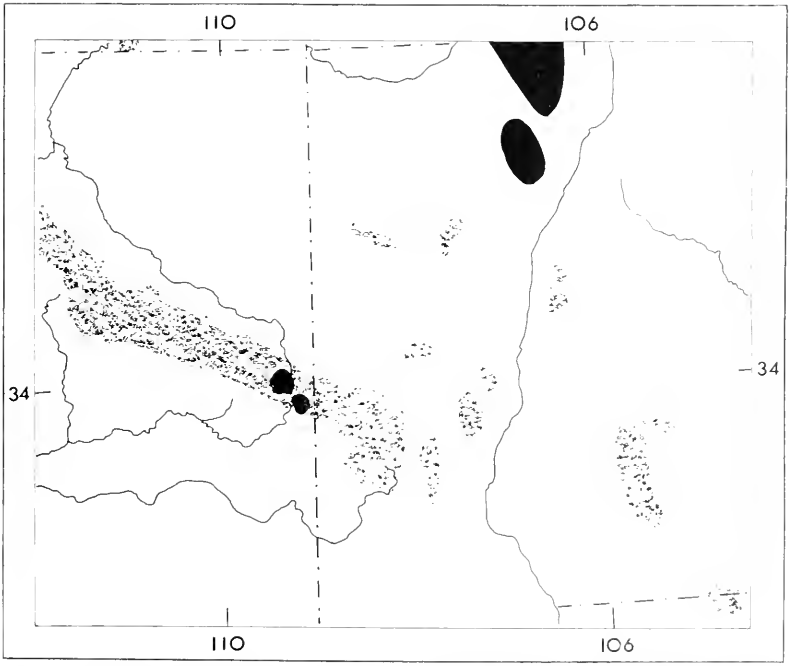

FIG. 3. Geographic distribution of two species of *Microtus*: black, *M. montanus*; blotched pattern, *M. mexicanus*.

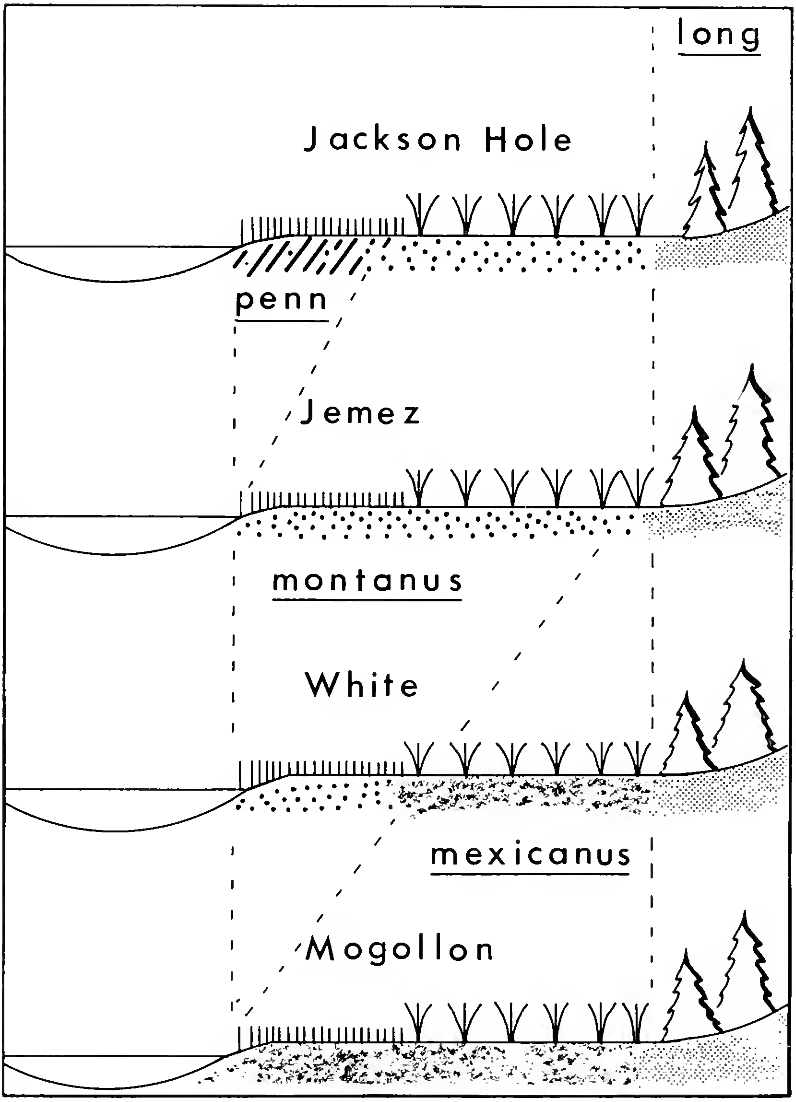

FIG. 4. Diagram of habitat relationships of four species of *Microtus* on three southwestern mountain ranges and in Jackson Hole, Wyoming.

ecological vicariants, *E. quadrivittatus, E. canipes,* and *E. bulleri,* is widespread in mixed coniferous and ponderosa forest. In the absence of *dorsalis,* the species *quadrivittatus* and *canipes* occur down to the lower edge of the woodland, and, in places, even into the grassland. *Eutamias minimus,* in the Southwest, is limited to some of the most mesic ranges, but farther north occurs over wide continuous areas, even into the sage-grassland in Wyoming and adjacent states. That the least chipmunk is well adapted to boreal conditions is suggested by its extensive postglacial spread across the Canadian coniferous forest.

Voles of the Genus *Microtus*

Figures 3 and 4 depict geographic and ecologic distribution of several species of *Microtus* in the Southwest. Again using the White Mountains as a focal point, we find there the northern species, *M. montanus,* living in the most mesic microtine habitat—grass-sedge meadows around streams and ponds. In drier grasslands at the same altitude, and down to the lower edge of ponderosa forest occurs *M. mexicanus.* The montane and Mexican voles seem to occupy somewhat analogous positions to the least and gray-necked chipmunks, respectively, but there is no microtine analog to the cliff chipmunk. If we look below the pine forest in the Southwest for a grazer that is a grass-tunnel dweller, we find various species of the cricetine genus *Sigmodon,* an animal much more tolerant of xeric conditions than any *Microtus.* Aside from its drought-tolerant qualities, *Sigmodon* is so *Microtus*-like in reduction of countershading, reduction of appendages, burrowing and tunnel-dwelling propensities, diurnal activity, grazing habit, and ability to respond to grass growth with population irruptions, that it might be thought of a "microtoid" cricetine. The species *M. longicaudus* is not primarily grass-dwelling, but rather a species of the forest edge, and thus does not enter directly into competition with the other two *Microtus,* nor is it closely related to them, usually being placed in another subgenus. Thus its distribution in the Southwest is not directly related to the history of the other two species. On those ranges where the montane vole is not found, the Mexican vole occupies the most mesic habitats as well as more xeric areas, and I earlier (Findley and Jones, 1962) postulated a competitive relationship between the two species, *mexicanus* invading those places in post-pluvial times where *montanus* had become extinct.

Rabbits of the Genus *Sylvilagus*

Geographic and ecologic distribution of three species of *Sylvilagus* in the Southwest is shown in Figures 5 and 6. The higher elevations of the White Mountains are inhabited by S. *nuttallii.*

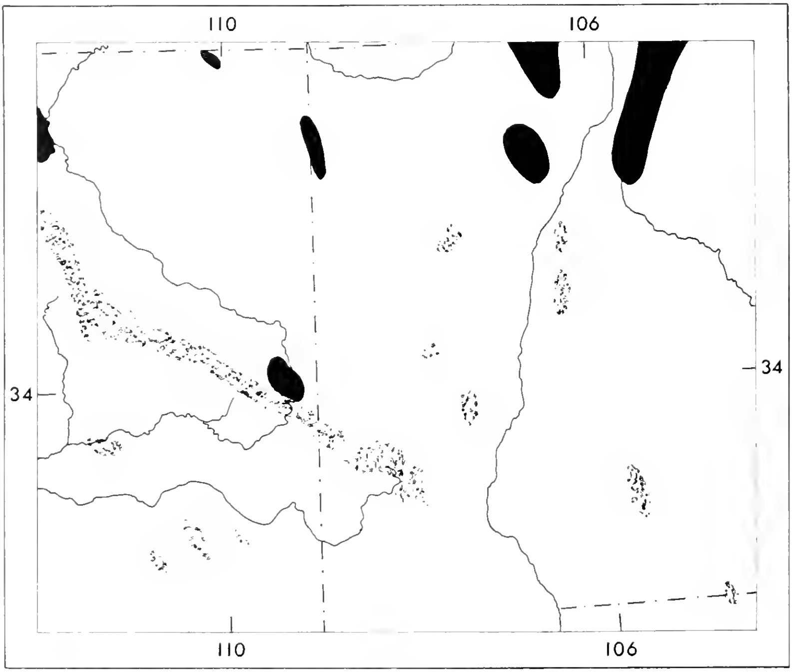

FIG. 5. Geographic distribution of three species of *Sylvilagus:* black, S. *nuttallii*; blotched, S. *floridanus;* white, S. *audubonii.*

More southerly and lower ranges are occupied by S. *floridanus,* which occurs so low as 2000 feet in Arizona (Hoffmeister and Lee, 1963). In the woodlands, grasslands, and deserts at all lower elevations in the Southwest occurs S. *audubonii.* Farther north S. *nuttallii* is more continuously distributed and often occurs at low elevations in the absence of the other two species. That S. *floridanus* is not, at first glance, a convincing analog of the *Eutamias quadrivitatus* group and *Microtus mexicanus* cannot be debated. *Sylvilagus floridanus* is widely distributed in the eastern United States and in Mexico, and attempting to derive the species by pluvial abandonment in the Southwest may seem to be in violation of the precepts of Occam's razor. However, the range of S. *floridanus* in the Southwest is highly disjunct, and western populations are largely separated from those to the east. The populations of the region, including those of Mexico, are quite variable, and it seems to me that the conspecificity of this widespread assemblage is far from obvious. There is at least a possibility that the montane, forest-

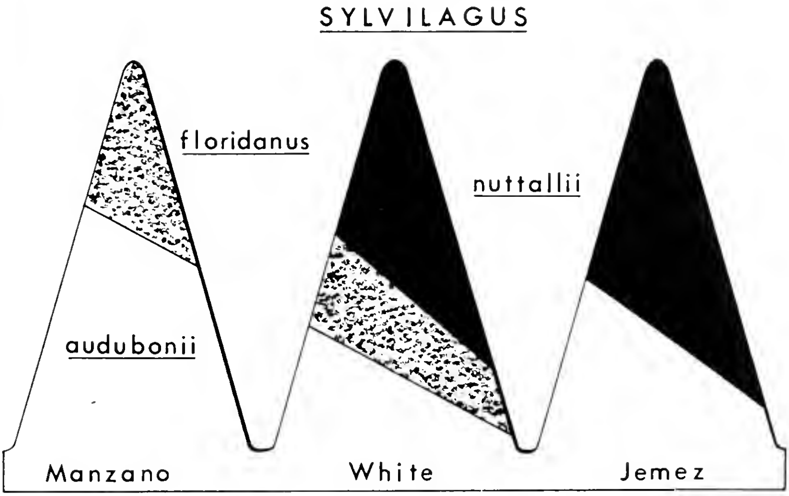

FIG. 6. Diagram of altitudinal relationships of three species of *Sylvilagus* on selected mountain ranges in the Southwest.

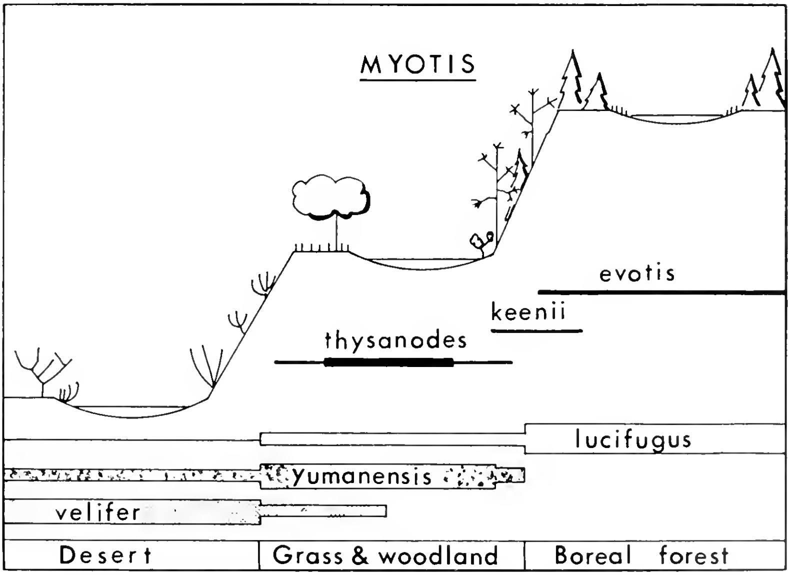

FIG. 7. Diagram of habitat relationships of six species of *Myotis* in the Southwest.

dwelling *S. floridanus* of the Southwest and the Sierra Madre Occidental is a derivative of the closely related *S. nuttallii.* Serological

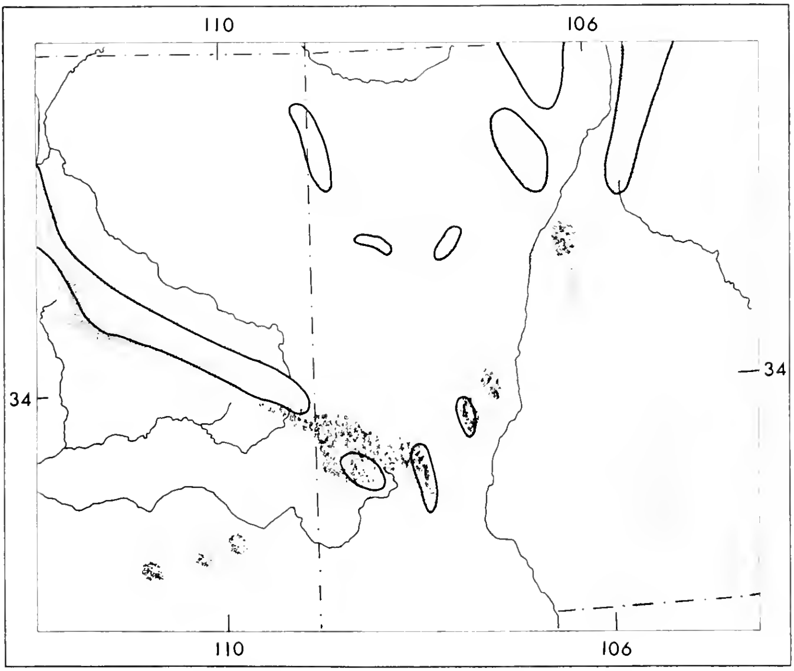

FIG. 8. Distribution of bats of the *Myotis evotis* group: solid lines enclose range of *M. evotis;* blotched pattern, *M. keenii;* stipple, *M. thysanodes.*

and karyological studies are strongly indicated for this group of mammals.

Bats of the Genus *Myotis*

Three groups of three species each may be delineated among the *Myotis* of the Southwest. (1) The *lucifugus* group, consisting of *lucifugus* (including *occultus*), *yumanensis,* and *velifer,* alike in having unkeeled calcars, large feet, relatively short ears, and relatively short broad rostra with relatively large molars, the paralophs, metalophs, and hypocones of which are well-developed. Usually these bats are found near sources of permanent water of relatively large size. (2) The *evotis* group, consisting of *evotis, keenii* (races *apache* and *auriculus*), and *thysanodes,* alike in having long ears, relatively long, slender rostra, slightly keeled or non-keeled calcars, a tendency to have a fringed trailing edge to the uropatagium, and upper molars with reduced or absent lophs, and a reduced hypocone. (3) The *volans* group, consisting of *volans, leibii* (formerly

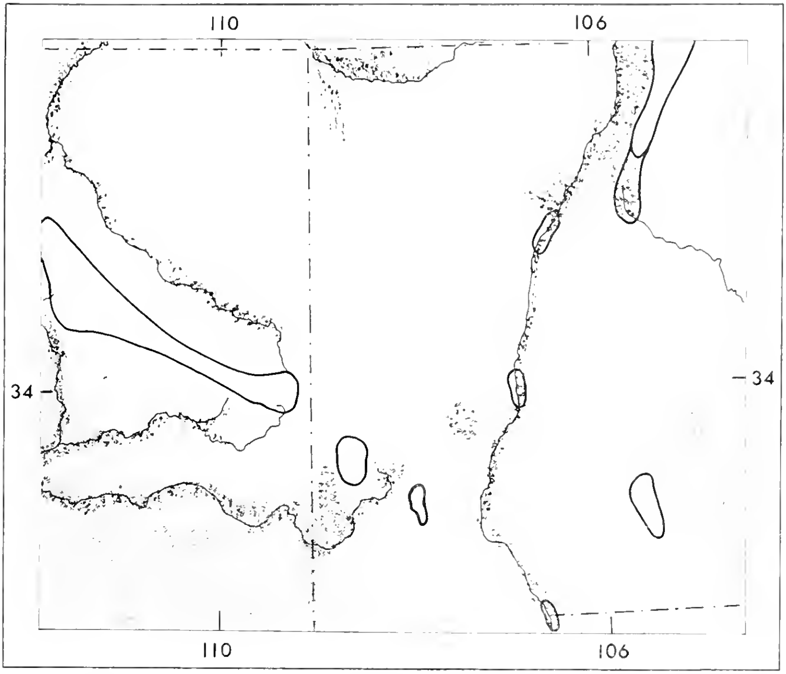

FIG. 9. Distribution of bats of the *Myotis lucifugus* group: solid lines enclose range of *M. lucifugus*; blotched pattern, *M. yumanensis;* stipple, *M. velifer.*

subulatus), and *californicus*, alike in small size, medium ears, strongly keeled calcar, small feet, and *lucifugus*-like molars. Summer geographic and ecologic distribution of some of these species in the Southwest is shown in Figures 7 through 9. In each case, one member of a species group is definitely boreal, one is most common at middle elevations in pine forests and woodlands, and one is a desert and grasslands species. The *lucifugus* group requires special comment in this regard. Maternity colonies of *M. lucifugus occultus* and *M. yumanensis* occur at some rather low elevations as at Socorro, New Mexico, and Blythe, California. Here, however, the colonies are located near large permanent bodies of water, the Rio Grande and the Colorado River. In the postpluvial retreat of these water-loving species, it might be expected that they would persist in the few water-rich lowland habitats, especially the more arid-adapted *yumanensis*, which, of course, is much more common in southwestern lowlands than is *lucifugus*.

THE DESERT PATTERNS

Desert mammals are those living in lowlands where aridity exerts a dominant limiting and molding force on the animals. Desert mammals in the region under consideration exist in an eastern (Chihuahuan) center and a western (Sonoran) center, and frequently extend from one center to the other through the lowland gap (the Deming Plain) extending across southwestern New Mexico and southeastern Arizona. Several patterns seem to recur among these mammals.

1. Widespread continuous distribution through both deserts with little striking geographic variation. *Dipodomys merriami* seems typical of this pattern. *Perognathus penicillatus* recently studied by Hoffmeister and Lee (1967) seems to show several concordant character shifts, one of which coincides with the Continental Divide. Other species include *Notiosorex crawfordi, Sylvilagus audubonii, Lepus californicus, Peromyscus eremicus, Onychomys torridus,* and *Neotoma albigula.*

2. As above but with one or more sharp character breaks, often in the area of the Continental Divide, or between southern and central Mexican Plateau populations. Unpublished results of a study by myself and Gerald L. Traut reveal that the desert bat *Pipistrellus hesperus,* while showing numerous local adaptations, is divisible into a large eastern and a small western population. Whereas in some areas size of this species is responsive to climate, this is not the explanation for the present distribution of the two populations. The two kinds contact, with a steep clinal change in size, along the Continental Divide (Fig. 10).

The widespread hispid cotton rat, *Sigmodon hispidus,* occurs in parts of the southwestern deserts where a cover of grass is available. While these animals extend across the Deming Plain, Mohlhenrich (1961) thought that they had entered this area recently, and Gennaro (1968) concurred as a result of his finding that cotton rats in the Deming Plain were not adaptively colored. Gennaro thought that these animals had entered the Deming Plain from both east and west. Recently Earl Zimmermann (personal communication) has revealed that animals from southern Arizona have a fundamental chromosome number of 38, while those from Lubbock, Texas, to the east have a fundamental number of 52 to 54. It may well be that the two differently colored hispid cotton rats of the Deming Plain also differ karyologically, providing an important example of this pattern.

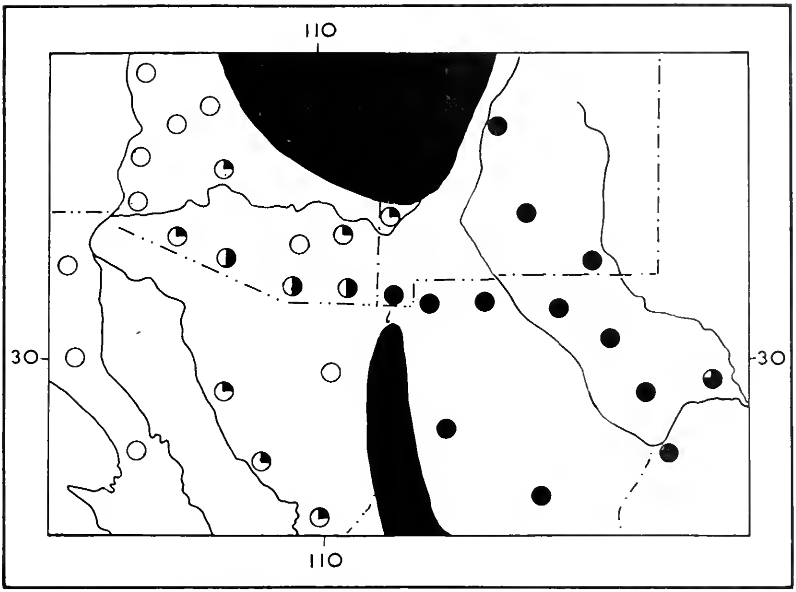

FIG. 10. Size in *Pipistrellus hesperus* based on 10 size variables. The darker the circle the larger the bats from that area. Black areas are forested highlands.

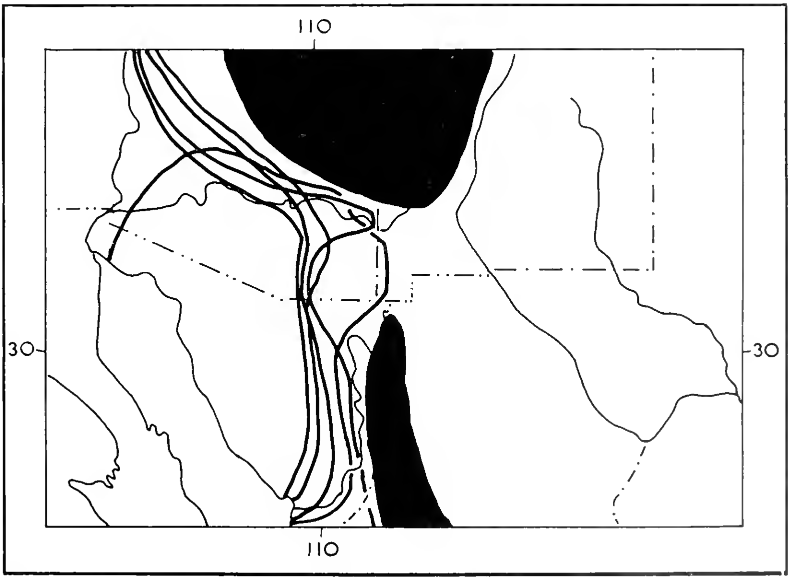

FIG. 11. Eastern limits of western desert species described in text. Black areas are forested highlands.

3. Largely confined to the Sonoran desert, barely extending to the Continental Divide area. Selected species are *Choeronycteris mexicana, Perognathus baileyi, Macrotus waterhousii, Spermophilus tereticaudus, Perognathus longimembris, Perognathus amplus, Dipodomys deserti,* and *Peromyscus merriami.* Eastern limits of selected species in this category are shown in Figure 11.

4. Largely confined to the Chihuahuan desert, barely extending into the Continental Divide area. Selected species are *Spermophilus spilosoma, Perognathus merriami, Perognathus flavus, Perognathus hispidus, Dipodomys spectabilis, Dipodomys ordii, Onychomys leucogaster, Reithrodontomys montanus, Peromyscus leucopus,* and *Neotoma micropus.* Western limits of selected species from this category are shown in Figure 12.

5. Like 3 or 4 above, but with a close relative in the other desert. Determination of this situation depends upon sound knowledge of relationships, frequently not available. That the white-sided jackrabbits, *Lepus callotis* and *L. alleni,* are closer to each other than to other species seems accepted by students of the group. Ranges of the two are basically Chihuahuan and Sonoran, respectively. The antelope squirrels, *Ammospermophilus,* show a similar pattern, more striking because of disjunction, and because the trans-Coloradan isolate, *A. leucurus,* has encircled the Chihuahuan desert from the north and thus closely approaches its Chihuahuan relative *(A. interpres). Perognathus intermedius* and *P. nelsoni* seem to fit this pattern although here the Sonoran isolate, *P. intermedius,* has extended well into the Chihuahuan desert, whereas its Chihuahuan relative, *P. nelsoni,* seems to have been rather sedentary. Ranges of two of these species pairs are shown in Figure 13.

DEVELOPMENT OF PATTERNS

That major ages of cool, moist climates, recurring during the Pleistocene, caused depression and coalescence of montane forests in the Southwest seems established beyond reasonable doubt. This is the only easily acceptable explanation for the existence of southwestern montane boreal islands.

If more than one cycle of pluvial-interpluvial conditions affected the Southwest, and if montane highlands existed there to act as interpluvial refugia for boreal organisms, it is possible to hypothesize a series of events that could have led to the present diversification of the southwestern boreal and sub-boreal mammalian fauna.

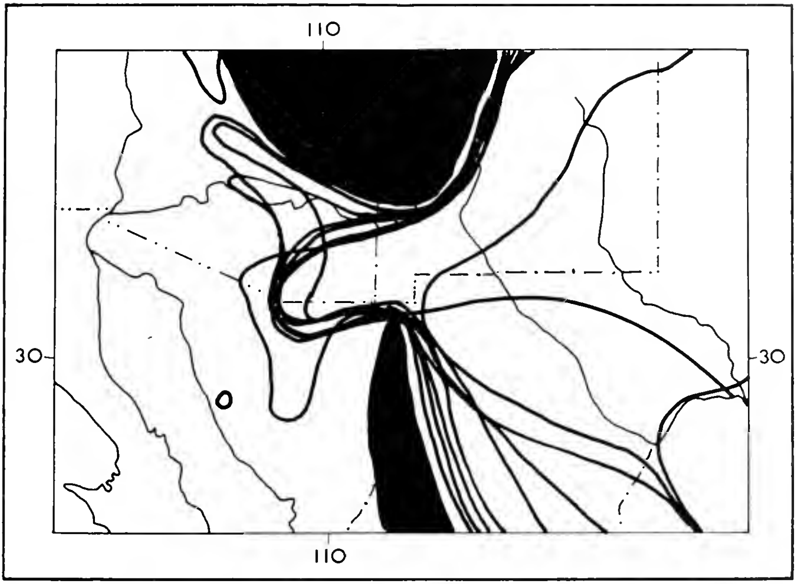

FIG. 12. Western limits of eastern desert and grassland species described in text. Black areas are forested highlands.

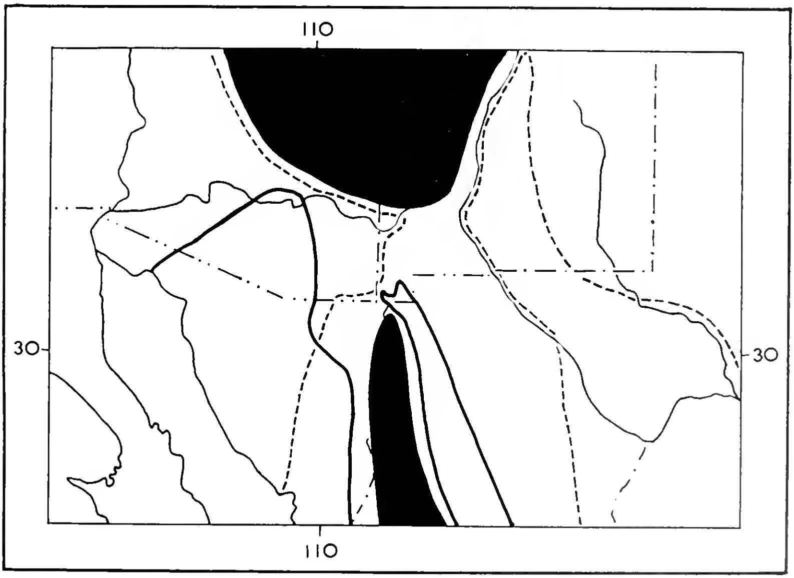

FIG. 13. Ranges of related pairs of species: solid lines, *Lepus alleni* (west) and *L. callotis* (east); dashed lines, *Ammospermophilus harrisii* (west) and *A. interpres* (east).

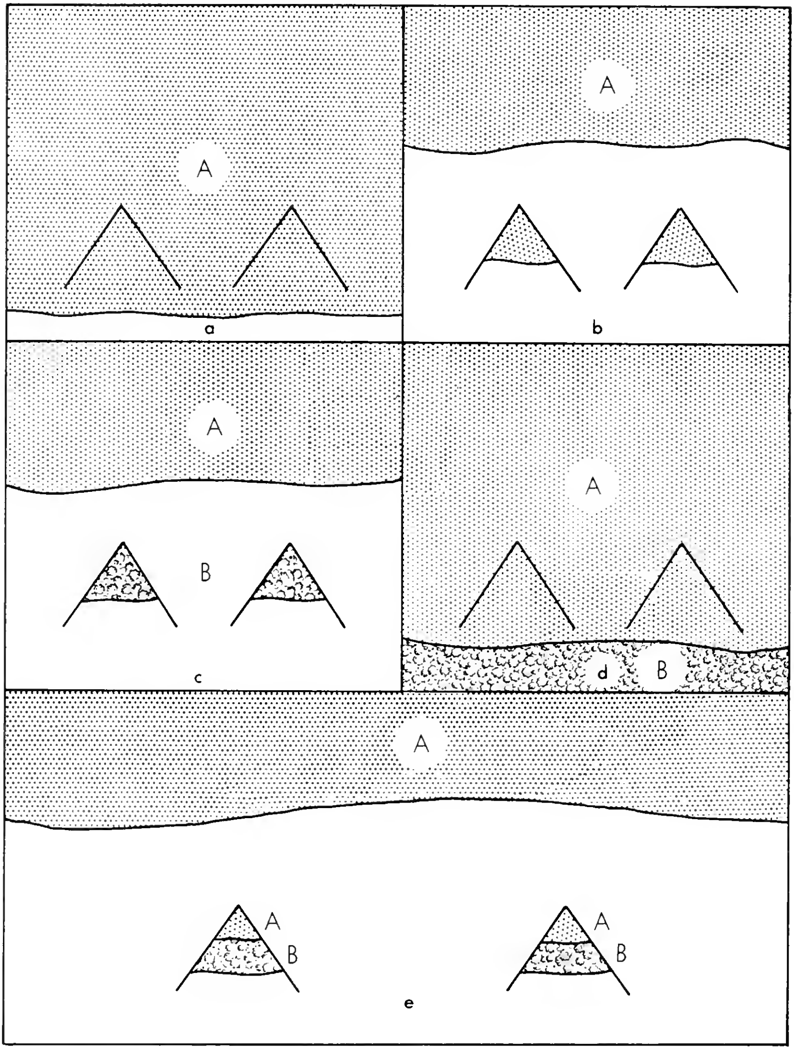

Fig. 14. Diagrams showing hypothetical sequence of events in development of zonation of boreal mammals in the Southwest. See text for explanation.

These hypothetical events are diagrammed in Figure 14, where the stippled pattern represents the distribution of a boreal mammalian taxon, moving northward and southward, as well as up and down mountain slopes, with Pleistocene climatic fluctuations. Figure 14A represents conditions during a pluvial time when boreal species A is continuously distributed in the Southwest. In figure 14B, interpluvial climates have resulted in northward and upward withdrawal of species A with its isolation on a mountain range. Figure 14C represents a later time during the interpluvial when the montane isolate has differentiated, perhaps in response to the arid marginally boreal conditions in which it was trapped as well as through the vagaries of random genetic phenomena, and now is different from its northern relative and hence designated B, and shown with a different pattern. Figure 14D shows another pluvial time. Species A and B have both moved southward, B, by virtue of its adaptation to less boreal ´conditions, being commonest in lower and more southern areas. Note that A and B may coexist and hence are considered to have speciated. Figure 14E depicts another interpluvial. Species A and B have moved northward and upward. On the mountain both are now isolated, A, still more borealy adapted than B, occupying higher more mesic areas. A continuation of this cycle of events might result in still more complex stratification of boreal mammals. Such a situation would result only if the taxon involved *could* adapt to the somewhat more arid conditions obtained on small boreal islands. Many boreal isolates would become extinct with each interpluvial, leaving no descendants.

If the postulated series of events ever took place, we might expect to find some cases of closely related, probably congeneric species occupying successive altitudinal zones, or at least local habitats differing in available moisture, on southwestern mountain ranges.

With each expansion of the boreal environment during pluvial times, the highlands of the Deming Plain must have been largely unavailable to desert mammals with the result that Sonoran and Chihuahuan segments of the ranges of many species must have been separated from one another. Under these circumstances, divergence of the two segments could have proceeded in response to differential selective pressures and random phenomena, with the following possible results. (1) Elimination of one segment of the population. With postpluvial spread of desert organisms the surviving population reoccupies the entire desert area, as has *Dipodomys merriami.* (2) The two segments differentiate but do not attain reproductive isolation, hence secondary intergradation takes place when they reestablish contact, as seems to be the case with *Pipistrellus hesperus.* (3) Only one population survives, but fails to reoccupy the entire desert area, perhaps because it has become too dependent on low or high desert conditions. Examples might be *Spermophilus terecti-*

caudus and *S. spilosoma.* (4) The two populations attain reproductive isolation. Perhaps there are no cases of this among mammals where the specific level of the populations is demonstrated by natural sympatry, though this may be an artifact of our imperfect knowledge of degrees of relationships between species. However, there seems little doubt that *Lepus callotis* and *L. alleni* are specifically distinct, and many species pairs such as the two *Onychomys* may be examples of this situation.

Some patterns suggest that in immediate postpluvial times eastern grassland species spread westward across the Deming Plain into the grasslands of southern Arizona. Subsequent progressive aridity limited these grassland species to grassland zones between desert and encinal on many desert mountain ranges, thus resulting in doughnut shaped relict ranges for some species such as *Dipodomys ordii* in southern Arizona. Of course, such grassland species may have existed on both sides of the Continental Divide during pluvial times, since pluvial grasslands were evidently widespread in southern Arizona and in Sonora.

It is evident that repeated dividing and reuniting of deserts could provide the mechanism for the proliferation of desert species.

SUMMARY

So far back in the Pleistocene as the present physiography has existed in the Southwest, we may imagine an oscillating series of boreal expansions coupled with desert contractions, alternating with desert expansions coupled with boreal retreats. The former phases resulted in desert speciation, the latter in boreal speciation. It seems to me likely that the majority of distribution and variation patterns in the Southwest and indeed in all of western North America will be found to be largely shaped by these events.

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HOLOTYPES OF RECENT MAMMALS IN THE MUSEUM OF NATURAL HISTORY, THE UNIVERSITY OF KANSAS

BY

J. Knox Jones, Jr., and Hugh H. Genoways

Various museums in recent years have published lists of type specimens housed in their collections. Such lists provide a useful point of reference for systematists and, for that reason, have been encouraged by the International Council of Museums. In 1968, that organization issued "A preliminary list of catalogues of type specimens in zoology and palaeontology," compiled by A. W. F. Banfield, and a revised list is planned for 1971. This catalogue of holotypes of mammals in The University of Kansas Museum of Natural History is particularly appropriate for the present volume, because Professor E. Raymond Hall was directly responsible for the descriptions of 20 taxa here listed, and was instrumental in arranging support for field work that resulted in the collection of many others.

The first type specimen of a mammal designated from the collections at Kansas was the holotype of "*Reithrodontomys dychei*," described by J. A. Allen (1895:120). This specimen, originally KU (old series) 5232, was renumbered as 10127/8431 in the mammal collection of the American Museum of Natural History, where it now is housed. Similarly, the holotype of "*Mimon cozumelae*," named by E. A. Goldman (1914:75), previously was in the collection at Kansas (original number, if any, unknown), but was presented to the U. S. National Museum, where it now is deposited as USNM 203191.

Ninety-nine holotypes and one allotype were among the nearly 120,000 specimens of Recent mammals housed in the Museum of Natural History as of December 31, 1968. These include two insectivores, 17 bats, five lagomorphs, 73 rodents, and two carnivores. Four of the holotypes—*Nycteris vinsoni* Dalquest, *Scotophilus alvenslebeni* Dalquest, *Eumops perotis renatae* Pirlot, and *Ochotona princeps howelli* Borell—were donated to the museum subsequent to the original description. Additionally, two holotypes of the rodent genus *Ochrotomys* are designated in this volume.

LIST OF HOLOTYPES

In the following list, holotypes are arranged under the name by which they were originally described. Condition of specimens and current nomenclatorial status of taxa are mentioned where appropriate. Under each ordinal name, genera are listed phylogenetically (those from North America after Hall and Kelson, 1959), whereas species and subspecies are arranged alphabetically.

INSECTIVORA

Cryptotis euryrhynchis Genoways and Choate, Proc. Biol. Soc. Washington, 80:203, December 1, 1967.

Holotype.—Adult male, skin and skull, KU 107143, from Volcán de Fuego (also called Volcán de Colima), 9800 ft., Jalisco; obtained July 10, 1966, by Percy L. Clifton, original number 11059.

Remarks.—Braincase of skull smashed and coronoid process of left ramus broken.

Scalopus montanus Baker, Univ. Kansas Publ., Mus Nat. Hist., 5:19, February 28, 1951.

Holotype.—Adult male, skin, skull, and body skeleton, KU 35668, from Club Sierra del Carmen, 2 mi. N and 6 mi. W Piedra Blanca, Coahuila; obtained April 7, 1950, by J. R. Alcorn, original number 11093.

CHIROPTERA

Nycteris vinsoni Dalquest, Jour. Mamm., 46:256, May 20, 1965.

Holotype.—Adult female, skin and skull, KU 105221, from S bank Save River, 212 km. SSW Beira, Mozambique; obtained October 8, 1963, by Walter W. Dalquest, original number 18739.

Leptonycteris nivalis longala Stains, Univ. Kansas Publ., Mus. Nat. Hist., 9:355, January 21, 1957.

Holotype.—Adult female, skin and skull, KU 33087, from 12 mi. S and 2 mi. E Arteaga, 7500 ft., Coahuila; obtained July 11, 1949, by W. K. Clark, original number 787.

Remarks.—Regarded as a synonym of *Leptonycteris nivalis* (Saussure, 1860) by Davis and Carter (1962:194).

Sturnira ludovici occidentalis Jones and Phillips, Univ. Kansas Publ., Mus. Nat. Hist., 14:477, March 2, 1964.

Holotype.—Adult female, skin and skull, KU 92798, from Plumosas, 2500 ft., Sinaloa; obtained August 31, 1962, by Percy L. Clifton, original number 2939.

Remarks.—Canine and first premolar of right ramus missing.

Natalus mexicanus saturatus Dalquest and Hall, Proc. Biol. Soc. Washington, 62:153, August 23, 1949.

Holotype.—Adult male, skin and skull, KU 23815, from 3 km. E San Andreas [=Andrés] Tuxtla, 1000 ft., Veracruz; obtained January 10, 1948, by Walter W. Dalquest, original number 8621.

Remarks.—Hole in the mid-ventral region of skin; left upper canine missing. Arranged as *Natalus stramineus saturatus* by Goodwin (1959:7).

Regarded as a synonym of *Natalus stramineus mexicanus* Miller, 1902, by Handley (1966:770).

Myotis argentatus Dalquest and Hall, Univ. Kansas Publ., Mus. Nat. Hist., 1:239, December 10, 1947.

Holotype.—Adult male, skin and skull, KU 19228, from 14 km. SW Coatzocoalcos, 100 ft., Veracruz; obtained February 2, 1947, by Walter W. Dalquest, original number 7052.

Myotis elegans Hall, Univ. Kansas Publ., Mus. Nat. Hist., 14:163, May 21, 1962.

Holotype.—Adult female, skin and skull, KU 88398, from 12½ mi. N Tihuatlán, 300 ft., Veracruz; obtained September 24, 1961, by Percy L. Clifton, original number 985.

Remarks.—Right upper incisors and canine, left upper canine and second small premolar, and lower left first molar missing, both zygomatic arches broken, and both auditory bullae separated from skull.

Myotis evotis auriculus Baker and Stains, Univ. Kansas Publ., Mus. Nat. Hist., 9:83, December 10, 1955.

Holotype.—Adult female, skin and skull, KU 55110, from 10 mi. W and 2 mi. S Piedra, 1200 ft., Sierra de Tamaulipas, Tamaulipas; obtained June 9, 1953, by Gerd H. Heinrich, original number 7061.

Remarks.—Skin with hole along ventral slit. Arranged as *Myotis keenii auriculus* by Findley (1960:18). Arranged as *Myotis auriculus auriculus* by Genoways and Jones (1969:10).

Myotis nigricans dalquesti Hall and Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:71, December 29, 1961.

Holotype.—Adult male, skin and skull, KU 23839, from 3 km. E San Andrés Tuxtla, 1000 ft., Veracruz; obtained January 5, 1948, by Walter W. Dalquest, original number 8444.

Remarks.—Skin with hole along right side; right zygomatic arch broken.

Myotis planiceps Baker, Proc. Biol. Soc. Washington, 68:165, December 31, 1955.

Holotype.—Adult male, skin and skull, KU 48242, from 7 mi. S and 4 mi. E Bella Unión, 7200 ft., Coahuila; obtained June 24, 1952, by Albert A. Alcorn, original number 920.

Remarks.—Parietals and major portion of frontals missing.

Myotis thysanodes pahasapensis Jones and Genoways, Jour. Mamm., 48:231, May 20, 1967.

Holotype.—Adult male, skin and skull, KU 100704, from 6 mi. N Newcastle, 6000 ft., Weston Co., Wyoming; obtained July 2, 1965, by Ronald W. Turner, original number 156.

Myotis velifer brevis Vaughan, Univ. Kansas Publ., Mus. Nat. Hist., 7:509, July 23, 1954.

Holotype.—Adult male, skin and skull, KU 22631, from Madera Canyon, 5000 ft., Santa Rita Mountains, Pima Co., Arizona; obtained March 12, 1948, by J. R. Alcorn, original number 5571.

Pipistrellus subflavus clarus Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:585, November 15, 1954.

Holotype.—Adult female, skin and skull, KU 48270, from 2 mi. W Jiménez, 850 ft., Coahuila; obtained June 19, 1952, by Rollin H. Baker, original number 2062.

Scotophilus alvenslebeni Dalquest, Jour. Mamm., 46:258, May 20, 1965.

Holotype.—Adult male, skin and skull, KU 105222, from S bank Save River, 212 km. SSW Beira, Mozambique; obtained October 9, 1963, by Walter W. Dalquest, original number 18767.

Remarks.—Regarded as synonym of *Scotophilus gigas* Dobson, 1875, by Dalquest (1966:134).

Lasiurus intermedius insularis Hall and Jones, Univ. Kansas Publ., Mus. Nat. Hist., 14:85, December 29, 1961.

Holotype.—Adult female, specimen stored in spirits with skull removed, KU 81666, from Cienfuegos, Las Villas Prov., Cuba; obtained January 3, 1948, by D. Gonzáles Muñoz, original number, if any, unknown.

Remarks.—Skull missing left auditory bulla.

Antrozous bunkeri Hibbard, Jour. Mamm., 15:227, August 10, 1934.

Holotype.—Adult female, skin and skull, KU 9302, from 7 mi. S [actually 4½ mi. S, ¼ mi. E] Sun City, Barber Co., Kansas; obtained September 2, 1933, by Hobart Smith and Claude W. Hibbard, original number 538 (Hibbard).

Remarks.—Arranged as *Antrozous pallidus bunkeri* by Krutzsch and Vaughan 1955:97, 99) and by Morse and Glass (1960:15). A corrected statement of the type locality was published by Jones *et al.* (1967:25).

Molossops greenhalli mexicanus Jones and Genoways, Proc. Biol. Soc. Washington, 80:207, December 1, 1967.

Holotype.—Adult male, skin and skull, KU 108609, from 7½ mi. SE Tecomate, 1500 ft., Jalisco; obtained December 7, 1966, by Percy L. Clifton, original number 11998.

Eumops perotis renatae Pirlot, Le Naturaliste Canadian, 92:5, January, 1965.

Holotype.—Adult female, specimen stored in spirits with skull removed, KU 115920, from Cumaná, Sucre, Venezuela; obtained on unknown date by R. P. C. Prieto, original number, if any, unknown.

Remarks.—Skull cracked across interorbital region and longitudinally along the palate; part of right maxillary, part of fourth upper premolar, and part of left parietal missing.

This specimen, which was originally deposited in the Collegio San José in Cumaná, Venezuela, was obtained for the Museum of Natural History by James D. Smith from R. P. C. Prieto. Smith entered the specimen in his field catalogue as number 2852. Pirlot (1968:90) claimed specific rank for *renatae.*

LAGOMORPHA

Ochotona princeps howelli Borell, Jour. Mamm., 12:306, August 24, 1931.

Holotype.—Adult male, skin and skull, KU 45705 (originally number 8744 in collection of Ralph Ellis), from summit of Smith Mountain (near head Bear Creek, S end of Seven Devils Mountains), 7500 ft., Adams Co., Idaho; obtained July 16, 1930, by Raymond M. Gilmore, original number 1325.

Ochotona princeps obscura Long, Univ. Kansas Publ., Mus. Nat. Hist., 14: 538, July 6, 1965.

Holotype.—Subadult male, skin and skull, KU 32918, from Medicine Wheel Ranch, 9000 ft., 28 mi. E Lovell, Big Horn Co., Wyoming; obtained July 7, 1949, by J. W. Twente, original number 232.

Remarks.—Braincase cracked but intact, tips of nasals and posterior extension of the left zygomatic arch missing.

Sylvilagus floridanus nelsoni Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:611, April 8, 1955.

Holotype.—Adult female, skin and skull, KU 57771, from 22 mi. S and 5 mi. W Ocampo, 5925 ft., Coahuila; obtained April 4, 1952, by Rollin H. Baker, original number 2571.

Remarks.—Posterior portion of right supraorbital process missing. Regarded as synonym of *Sylvilagus floridanus robustus* (Bailey, 1905) by Raun (1965: 521).

Lepus americanus seclusus Baker and Hankins, Proc. Biol. Soc. Washington, 63:63, May 25, 1950.

Holotype.—Adult male, skin and skull, KU 20897, from 12 mi. E and 2 mi. N Shell, 7900 ft., Bighorn Mts., Big Horn Co., Wyoming; obtained July 8, 1947, by Gilbert Winemiller, original number 22 of João Moojen.

Remarks.—Baker (1959:145) believed *seclusus* to be preoccupied by *Lepus timidus seclusus* Degerbøl, 1940, and therefore proposed the replacement name *Lepus americanus setzeri* for this subspecies. Long (1965a:548; 1965b:125-126) considered the name *Lepus americanus seclusus* Baker and Hankins not to be preoccupied by *Lepus timidus seclusus* Degerbøl because the latter name pertains to a "variety" or "forma," which have no standing under the Code; therefore he regarded *Lepus americanus setzeri* Baker as a junior synonym of *L. a. seclusus.*

Lepus californicus curti Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:42, October 1, 1951.

Holotype.—Adult female, skin and skull, KU 35470, from an island, 88 mi. S and 10 mi. W Matamoros, Tamaulipas; obtained March 19, 1950, by E. R. Hall, original number 6783.

RODENTIA

Eutamias minimus silvaticus White, Univ. Kansas Publ., Mus. Nat. Hist., 5:261, April 10, 1952.

Holotype.—Adult female, skin and skull, KU 20050, from 3 mi. NW Sundance, 5900 ft., Crook Co., Wyoming; obtained July 4, 1947, by H. W. Setzer, original number 1692.

Eutamias umbrinus fremonti White, Univ. Kansas Publ., Mus. Nat. Hist., 5:575, December 1, 1953.

Holotype.—Adult male, skin, skull, and prepared baculum, KU 41790, from 31 mi. N Pinedale, 8025 ft., Sublette Co., Wyoming; obtained July 8, 1951, by Rollin H. Baker, original number 1596.

Eutamius umbrinus montanus White, Univ. Kansas Publ., Mus. Nat. Hist., 5:576, December 1, 1953.

Holotype.—Adult male, skin, skull, and prepared baculum, KU 20105, from ½ mi. E and 3 mi. S Ward, 9400 ft., Boulder Co., Colorado; obtained August 1, 1947, by E. L. Cockrum, original number 721.

Marmota monax bunkeri Black, Jour. Mamm., 16:319, November 15, 1935.

Holotype.—Adult female, skin and skull, KU 3089, from 7 mi. SW Lawrence, Douglas Co., Kansas; obtained March 8, 1920, by Fred Hastie, original number, if any, unknown.

Spermophilus spilosoma oricolus Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:123, March 7, 1962.

Holotype.—Adult female, skin and skull, KU 55497, from 1 mi. E La Pesca, Tamaulipas; obtained March 27, 1953, by Gerd H. Heinrich, original number 6933.

Thomomys bottae angustidens Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:508, June 1, 1953.

Holotype.—Adult male, skin and skull, KU 48481, from Sierra del Pino, 6 mi. N and 6 mi. W Acebuches, Coahuila; obtained July 3, 1952, by Rollin H. Baker, original number 2141.

Remarks.—Hall and Kelson (1959:416) arranged this and other subspecies of *Thomomys bottae* as races of *Thomomys umbrinus*; however, several recent authors (Anderson, 1966:189; Dunnigan, 1967:144; Patton and Dingman, 1968:2) have shown the two species to be distinct.

Thomomys bottae caneloensis Lange, Proc. Biol. Soc. Washington, 72:131, November 4, 1959.

Holotype.—Adult male, skin and skull, KU 51788, from Huachuca Mountains, west foothills, Canelo, 10 mi. S Elgin, 5100 ft., Santa Cruz Co., Arizona; obtained November 30, 1952, by Gerd H. Heinrich, original number 5551.

Allotype.—Adult female, skin and skull, KU 51786; obtained November 29, 1952, by Gerd H. Heinrich, original number 5549.

Thomomys bottae humulis Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:503, June 1, 1953.

Holotype.—Adult male, skin and skull, KU 35746, from 3 mi. W Hda. [Hacienda] San Miguel, 2200 ft., Coahuila; obtained April 4, 1950, by J. R. Alcorn, original number 11039.

Thomomys bottae retractus Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:507, June 1, 1953.

Holotype.—Adult male, skin and skull, KU 44826, from Fortín, 3300 ft., 33 mi. N and 1 mi. E San Gerónimo, Coahuila; obtained March 29, 1952, by Rollin H. Baker, original number 1971.

Thomomys bottae rubidus Youngman, Univ. Kansas Publ., Mus. Nat. Hist., 9:376, February 21, 1958.

Holotype.—Adult female, skin and skull, KU 72954, from 2 9/10 mi. E Cañon City, 5344 ft., Fremont Co., Colorado; obtained March 17, 1957, by Richard S. Miller and Phillip M. Yougman, original number 253 (Youngman).

Thomomys bottae villai Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:505, June 1, 1953.

Holotype.—Adult female, skin and skull, KU 44816, from 7 mi. S and 2 mi. E Boquillas, 1800 ft., Coahuila; obtained March 1, 1952, by Rollin H. Baker, original number 1816.

Thomomys talpoides attenuatus Hall and Montague, Univ. Kansas Publ., Mus. Nat. Hist., 5:29, February 28, 1951.

Holotype.—Adult male, skin and skull, KU 15095, from 3½ mi. W Horse Creek Post Office, 7000 ft., Laramie Co., Wyoming; obtained July 16, 1945, by Henry W. Setzer, original number 629.

Thomomys talpoides meritus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:221, December 15, 1951.

Holotype.—Adult male, skin and skull, KU 25628, from 8 mi. N and 19½ mi. E Savery, 8800 ft., Carbon Co., Wyoming; obtained July 19, 1948, by George M. Newton, original number 4.

Thomomys talpoides rostralis Hall and Montague, Univ. Kansas Publ., Mus. Nat. Hist., 5:27, February 28, 1951.

Holotype.—Adult female, skin and skull, KU 17096, from 1 mi. E Laramie, 7164 ft., Albany Co., Wyoming; obtained August 26, 1946, by C. Howard Westman, original number 320.

Remarks.—The date on which the holotype was captured was incorrectly given as July 16, 1945, in the original description.

Thomomys umbrinus varus Hall and Long, Proc. Biol. Soc. Washington, 73:35, August 10, 1960.

Holotype.—Adult male, skin and skull, KU 75271, from 1 mi. S El Dorado, Sinaloa; obtained November 14, 1957, by William L. Cutter, original number 1452.

Remarks.—Left upper premolar missing. Regarded as a synonym of *Thomomys bottae sinaloae* Merriam, 1901, by Dunnigan (1967:149).

Geomys bursarius industrius Villa-R. and Hall, Univ. Kansas Publ., Mus. Nat. Hist., 1:226, November 29, 1947.

Holotype.—Adult male, skin and skull, KU 14083, from 1½ mi. N Fowler, Meade Co., Kansas; obtained December 30, 1941, by H. H. Hildebrand, original number 16.

Remarks.—Exposed portion of right upper premolar missing.

Heterogeomys hispidus latirostris Hall and Alvarez, An. Escuela Nac. Cien. Biol., 10:121, December 20, 1961.

Holotype.—Adult female, skin and skull, KU 82968, from Hacienda Tamiahua, Cabo Rojo, Veracruz; obtained April 2, 1960, by M. R. Lee, original number 1822.

Remarks.—Catalogue number of the holotype was incorrectly listed in the original description as 83968. Arranged as *Orthogeomys hispidus latirostris* by Russell (1968a:531).

Pappogeomys alcorni Russell, Univ. Kansas Publ., Mus. Nat. Hist., 9:359, January 21, 1957.

Holotype.—Adult female, skin and skull, KU 39806, from 4 mi. W Mazamitla, 6600 ft., Jalisco; obtained October 18, 1950, by J. R. Alcorn, original number 12835.

Pappogeomys bulleri infuscus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:610, August 5, 1968.

Holotype.—Adult male, skin and skull, KU 33451, from Cerro Tequila, 10,000 ft., 7 mi. S and 2 mi. W Tequila, Jalisco; obtained May 13, 1949, by J. R. Alcorn, original number 9186.

Pappogeomys bulleri lutulentus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:612, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 92984, from Sierra de Cuale, 7300 ft., 9 km. N El Teosinte (=Desmoronado), Jalisco; obtained October 28, 1962, by Percy L. Clifton, original number 3236.

Pappogeomys castanops elibatus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:672, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 58092, from 12 mi. W San Antonio de las Alazanas, about 7500 ft., Coahuila; obtained January 10, 1954, by Robert W. Dickerman, original number 2268.

Pappogeomys castanops parviceps Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:673, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 87152, from 18 mi. SW Alamogordo, 4400 ft., Otero Co., New Mexico; obtained June 30, 1961, by M. Raymond Lee, original number 4067.

Pappogeomys castanops perexiguus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:676, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 55584, from 6 mi. E Jaco, Chihuahua, 4500 ft., *in* Coahuila; obtained March 18, 1953, by Gerd H. Heinrich, original number 6262.

Pappogeomys castanops pratensis Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:653, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 52051, from 8 mi. W and 3 mi. S Alpine, 5100 ft., Brewster Co., Texas; obtained December 30, 1952, by Gerd H. Heinrich, original number 5684.

Pappogeomys castanops surculus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:688, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 62470, from La Zarca, Durango; obtained May 29, 1954, by Robert W. Dickerman, original number 3361.

Remarks.—Left upper premolar missing.

Pappogeomys castanops torridus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:665, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 84461, from 3 mi. E Sierra Blanca, about 4000 ft., Hudspeth Co., Texas; obtained August 13, 1960, by M. R. Lee, original number 2659.

Pappogeomys tylorhinus brevirostris Russell, Univ. Kansas Publ., Mus. Nat. Hist., 16:733, August 5, 1968.

Holotype.—Adult female, skin and skull, KU 66151, from 2 mi. E Celaya, 5800 ft., Guanajuato; obtained January 17, 1955, by Robert W. Dickerman, original number 4844.

Remarks.—Tips of upper incisors missing.

Cratogeomys castanops bullatus Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:597, March 15, 1955.

Holotype.—Adult female, skin and skull, KU 48498, from 2 mi. S and 6½ mi. E Nava, 810 ft., Coahuila; obtained June 16, 1952, by Robert J. Russell, original number 276.

Remarks.—Exposed portion of third upper molar missing on both sides. Arranged as *Pappogeomys castanops bullatus* by Russell (1968b:632).

Cratogeomys castanops jucundus Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:599, March 15, 1955.

Holotype.—Adult female, skin and skull, KU 56603, from Hermanas, 1205 ft., Coahuila; obtained December 5, 1953, by Robert W. Dickerman, original number 2051.

Remarks.—Arranged as *Pappogeomys castanops jucundus* by Russell (1968b:648).

Cratogeomys castanops sordidulus Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:600, March 15, 1955.

Holotype.—Adult female, skin and skull, KU 56614, from 1½ mi. NW Ocampo, 3300 ft., Coahuila; obtained December 16, 1953, by Robert W. Dickerman, original number 2164.

Remarks.—Arranged as *Pappogeomys castanops sordidulus* by Russell (1968b:658).

Cratogeomys castanops ustulatus Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:598, March 15, 1955.

Holotype.—Adult female, skin and skull, KU 34589, from Don Martín, 800 ft., Coahuila; obtained August 19, 1949, by W. Kim Clark, original number 1034.

Remarks.—Arranged as *Pappogeomys castanops ustulatus* by Russell (1968b: 667).

Cratogeomys gymnurus atratus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 5:539, October 15, 1953.

Holotype.—Adult female, skin and skull, KU 31880, from top of Cerro Viejo de Cuyutlán, 9700 ft., 19 mi. S and 9 mi. W Guadalajara, Jalisco; obtained February 17, 1949, by J. R. Alcorn, original number 7902.

Remarks.—Arranged as *Pappogeomys tylorhinus atratus* by Russell (1968b: 731).

Cratogeomys gymnurus tellus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 5:537, October 15, 1953.

Holotype.—Adult female, skin and skull, KU 33454, from 3 mi. W Tala, 4300 ft., Jalisco; obtained June 2, 1949, by J. R. Alcorn, original number 9376.

Remarks.—Arranged as *Pappogeomys gymnurus tellus* by Russell (1968a: 482, 571; 1968b:756).

Cratogeomys zinseri morulus Russell, Univ. Kansas Publ., Mus. Nat. Hist., 5:541, October 15, 1953.

Holotype.—Adult male, skin and skull, KU 36679, from N end Lago Sayula, 4400 ft., 9 mi. N and 2 mi. E Atoyac, Jalisco; obtained March 23, 1950, by J. R. Alcorn, original number 10889.

Remarks.—Exposed portion of left upper incisor missing. Considered a synonym of *Pappogeomys gymnurus gymnurus* (Merriam, 1892) by Russell (1968b:751).

Cratogeomys zinseri zodius Russell, Univ. Kansas Publ., Mus. Nat. Hist., 5:540, October 15, 1953.

Holotype.—Adult male, skin and skull, KU 31879, from 13 mi. S and 15 mi. W Guadalajara, Jalisco; obtained February 6, 1949, by J. R. Alcorn, original number 7747.

Remarks.—Exposed portion of left upper incisor and left lower third molar missing. Arranged as *Pappogeomys tylorhinus zodius* by Russell (1968a:535; 1968b:742).

Perognathus flavescens cockrumi Hall, Univ. Kansas Publ., Mus. Nat. Hist., 7:589, November 15, 1954.

Holotype.—Subadult female, skin and skull, KU 13045, from 4½ mi. NE Danville, Harper Co., Kansas; obtained December 1, 1939, by Sam Tihen, original number 99 of J. A. Tihen.

Remarks.—Both zygomatic arches missing.

Perognathus flavus bunkeri Cockrum, Univ. Kansas Publ., Mus. Nat. Hist., 5:205, December 15, 1951.

Holotype.—Adult female, skin and skull, KU 11716, from Conrad Farm, 1 mi. E Coolidge, Hamilton Co., Kansas; obtained July 1, 1936, by F. Parks and C. W. Hibbard, original number 894 (Hibbard).

Remarks.—Left zygomatic arch missing, right ramus broken, and hole in right parietal.

Perognathus flavus medius Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:343, February 15, 1954.

Holotype.—Adult female, skin and skull, KU 48583, from 1 mi. S and 6 mi. E Rincón de Romos, 6550 ft., Aguascalientes; obtained July 14, 1952, by Rollin H. Baker, original number 2215.

Remarks.—Right zygomatic arch missing.

Perognathus flavus pallescens Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:345, February 15, 1954.

Holotype.—Adult male, skin and skull, KU 40298, from 1 mi. SW San Pedro de las Colonias, 3700 ft., Coahuila; obtained February 9, 1951, by J. R. Alcorn, original number 14177.

Perognathus flavus parviceps Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:344, February 15, 1954.

Holotype.—Adult female, skin and skull, KU 38402, from 4 mi. W and 2 mi. S Guadalajara, 5100 ft., Jalisco; obtained June 15, 1950, by J. R. Alcorn, original number 12020.

Remarks.—Right zygomatic arch missing.

Dipodomys ordii largus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:40, October 1, 1951.

Holotype.—Adult female, skin and skull, KU 27234, from Mustang Island, 14 mi. SW Port Aransas, Aransas Co., Texas; obtained June 30, 1948, by W. K. Clark, original number 543.

Dipodomys ordii parvabullatus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:38, October 1, 1951.

Holotype.—Adult male, skin and skull, KU 35454, from an island, 88 mi. S and 10 mi. W Matamoros, Tamaulipas; obtained March 19, 1950, by E. R. Hall and Curt von Wedel, original number 6778 (Hall).

Remarks.—Both zygomatic arches missing and hole in right parietal.

Reithrodontomys fulvescens meridionalis Anderson and Jones, Univ. Kansas Publ., Mus. Nat. Hist., 9:522, January 14, 1960.

Holotype.—Adult male, skin and skull, KU 71388, from 9 mi. NNW Estelí, Estelí, Nicaragua; obtained July 15, 1956, by J. R. Alcorn, original number 21464.

Reithrodontomys gracilis insularis Jones, Proc. Biol. Soc. Washington, 77:123, June 26, 1964.

Holotype.—Adult male, skin and skull, KU 92262, from 8 mi. ENE Ciudad del Carmen, Isla del Carmen, Campeche; obtained July 7, 1962, by William C. Stanley, original number 373.

Reithrodontomys spectabilis Jones and Lawlor, Univ. Kansas Publ., Mus. Nat. Hist., 16:413, April 13, 1965.

Holotype.—Adult male, skin and skull, KU 92294, from 2½ km. N San

Miguel, Isla Cozumel, Quintana Roo; obtained August 8, 1962, by Ticul Alvarez, original number 848.

Peromyscus angustirostris Hall and Alvarez, Proc. Biol. Soc. Washington, 74:203, August 11, 1961.

Holotype.—Old adult male, skin and skull, KU 83226, from 3 km. W Zacaulpan, 6000 ft., Veracruz; obtained April 12, 1960, by M. Raymond Lee, original number 1886.

Remarks.—Regarded as a synonym of *Peromyscus furvus* J. A. Allen and Chapman, 1897, by Musser (1964:12).

Peromyscus boylii cansensis Long, Univ. Kansas Publ., Mus. Nat. Hist., 14:101, December 29, 1961.

Holotype.—Adult male, skin and skull, KU 81830, from 4 mi. E Sedan, Chautauqua Co., Kansas; obtained December 30, 1959, by C. A. Long, original number 456.

Remarks.—Both zygomatic arches broken. Regarded as a synonym of *Peromyscus boylii attwateri* J. A. Allen, 1895, by Choate *et al.* (1967:312).

Peromyscus difficilis petricola Hoffmeister and de la Torre, Proc. Biol. Soc. Washington, 72:167, November 4, 1959.

Holotype.—Adult female, skin and skull, KU 33239, from 12 mi. E San Antonio de las Alazanas, 9000 ft., Coahuila; obtained August 2, 1949, by W. Kim Clark, original number 979.

Remarks.—Left ramus broken.

Peromyscus maniculatus ozarkiarum Black, Jour. Mamm., 16:144, May 15, 1935.

Holotype.—Adult male, skin and skull, KU 10104, from 3 mi. S Winslow, Washington Co., Arkansas; obtained August 30, 1934, by Ruby Black, original number 853 of J. D. Black.

Remarks.—Right zygomatic arch broken.

Peromyscus melanophrys coahuilensis Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:257, April 10, 1952.

Holotype.—Adult female, skin and skull, KU 35019, from 7 mi. S and 1 mi. E Gómez Farías, 6500 ft., Coahuila; obtained November 20, 1949, by W. K. Clark, original number 1293.

Remarks.—Skin with slippage on belly and right flank. In the original description in the statement of particulars about the holotype, the locality of capture was incorrectly given as "Gomez Farias, 6500 ft., Coahuila," although elsewhere in the paper it is located correctly.

Peromyscus melanophrys micropus Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:255, April 10, 1952.

Holotype.—Adult male, skin and skull, KU 31760, from 3 mi. N Guadalajara, Jalisco; obtained January 18, 1949, by J. R. Alcorn, original number 7402.

Remarks.—The date on which the holotype was obtained was incorrectly given in the original description as January 11, 1949.

Peromyscus ochraventer Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:213, December 15, 1951.

Holotype.—Adult female, skin and skull, KU 36958, from 70 km. [by highway] S Ciudad Victoria and 6 km. W of the [Pan American] highway [at El Carrizo], Tamaulipas; obtained January 12, 1950, by William J. Schaldach, Jr., original number 566.

Peromyscus truei erasmus Finley, Univ. Kansas Publ., Mus. Nat. Hist., 5:265, May 23, 1952.

Holotype.—Young adult female, skin and skull, KU 34417, from 8 mi. NE Durango, 6200 ft., Durango; obtained August 16, 1949, by J. R. Alcorn, original number 10255.

Remarks.—Right zygomatic arch broken. Regarded as a synonym of *Peromyscus truei gentilis* Osgood, 1904, by Baker (1960:321).

Baiomys musculus pullus Packard, Univ. Kansas Publ., Mus. Nat. Hist., 9:401, December 19, 1958.

Holotype.—Adult female, skin and skull, KU 71605, from 8 mi. S Condega, Estelí, Nicaragua; obtained July 15, 1956, by A. A. Alcorn, original number 4218.

Baiomys taylori canutus Packard, Univ. Kansas Publ., Mus. Nat. Hist., 9:643, June 16, 1960.

Holotype.—Adult male, skin and skull, KU 62075, from 1 mi. S Pericos, Sinaloa; obtained June 14, 1954, by A. A. Alcorn, original number 1754.

Remarks.—Left ear missing and some slippage of pelage on left shoulder.

Baiomys taylori fuliginatus Packard, Univ. Kansas Publ., Mus. Nat. Hist., 9:645, June 16, 1960.

Holotype.—Adult male, skin and skull, KU 36765, from 10 mi. E and 2 mi. N Ciudad de Maíz, 4000 ft., San Luis Potosí; obtained January 17, 1950, by J. R. Alcorn, original number 10400.

Sigmodon hispidus solus Hall, Univ. Kansas Publ., Mus. Nat. Hist., 5:42, October 1, 1951.

Holotype.—Adult male, skin and skull, KU 35468, from an island, 88 mi. S and 10 mi. W Matamoros, Tamaulipas; obtained March 22, 1950, by E. R. Hall and Curt von Wedel, original number 6806 (Hall).

Remarks.—Hole in left orbit and left zygomatic arch cracked in region of infraorbital foramen.

Neotoma albigula subsolana Alvarez, Univ. Kansas Publ., Mus. Nat. Hist., 14:141, April 30, 1962.

Holotype.—Adult male, skin and skull, KU 56950, from Miquihuana, 6400 ft., Tamaulipas; obtained July 20, 1953, by Gerd H. Heinrich, original number 7553B.

Neotoma angustapalata Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:217, December 15, 1951.

Holotype.—Subadult male, skin, skull, and prepared baculum, KU 36976, from 70 km. [by highway] S Ciudad Victoria and 6 km. W of the [Pan American] highway [at El Carrizo], Tamaulipas; obtained January 14, 1950, by William J. Schaldach, Jr., original number 578.

Neotoma mexicana eremita Hall, Jour. Washington Acad. Sci., 45:328, October 31, 1955.

Holotype.—Adult female, skin, skull, and body skeleton, KU 64532, from 1 mi. S San Francisco, 50 ft., Nayarit; obtained January 27, 1955, by J. R. Alcorn, original number 17830.

Neotoma mexicana scopulorum Finley, Univ. Kansas Publ., Mus. Nat. Hist., 5:529, August 15, 1953.

Holotype.—Old adult male, skin and skull, KU 37137, from 37° 47′ N, 103° 28′ W, 3 mi. NW Higbee, 4300 ft., Otero Co., Colorado; obtained May 16, 1950, by R. B. Finley, Jr., original number 500516-1.

Remarks.—Left upper first molar appears to have been lost in life.

Nelsonia neotomodon cliftoni Genoways and Jones, Proc. Biol. Soc. Washington, 81:97, April 30, 1968.

Holotype.—Adult female, skin and skull, KU 109437, from 2½ mi. ENE Jazmín, 6800 ft., Jalisco; obtained October 20, 1966, by Percy L. Clifton, original number 11706.

Microtus montanus codiensis Anderson, Univ. Kansas Publ., Mus. Nat. Hist., 7:497, July 23, 1954.

Holotype.—Adult female, skin and skull, KU 27578, from 3 1/5 mi. E and 3/5 mi. S Cody, 5020 ft., Park Co., Wyoming; obtained August 11, 1948, by James W. Bee, original number 18-8-11-48.

Microtus montanus pratincolus Hall and Kelson, Univ. Kansas Publ., Mus. Nat. Hist., 5:75, October 1, 1951.

Holotype.—Adult female, skin and skull, KU 34004, from 6 mi. E Hamilton, 3700 ft., Ravalli Co., Montana; obtained August 14, 1949, by John A. White, original number 477.

Remarks.—Subspecific name emended to *pratincola* by Hall and Cockrum (1953:417).

Microtus montanus zygomaticus Anderson, Univ. Kansas Publ., Mus. Nat. Hist., 7:500, July 23, 1954.

Holotype.—Adult male, skin and skull, KU 32761, from Medicine Wheel Ranch, 9000 ft., 28 mi. E Lovell, Big Horn Co., Wyoming; obtained July 8, 1949, by R. Freiburg, original number 105.

Microtus ochrogaster taylori Hibbard and Rinker, Univ. Kansas Sci. Bull., 29:256, October 15, 1943.

Holotype.—Adult female, skin and skull, KU 14126, from 1½ mi. N Fowler, Meade Co., Kansas; obtained June 17, 1942, by George C. Rinker, original number 1195 of C. W. Hibbard.

Remarks.—Hole in left auditory bulla.

Microtus pennsylvanicus alcorni Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:105, November 28, 1951.

Holotype.—Adult female, skin and skull, KU 21552, from 6 mi. SW Kluane, 2550 ft., Yukon Territory, Canada; obtained August 24, 1947, by J. R. Alcorn, original number 5240.

Microtus pennsylvanicus finitus Anderson, Univ. Kansas Publ., Mus. Nat. Hist., 9:96, May 10, 1956.

Holotype.—Adult female, skin and skull, KU 50204, from 5 mi. N and 2 mi. W Parks, Dundy Co., Nebraska; obtained August 16, 1952, by J. Knox Jones, Jr., original number 906.

Remarks.—Right zygomatic arch broken.

Microtus pennsylvanicus pullatus Anderson, Univ. Kansas Publ., Mus. Nat. Hist., 9:97, May 10, 1956.

Holotype.—Adult male, skin and skull, KU 37873, from 12 mi. N and 2 mi. E Sage, 6100 ft., Lincoln Co., Wyoming; obtained July 19, 1950, by Rollin H. Baker, original number 1343.

Microtus pennsylvanicus tananaensis Baker, Univ. Kansas Publ., Mus. Nat. Hist., 5:107, November 28, 1951.

Holotype.—Adult female, skin and skull, KU 21509, from Yerrick Creek, 21 mi. W and 4 mi. N Tok Junction, Alaska; obtained July 20, 1947, by J. R. Alcorn, original number 5023.

Remarks.—Left auditory bulla broken.

Microtus pennsylvanicus uligocola Anderson, Univ. Kansas Publ., Mus. Nat. Hist., 9:94, May 10, 1956.

Holotype.—Adult male, skin and skull, KU 26898, from 6 mi. W and ½ mi. S Loveland, 5200 ft., Larimer Co., Colorado; obtained July 26, 1948, by James O. Lounquist, original number 349.

Synaptomys cooperi paludis Hibbard and Rinker, Univ. Kansas Sci. Bull., 28:26, May 15, 1942.

Holotype.—Adult male, skin and skull, KU 13713, from Meade County State Park, 14 mi. SW Meade, Meade Co., Kansas; obtained July 12, 1941, by Claude W. Hibbard, original number 528.

Synaptomys cooperi relictus Jones, Univ. Kansas Publ., Mus. Nat. Hist., 9:387, May 12, 1958.

Holotype.—Adult female, skin and skull, KU 51617, from Rock Creek Fish Hatchery, 5 mi. N and 2 mi. W Parks, Dundy Co., Nebraska; obtained November 1, 1952, by J. Knox Jones, Jr., original number 995.

Zapus hudsonius pallidus Cockrum and Baker, Proc. Biol. Soc. Washington, 63:1, April 26, 1950.

Holotype.—Adult male, skin, skull, and body skeleton, KU 22953, from NW corner sec. 4, T. 12 S, R. 20 E, 5½ mi. N and 1¾ mi. E Lawrence, Douglas Co., Kansas; obtained May 4, 1948, by E. Lendell Cockrum and Rollin H. Baker, original number 916 (Cockrum).

CARNIVORA

Taxidea taxus kansensis Schanz, Jour. Mamm., 31:346, August 21, 1950.

Holotype.—Adult female, tanned (cased) skin and skull, KU 21989, from 4 mi. SE McLouth, Leavenworth Co., Kansas; obtained November 30, 1947, by Henry Murr and prepared by James O. Lounquist, original number 46.

Remarks.—Bullet hole entering skull through right parietal and leaving through right alisphenoid, but braincase intact. The taxonomic status of this nominal subspecies is uncertain because the species is in need of systematic review.

Mephitis macroura eximius Hall and Dalquest, Univ. Kansas Publ., Mus. Nat. Hist., 1:579, January 20, 1950.

Holotype.—Adult female, skin and skull, KU 19272, from 15 km. W Piedras Negras, 300 ft., Veracruz; obtained January 13, 1947, by J. Mazza and Walter W. Dalquest, original number 7017 (Dalquest).

GEOGRAPHIC ORIGIN OF TYPE SPECIMENS

The countries, states, and territories whence originated the holotypes in the foregoing list are here arranged alphabetically. Names of species and subspecies are listed alphabetically, in the combination used in the original description, under the place names.

CANADA
- Yukon Territory
  - *Microtus pennsylvanicus alcorni* Baker

CUBA
- *Lasiurus intermedius insularis* Hall and Jones

MEXICO
- Aguascalientes
  - *Perognathus flavus medius* Baker
- Campeche
  - *Reithrodontomys gracilis insularis* Jones
- Coahuila
  - *Cratogeomys castanops bullatus* Russell and Baker
  - *Cratogeomys castanops jucundus* Russell and Baker
  - *Cratogeomys castanops sordidulus* Russell and Baker
  - *Cratogeomys castanops ustulatus* Russell and Baker
  - *Leptonycteris nivalis longala* Stains
  - *Myotis planiceps* Baker
  - *Pappogeomys castanops elibatus* Russell
  - *Pappogeomys castanops perexiguus* Russell
  - *Perognathus flavus pallescens* Baker
  - *Peromyscus difficilis petricola* Hoffmeister and de la Torre
  - *Peromyscus melanophrys coahuilensis* Baker
  - *Pipistrellus subflavus clarus* Baker
  - *Scalopus montanus* Baker
  - *Sylvilagus floridanus nelsoni* Baker
  - *Thomomys bottae angustidens* Baker
  - *Thomomys bottae humulis* Baker
  - *Thomomys bottae retractus* Baker
  - *Thomomys bottae villai* Baker
- Durango
  - *Pappogeomys castanops surculus* Russell
  - *Peromyscus truei erasmus* Finley
- Guanajuato
  - *Pappogeomys tylorhinus brevirostris* Russell
- Jalisco
  - *Cratogeomys gymnurus atratus* Russell
  - *Cratogeomys gymnurus tellus* Russell
  - *Cratogeomys zinseri morulus* Russell
  - *Cratogeomys zinseri zodius* Russell
  - *Cryptotis euryrhynchis* Genoways and Choate
  - *Molossops greenhalli mexicanus* Jones and Genoways
  - *Nelsonia neotomodon cliftoni* Genoways and Jones
  - *Pappogeomys alcorni* Russell
  - *Pappogeomys bulleri infuscus* Russell
  - *Pappogeomys bulleri lutulentus* Russell
  - *Perognathus flavus parviceps* Baker
  - *Peromyscus melanophrys micropus* Baker
- Nayarit
  - *Neotoma mexicana eremita* Hall
- Quintana Roo
  - *Reithrodontomys spectabilis* Jones and Lawlor
- San Luis Potosí
  - *Baiomys taylori fuliginatus* Packard
- Sinaloa
  - *Baiomys taylori canutus* Packard
  - *Sturnira ludovici occidentalis* Jones and Phillips
  - *Thomomys umbrinus varus* Hall and Long

Tamaulipas
- *Dipodomys ordii parvabullatus* Hall
- *Lepus californicus curti* Hall
- *Myotis evotis auriculus* Baker and Stains
- *Neotoma albigula subsolana* Alvarez
- *Neotoma angustapalata* Baker
- *Peromyscus ochraventer* Baker
- *Sigmodon hispidus solus* Hall
- *Spermophilus spilosoma oricolus* Alvarez

Veracruz
- *Heterogeomys hispidus latirostris* Hall and Alvarez
- *Mephitis macroura eximius* Hall and Dalquest
- *Myotis argentatus* Dalquest and Hall
- *Myotis elegans* Hall
- *Myotis nigricans dalquesti* Hall and Alvarez
- *Natalus mexicanus saturatus* Dalquest and Hall
- *Peromyscus angustirostris* Hall and Alvarez

MOZAMBIQUE
- *Nycteris vinsoni* Dalquest
- *Scotophilus alvenslebeni* Dalquest

NICARAGUA
- *Baiomys musculus pullus* Packard
- *Reithrodontomys fulvescens meridionalis* Anderson and Jones

UNITED STATES

Alaska
- *Microtus pennsylvanicus tananaensis* Baker

Arizona
- *Myotis velifer brevis* Vaughan
- *Thomomys bottae caneloensis* Lange

Arkansas
- *Peromyscus maniculatus ozarkiarum* Black

Colorado
- *Eutamias umbrinus montanus* White
- *Microtus pennsylvanicus uligocola* Anderson
- *Neotoma mexicana scopulorum* Finley
- *Thomomys bottae rubidus* Youngman

Idaho
- *Ochotona princeps howelli* Borell

Kansas
- *Antrozous bunkeri* Hibbard
- *Geomys bursarius industrius* Villa-R. and Hall
- *Marmota monax bunkeri* Black
- *Microtus ochrogaster taylori* Hibbard and Rinker
- *Perognathus flavescens cockrumi* Hall
- *Perognathus flavus bunkeri* Cockrum
- *Peromyscus boylii cansensis* Long
- *Synaptomys cooperi paludis* Hibbard and Rinker
- *Taxidea taxus kansensis* Schanz
- *Zapus hudsonius pallidus* Cockrum and Baker

Montana
- *Microtus montanus pratincolus* Hall and Kelson

Nebraska
- *Microtus pennsylvanicus finitus* Anderson
- *Synaptomys cooperi relictus* Jones

New Mexico
- *Pappogeomys castanops parviceps* Russell

Texas

Dipodomys ordii largus Hall
Pappogeomys castanops pratensis Russell
Pappogeomys castanops torridus Russell

Wyoming

Eutamias minimus silvaticus White
Eutamias umbrinus fremonti White
Lepus americanus seclusus Baker and Hankins
[=*Lepus americanus setzeri* Baker]
Microtus montanus codiensis Anderson
Microtus montanus zygomaticus Anderson
Microtus pennsylvanicus pullatus Anderson
Myotis thysanodes pahasapensis Jones and Genoways
Ochotona princeps obscura Long
Thomomys talpoides attenuatus Hall and Montague
Thomomys talpoides meritus Hall
Thomomys talpoides rostralis Hall and Montague

VENEZUELA

Eumops perotis renatae Pirlot

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ECOLOGY OF POCKET GOPHERS OF MESA VERDE, COLORADO

BY

CHARLES L. DOUGLAS

The Mesa Verde land mass consists of about 200 square miles of plateau country in southwestern Colorado near the Four Corners, where Colorado, Utah, Arizona, and New Mexico have a common boundary. The Mesa Verde, named by early Spanish explorers of the Southwest, is the remnant of a plateau laid down by late Cretaceous seas. Erosion has dissected the plateau until it is now a cuesta consisting of long, finger-like mesas joined at their northern ends but otherwise separated from each other by deep canyons (Figs. 1-3). In 1906, part of the land mass was set aside, by Congress, as Mesa Verde National Park in order to preserve dwellings of prehistoric Indians, for which the area is famous. Today, more than 52,000 acres are included within the boundaries of the park.

Elevations in Mesa Verde National Park range from 8572 feet at Park Point down to about 6500 feet at the southern ends of the mesas, where the canyons are from 600 to 900 feet deep. Mesa Verde is in the pinyon-juniper climax region that extends through much of the Southwest; and pinyon-juniper woodland is the dominant canopy cover on the tops of the mesas. Oak chaparral and mixed shrubs occur on slopes. Past fires apparently have permitted establishment of a shrub zone at some of the higher elevations. Sagebrush grows in the bottoms of canyons and in many of the drainages on top of the mesas, and also persists as a late successional stand on the disturbed soil around prehistoric surface dwellings. Stands of Douglas fir occurs on many of the cooler north-facing slopes where micro-climates are favorable for its growth. Individual trees and small stands of ponderosa pine are found in sheltered places throughout the Mesa Verde.

Climatically the Mesa Verde is semi-arid. Precipitation has averaged about 18 inches each year for the past 45 years, with July and August generally having the most precipitation. Precipitation is heavier on the higher, northern end of the park than on the southern end, owing to the proximity of the northern parts of the park to the nearby La Plata Mountains.

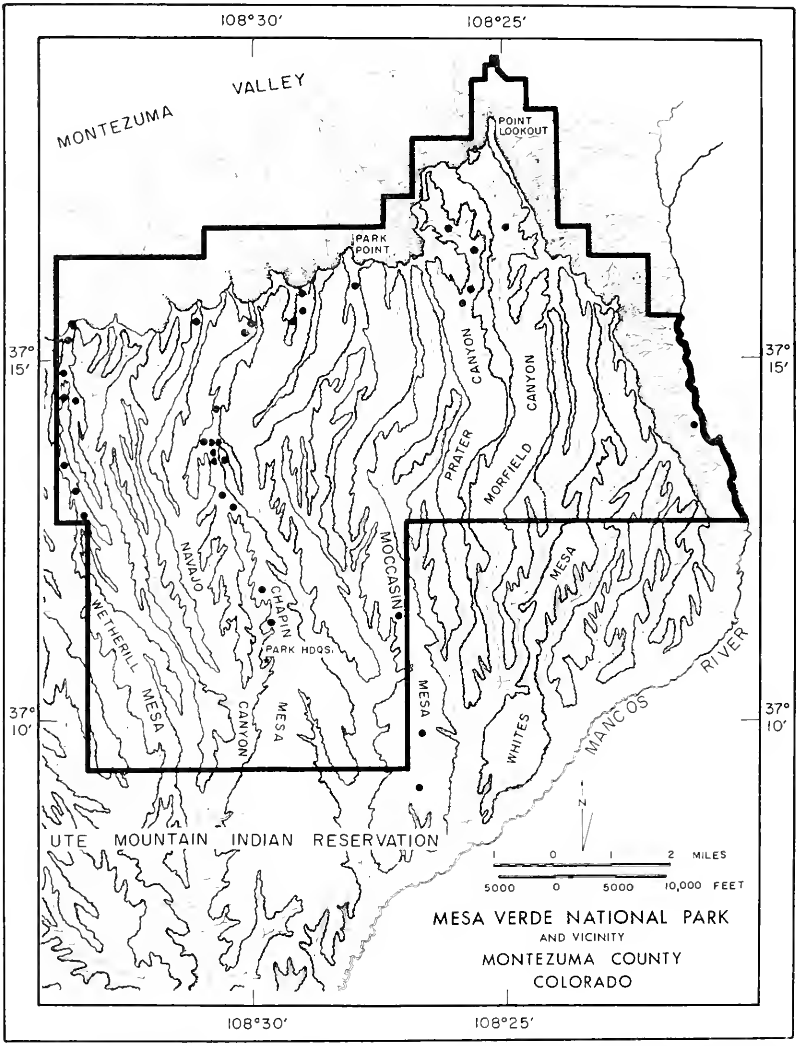

FIG. 1. Map of Mesa Verde National Park and vicinity, showing localities at which specimens of pocket gophers have been collected.

Interdisciplinary research recently conducted under the auspices of the Wetherill Mesa Archeological Project has resulted in reports on mammals of the park (Douglas, 1963, 1967a, 1967b), on amphibians and reptiles (Douglas, 1966), on plants (Erdman, 1962; Erdman *et al.*, 1962; Welsh and Erdman, 1964; Fritts *et al.*, 1965; Douglas and Erdman, 1967), and a report on climatic conditions in the park is in press. Earlier zoological studies include a report on mammals by Anderson (1961).

Pocket gophers, *Thomomys bottae aureus*, are found in Mesa Verde along roadsides where soil has been disturbed, in grassy meadows, in stands of sagebrush, and in the shrub zone along the north rim of the park. Gophers occasionally are found in openings in the pinyon-juniper woodland, in oak brush, and in rocky areas that do not appear to offer adequate conditions for fossorial animals. The diversity of habitats used by gophers led me to study their ecology in Mesa Verde. This report is the first to result from these studies.

Gophers were studied periodically from 1962 through 1967. Field notes were kept on locations and activities of colonies and individuals from 1961 through 1963. Trapping and analyses of habitats was begun in 1963 and continued through 1967. Most of the gophers trapped for use in this study were caught in 1965 and 1967. Twenty-eight months were spent in residence in Mesa Verde National Park from 1961 through 1964; also, I visited the park from August 10 to 16, 1965, April 18 to May 5, 1967, and September 18 to 30, 1967, to study pocket gophers.

DISTRIBUTION OF GOPHERS IN MESA VERDE

Gophers have been collected in Mesa Verde at the places shown in Figure 1; the localities are listed below under "specimens examined" and "other locality records." Specimens listed under the latter heading have not been examined by me. Specimens housed in various collections are designated as follows: Museum of Natural History, University of Kansas (KU); United States National Museum (USNM); Mesa Verde National Park (MV); Museum of Vertebrate Zoology, University of California (MVZ). Specimens presently in my personal collection are listed by locality, followed in parentheses by the number of individuals. A total of 132 specimens from Mesa Verde were examined and measured. To the best of my knowledge, the specimens listed below represent all gophers that have been taken in the park.

Specimens examined.—Total 132, as follows: Mancos River, 6200 ft. (KU 69307-69315); head Prater Canyon, 7700 ft. (13); Upper Well, Prater Canyon, 7575 ft. (KU 69279); Prater Canyon, 7500 ft. (KU 75977); ¼ mi. N Middle Well, Prater Canyon, 7500 ft. (KU 69280); Middle Well, Prater Canyon, 7500 ft. (KU 69281-69285); 6.8 mi. S North Rim, Moccasin Mesa (KU 102058); 8 mi. S North Rim, Moccasin Mesa (20 and also KU 102059-102061); 9 mi. S North Rim, Moccasin Mesa (2); Morfield Canyon, 7600 ft. (KU 75978);

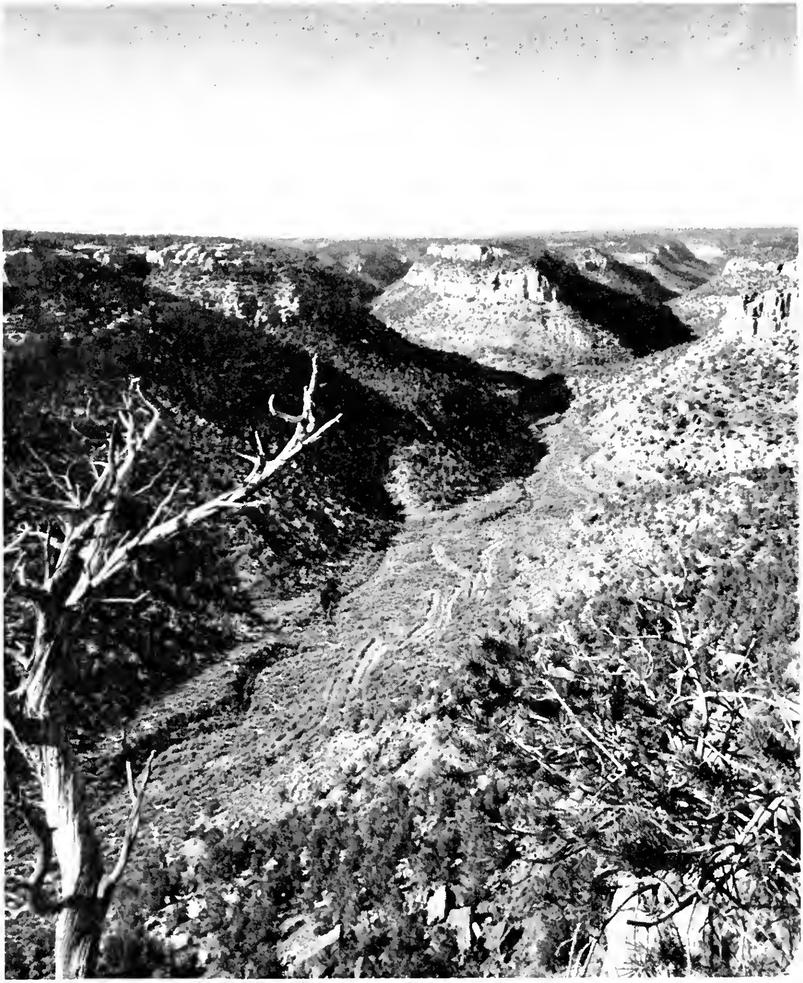

FIG. 2. View of Navajo Canyon looking northward toward the confluence with Spruce Canyon. At this point, the canyon bottom is 600 feet lower than the tops of the mesas.

Park Point, 8400-8500 ft. (16 and also KU 102047-102048, 102050-102057); ¾ mi. S, 1¾ mi. W Park Point, 8000 ft. (KU 69286-69288); 1¼ mi. S, 1¾ mi. W Park Point, 8000 ft. (KU 69289); 1½ mi. S, 2 mi. W Park Point, 8075 ft. (KU 69290); sec. 27, head East Fork, Navajo Canyon, 7900 ft. (KU 69291-69292); sec. 27, head East Fork, Navajo Canyon, 7875 ft. (1); head West Fork, Navajo Canyon (1); ½ mi. N Far View Ruins, 7825 ft. (KU 69293); Far View Ruins, 7700 ft. (KU 69294); 100 yds. W Far View Ruins (1); 200 yds. W Far View Ruins (6); 300 yds. W Far View Ruins (3); Far View Ruins, ¼ mi. W Highway (1); Drainage ¼ mi. S Far View Ruins (1); 200 yds. S Far View Ruins (1);

¼ mi. S Far View Ruins Road, 30 ft., E Highway (2); 1 mi. SW Far View Ruins (2); 1.2 mi. S Far View Ruins Road (1 and KU 102062); 100 yds. N Wetherill Lab, 7050 ft., Chapin Mesa (2); Residence Area, 7000 ft., Chapin Mesa (1); N Rim, Wetherill Mesa, 8239 ft. (2); 3 mi. N Rock Springs, 8200 ft. (KU 69295-69298); 2.2 mi. N Rock Springs (1); 2½ mi. N, ½ mi. W Rock Springs, 8100 ft. (KU 69299-69301); 2 mi. N, ¼ mi. W Rock Springs, 7900 ft. (KU 69302-69303); 1 mi. NNW Rock Springs, 7600 ft. (KU 69304); ½ mi. NNW Rock Springs, 7500 ft. (KU 69305); Rock Springs, 7400 ft. (1 and KU 69306).

Other locality records.—Prater Canyon, 7600 ft. (MVZ 74408-74410); Far View Ruins, 7700 ft. (MV 7852/507, 7853/507); Mesa Verde, northern end, 8100 ft. (USNM 149087).

The distribution of gophers is influenced by a complex interrelationship of edaphic and climatic factors. Since gophers spend most of their lives in subterranean tubes, it is important that the soil in which they live be of sufficient depth to permit development of feeding tunnels as well as deeper living chambers where microenvironmental variables are more constant. Friability and constituency of soils influence the ability of gophers to dig new tunnels and the amount of friability undoubtedly affects gaseous exchanges between air in the tunnels and air in the interstices of the soil (see Kennerly, 1964).

Soils on mesa tops are loessal in origin; the earliest preserved loess in Mesa Verde probably is Sangamon in age (Arrhenius and Bonatti, 1965). Soils in Mesa Verde generally are shallow, although deeper soils occur in some saddles between ridges along the northern rim of the land mass, and in the bottoms of canyons where deep, sandy alluvial terraces occur.

It was observed early in the study that gophers occurred in a variety of vegetational associations within Mesa Verde. Soils in these associations ranged from deep, sandy alluvium found in drainages, to the shallow soils of the pinyon-juniper woodland. In some places, gophers dug tunnels through hard layers of subsurface caliche, and numerous pieces of it were present in their mounds. In a former gravel storage area, gophers dug to the surface through about one foot of hard-packed gravel that was almost impossible to excavate with a shovel. On Park Point, individuals dug through a residual layer of loose rock to deposit rock-filled soil above ground. In other areas on Park Point they dug small contorted tunnels around and between subsurface boulders in areas that offered little in the way of soil and vegetation.

In order to learn more about the composition of soils in gopher habitats, samples of soil were collected from the top two inches of

FIG. 3. Prater Canyon near upper well, looking southward. Pocket gophers live in the sedge- and grass-covered soils of the canyon.

the surface in 18 of the major trapping localities (Table 1). These samples were analyzed for particle size by the hydrometer method, which permits rapid determinations of percentages of clay, silt, and sand (Bouyoucos, 1967).

The results of the hydrometer analyses are given in Table 1. Each of the values listed in this table represents an average of duplicate samples. The soils from various gopher habitats are moderately fine to medium in texture, and are classified as silty clay loam (27 to 40 per cent clay), silty loam (40 per cent or more silt), or as sandy clay loam (up to 39 per cent silt). Of much more importance than the classification of the soils is the fact that moderately fine to medium soils have excellent capacities for retaining moisture, being surpassed only by fine soils containing more than 40 per cent clay. Available moisture is defined as that percentage between field capacity and wilting point, and is expressed in inches of moisture per foot of soil. The range and average values of available moisture for soils in the state of Colorado are as follows: moderately fine, 1.6-2.5, average 2.2; medium (40 per cent or more silt), 1.6-2.5, average 2.3; medium (0 to 39 per cent silt), 1.5-2.4, average 1.9 inches per foot (Orville Parsons, personal communication).

TABLE 1.—PERCENTAGES OF CLAY, SILT, AND SAND OCCURRING IN SOIL SAMPLES FROM VARIOUS LOCALITIES IN MESA VERDE NATIONAL PARK, AS DETERMINED BY THE HYDROMETER METHOD.

Locality	Clay	Silt	Sand
Park Point	23.60	43.10	33.30
Park Point, 8500 ft.	16.10	29.10	54.80
Park Point, 8400 ft.	11.60	45.55	42.85
200 yds. W Far View Ruins	16.40	36.85	46.75
300 yds. W Far View Ruins	24.15	30.15	45.70
300 yds. W Far View Ruins	31.70	32.90	35.40
1 mi. SW Far View Ruins	26.10	35.10	38.80
200 yds. W Far View Ruins	19.50	39.25	41.25
North Rim Wetherill Mesa	12.60	48.10	39.30
2.2 mi. N Rock Springs	15.10	50.60	34.30
Prater Canyon, 7600 ft.	17.30	23.90	58.80
Prater Canyon, 200 yds. S Highway	30.00	37.00	33.00
Moccasin Mesa, northern end	11.30	52.70	36.00
Head Meadow, 8 mi. S North Rim, Moccasin Mesa	20.80	45.75	33.45
Meadow, Moccasin Mesa, 8 mi. S North Rim	25.65	43.05	31.30
Meadow, Moccasin Mesa, 8 mi. S North Rim	27.00	45.20	27.80
Meadow, Moccasin Mesa, 8 mi. S North Rim	24.00	51.20	24.80
100 yds., N Wetherill Lab, Capin Mesa	18.50	33.80	47.70

It was somewhat unexpected to find so much variation in samples from the same general area. Nevertheless, soils in Mesa Verde are known to occur in mozaic patterns, and variation in soil composition within a valley, or between various elevations on a ridge, such as Park Point, probably is to be expected.

Probably the most important factor determining distribution of gophers is vegetational ground cover. Distribution of various plants of importance to gophers is regulated by the distribution of soils suitable for their growth and by amounts of nutrients and moisture available in such soils. Factors such as the tolerance of a plant for shade or sunlight, the seral stage in which the plant usually occurs, kinds of dispersal agents, chemical factors in the soil, and more, play regulatory roles in the ability of plants to invade certain areas. When species of plants are heavily cropped by gophers, the ability to grow new roots may be a limiting factor in the survival of such species in areas used by gophers.

Some plants, such as *Poa fendleriana,* are common to various vegetational associations within Mesa Verde, whereas others are restricted to a particular association. In order to analyze the relationship of plants to the distribution of gophers. the vegetation was analyzed at each major trapping locality. Nineteen of the trapping sites were chosen for intensive analysis of the vegetation. The sites were selected to include various associations, and all localities at which particle sizes of the soils had been analyzed. The dominant and codominant species of plants were determined at each site, then other species were listed in order of their relative abundance. More than 70 species of plants were recorded from the 19 sites. The most abundant plants in gopher habitats consisted of about 30 species; these are listed below in order of their relative number of occurrences:

Poa fendleriana
Eriogonum racemosum
Penstemon linarioides
Amelanchier utahensis
Solidago petradoria
Pinus edulis
Juniperus osteosperma
Aster bigelovii
Chrysothamnus depressus
Lupinus argenteus
Astragalus scopulorum
Artemisia tridentata
Artemisia nova
Lithospermum ruderale
Purshia tridentata
Erigeron speciosus
Artemisia ludoviciana
Eriogonum umbellatum
Sphaeralcea coccinea
Tragopogon pratensis
Achillea millefolium
Chenopodium sp.
Chrysothamnus nauseosus
Comandra umbellata
Koeleria cristata
Stipa comata
Opuntia sp.
Castilleja chromosa
Erigeron flagellaris
Fendlera rupicola

The ground cover at the head of Prater Canyon was composed mostly of *Carex praegracilis, Equisetum* sp., and *Agropyron desertorum.* Although these species were of major importance to a large colony of gophers at this site, they were found only at this locality and therefore did not rank among the 30 most abundant species listed above.

The first 10 species of plants listed above are widely distributed in Mesa Verde. Of these, six species (or in two cases closely related species) were eaten by captive gophers (Table 2). It seems reasonable to assume that when a species is found in more than half of the 19 localities it is utilized by gophers. Plants such as *Chrysothamnus* sp., having numerous, succulent roots, probably are utilized more than plants such as *Aster bigelovii*, which has only one major root. Plants with widespreading root systems can be cropped repeatedly whereas plants with fewer roots may be killed after the first severe cropping.

Gophers influenced changes in vegetation from year to year by their selection of certain species. This was especially evident in the meadow of Moccasin Mesa. In 1965, tunnels of gophers were found under almost every clump of cactus (*Opuntia* sp.) occurring in the meadow. In some cases the entire underground parts of the plants were eaten and the part above ground was pulled partly into a

TABLE 2.—FOOD ITEMS CONSUMED BY CAPTIVES OF *Thomomys bottae* (+, EATEN; O, NOT EATEN; —, NOT OFFERED).

Plant	Roots	Stem	Leaves	Other
Artemisia frigida	—	+	+	—
Artemisia ludoviciana	+	+	o	—
Aster bigelovii	+	+	+	flowers
Astragalus scopulorum	+	+	o	—
Castilleja chromosa	+	+	+	—
Chrysopsis villosa	+	+	+ (basal)	—
Chrysothamnus nauseosus	+	+	—	—
Equisetum sp.	+	—	—	—
Fendlera rupicola	—	+	—	—
Lupinus caudatus	+	+	—	—
Pedicularis centranthera	+	+	+	—
Penstemon linarioides	+	+	+	—
Quercus gambelii	+	—	—	acorns
Solidago petradoria	+	+	—	—
Sphaeralcea coccinea	+	o	o	—

burrow. Some clumps of cacti recovered by 1967, but others died out completely and the area was invaded by primary successional species such as *Sphaeralcea coccinea.*

Climatic factors affecting plants may also cause gophers to shift their area of activity, thereby allowing recovery of the vegetation in the former area of concentration. In 1965, moisture from heavy winter snows and spring rains promoted a luxuriant growth of grasses and herbs on Moccasin Mesa (see Fig. 4). In the autumn of that year, vegetation in the meadow was dense and gophers were concentrated around the periphery of the meadow at the edges of the pinyon-juniper woodland. Only a few gophers were found in the meadow. In this case, many more roots were available in the meadow than in the relatively sparse ground cover of the woodland. The next year vegetation in the meadow was more normal in density, and gophers were again concentrated there. I suppose that gophers preferred the deeper soils and more abundant plants in the meadow, but were concentrated in the more sparsely vegetated areas when plants in the meadow became too dense for unhampered movement or vision above ground, because gophers appear to avoid tall, dense vegetation.

Gophers move tons of soil each year (Kennerly, 1964; Downhower and Hall, 1966). Mounds often cover the surface sufficiently to prevent further growth of the underlying vegetation. Succession of plants on mounds then progresses as it would on any denuded ground, but because of the relatively small area covered by each mound, succession is fairly rapid. Mound obliteration in Mesa Verde customarily takes two or three years, whereas larger denuded

FIG. 4. Meadow on Moccasin Mesa, 8 mi. S North Rim. Heavy precipitation in winter and spring of 1967 promoted the unusually luxuriant growth of grasses shown here.

areas require longer to recover. An example of the slow rate of succession in Mesa Verde is seen on the northern part of Wetherill Mesa, which burned in 1934. In 1967 this area supported shrubs, grasses, and herbaceous species, but pinyon and juniper seedlings had not become re-established despite the presence of unburned woodland adjoining the area. Likewise, in 1961, seedlings of pinyon and juniper were just becoming established in a large area on Chapin Mesa that was burned in 1858.

In June of 1964, stakes were placed beside each of 20 new gopher mounds in the meadow on Moccasin Mesa (see Fig. 5). These mounds were inspected in the autumn of 1964 and again in 1965 and 1967, in order to learn which species of plants were early invaders of such disturbed soil. No new vegetation appeared on the mounds in 1964. In August, 1965, *Sphaeralcea coccinea* and *Tragopogon pratensis* were present. In May, 1967, *Sphaeralcea coccinea*, *Tragopogon pratensis*, *Artemisia dracunculus*, and *Poa pratensis* grew on the mounds.

FIG. 5. Photograph of gopher habitat in meadow on Moccasin Mesa. Mounds made, and staked, in 1965 were nearly obliterated in two years time (photograph taken in September, 1967).

Individuals of *Thomomys* browse above ground around the openings of burrows. Evidence of feeding usually is found on plants within a six- to 12-inch radius around the opening of the burrow. Such grazing was especially evident in areas where rabbit brush, *Chrysothamnus nauseosus*, occurred. Gophers appear to relish the above-ground parts of this plant as well as its roots, as was verified by the feeding of captives (Table 2). Gophers also harvested sweet vetch, *Astragalus scopulorum*, and Indian rice grass, *Oryzopsis hymenoides*, and aerial parts of these plants were found in tunnels. Such aerial parts were cut into lengths of six or seven inches before being taken below ground.

Side tunnels of burrows often were packed with small pieces (one to two inches long) of roots and grass stems. These accumulations probably represent food caches that are stored for later use. All such caches filled with vegetation and soil were found within one or two feet of a burrow opening. Several cones and numerous nuts of pinyon pine, *Pinus edulis*, were found in the cache of one gopher.

The cones had been opened and most of the nuts had been removed and eaten; the chewed coats of seeds remained in the tunnel. This was especially interesting because the nearest pinyon pine was about 30 feet from the opening of the burrow; the opening was also at that part of the tunnel nearest the woodland.

Captive gophers soon die if they are not given succulent plants or roots to eat. On the other hand, captives gain weight and thrive on a diet of potatoes and rolled oats, supplemented with fresh green vegetation. Gophers probably do not produce much if any, metabolic water. Roots found in cheek pouches and in tunnels indicate that they prefer non-woody, succulent roots that can be eaten easily. Few woody roots were recovered from cheek pouches or from tunnels. Captives chewed the softer parts of roots and stems, but rarely bothered with woody roots when other foods were available. All stomach contents of *Thomomys* that I have seen always were green in color, indicating extensive foraging on aerial parts of plants.

The fossorial mode of life permits *Thomomys* to avoid the problems of thermo-regulation that would be attendant with living on the surface. Fossorial forms are known to have poor thermo-regulation and a generally low tolerance to high temperatures. The maintenance of water balance also can be a pressing problem facing species living in arid environments. Relative humidity is more constant in burrows than it is at the surface (Kennerly, 1964); thus living in subterranean tunnels permits gophers to avoid desiccation and the need for obtaining larger amounts of moisture to facilitate osmoregulation.

The storage of roots and stems underground provides a source of moist vegetation for gophers. This would be advantageous to them in the hottest months of summer and during periods of drought when aerial parts of plants, and perhaps many root systems are reduced in moisture content. *Thomomys bottae* apparently is well adapted to life in arid environments because of its behavior, rather than because of its physiological adaptations.

Thomomys bottae is coprophagic, and captives often were observed to eat feces. This was accomplished in such a way that it has not been possible to determine whether this species produces two kinds of droppings, as do rabbits. At any rate, captive individuals produce copious droppings and, as would be expected, the caecum is large and probably contains bacteria that break down cellulose.

REPRODUCTION, GROWTH, AND DEVELOPMENT

In Mesa Verde, reproduction in *Thomomys* occurs only in spring. Pregnant females were taken in late April and early May; females with enlarged uteri were taken in April, August, and September, indicating that reproductive activity probably begins in March, or perhaps late in February. The gestation period for *T. bottae* is about 18 to 19 days (Schramm, 1961). Lactating females were taken in early May, but none of 31 females taken in August or September was lactating (Fig. 6). Four females had from two to four embryos each (average three). Two other females each had

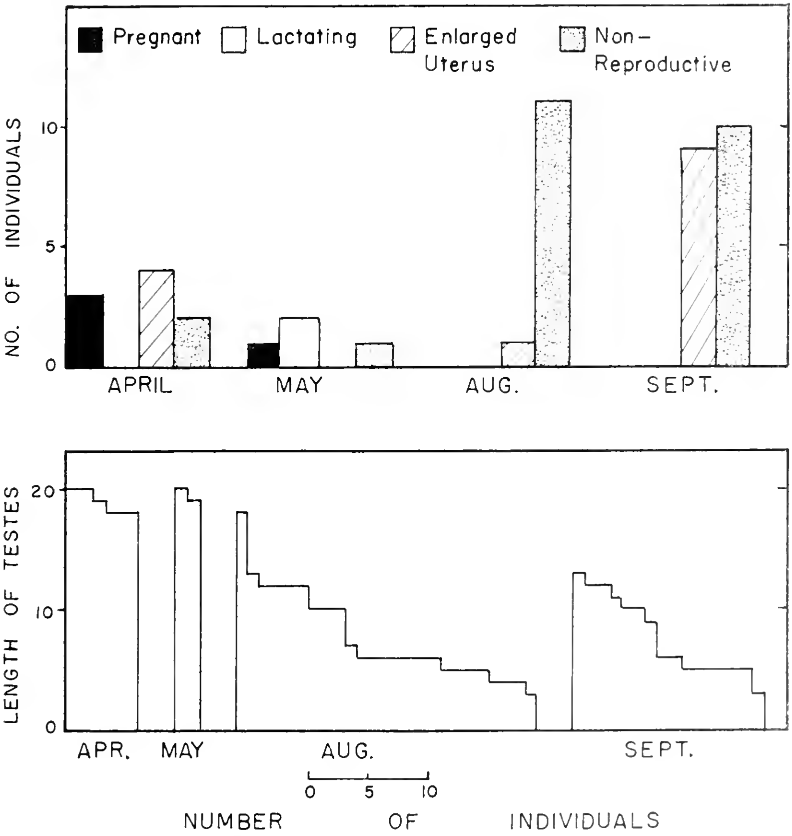

FIG. 6. Condition of reproductive organs of dissected gophers collected in Mesa Verde from 1965 through 1967. Reproductive condition of females (upper) in various months; size of testes of males (lower) collected in various months.

three placental scars. Howard and Childs (1959:295) reported an average litter size of 4.6 for *T. b. mewa* from California. Young of the year appeared in traps in April, May, August, and September. Unfortunately, no gophers have been trapped in Mesa Verde earlier than April and none has been taken in June or July; the data on reproduction are therefore incomplete.

Eight males taken in late April and early May of 1967 were in breeding condition. Howard and Childs (1959:300) separated kill-trapped individuals of *T. bottae* into three age classes by the size of the testes. Testes of animals less than five months of age were between one and 10 millimeters in length (average 4.5 mm.). Males nine months or older had testes 12 millimeters or longer. Figure 6 shows the length of testes in males taken in Mesa Verde in various months of the year. Testes of adults taken in spring were engorged, highly vascularized, and scrotal, whereas those of adults taken in August or September were flaccid, wrinkled, and less vascularization was present. Testes of young males were not apparent externally and it is difficult to sex such young animals without dissecting them.

Figure 7 shows the distribution of sizes of males and females taken from Mesa Verde, and the months in which they were taken. Although the samples are somewhat limited, it is apparent that young of the year grow rapidly and attain adult size by autumn, when separation of young and adult individuals can best be accomplished by examining reproductive tracts. Apparently, few females breed in the first year, whereas all individuals a year old or older evidence reproductive activity. This agrees with reports in the literature (Howard and Childs, 1959:302).

Table 3 summarizes measurements taken on 122 specimens examined in this study. Measurements for young of the year (young and subadult individuals) are given separately from those of adults.

Juveniles are those animals that are still in the nest, or that have juvenal pelage. These individuals can be distinguished easily from adults, but seldom appear in traps. Young individuals are those that are moving about on their own, and those in which the juvenal pelage is being replaced. Subadults are those young of the year that have reached adult proportions but have not yet bred. Adults are those individuals showing signs of reproductive activity. In some cases, young of the year may breed and thus would then be classified as adults, but breeding in the first season probably is an unusual occurrence in Mesa Verde.

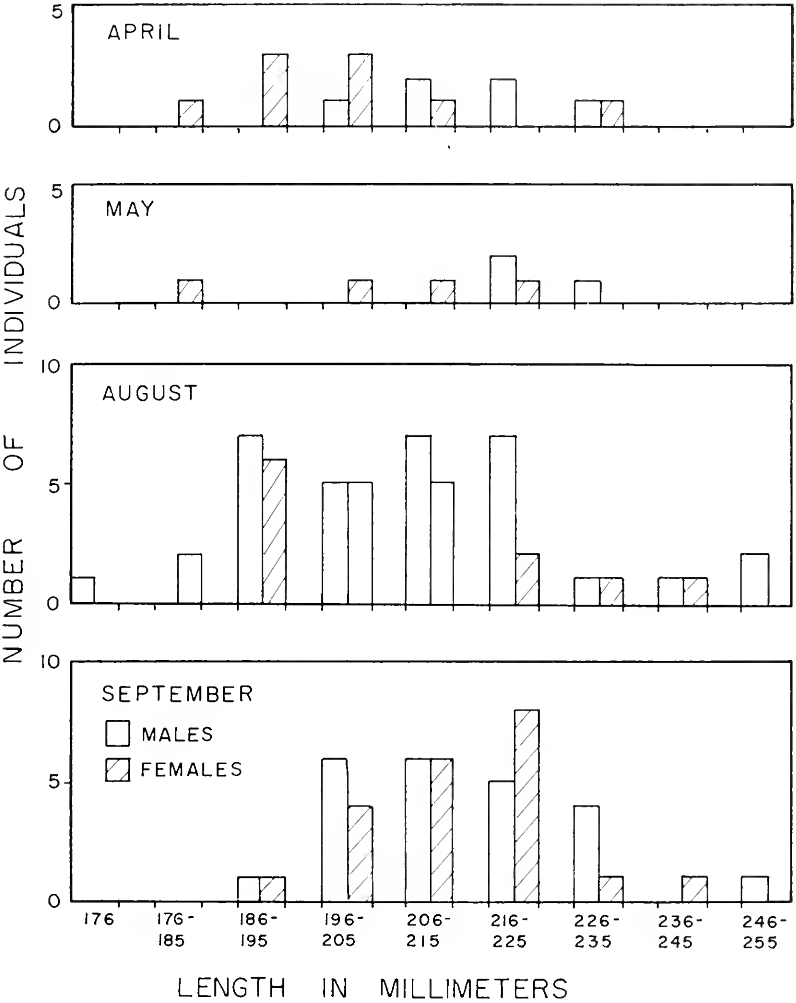

FIG. 7. Size distribution of 63 male and 57 female pocket gophers taken in Mesa Verde National Park and vicinity.

In young females the pubic symphysis is not fully absorbed, the nipples are not enlarged, and the uterus usually is not dilated nor does it show other evidence of breeding activity. Individuals meeting these criteria were considered to be young of the year, irrespective of their external size or dimensions of the skull. Three young females taken in late April measured 177 to 197 millimeters in total length (average 187 mm.), indicating the rapid growth achieved by

TABLE 3.—MEASUREMENTS, IN MILLIMETERS, OF *Thomomys bottae*. ADULT INDIVIDUALS WERE THOSE EXHIBITING EVIDENCE OF REPRODUCTIVE ACTIVITY; YOUNG INDIVIDUALS WERE THOSE JUVENILES AND YOUNG OF THE YEAR SHOWING NO REPRODUCTIVE ACTIVITY. MEAN, MAXIMUM AND MINIMUM ARE GIVEN IN THAT ORDER FOR EACH MEASUREMENT.

Measurement	30 adult females	28 young females	37 adult males	27 young males
Total length	211	201	220	203
	240	220	250	225
	185	175	187	174
Length of tail	57	57	62	60
	66	71	79	83
	42	48	48	50
Length of hind foot	29	28	29	29
	32	30	35	33
	26	24	27	25
Condylobasal length	37.4	35.8	39.3	35.5
	40.6	38.5	44.9	39.9
	34.1	32.0	34.4	30.8
Palatal length	22.0	21.0	23.4	20.9
	23.9	23.6	26.7	23.5
	20.3	17.9	19.6	17.5
Length of nasal	11.9	11.2	12.9	11.3
	13.4	12.5	15.3	13.8
	10.7	9.4	10.2	8.7
Zygomatic breadth	23.6	22.6	24.9	22.0
	25.6	24.6	28.4	25.5
	21.5	19.3	22.6	19.6
Mastoidal breadth	19.4	19.1	20.3	18.6
	20.9	20.1	23.0	21.0
	18.0	15.9	16.8	16.3
Least interorbital breadth	6.3	6.3	6.1	6.3
	6.8	6.8	6.9	6.8
	5.6	5.7	5.3	5.8
Alveolar length of maxillary toothrow	7.4	7.3	7.7	7.2
	8.7	8.3	8.9	8.1
	6.6	6.2	6.5	6.5
Length of mandible	25.3	24.4	26.9	24.6
	28.6	27.3	31.8	27.5
	22.9	20.1	22.4	21.2
Capacity of braincase (cc.)	1.3	1.2	1.3	1.3
	1.5	1.4	1.6	1.4
	1.1	1.0	1.1	1.1

young individuals in the first several months of life. Twenty-three young females taken in August and September measured from 178 to 219 millimeters in total length (average 202), whereas 27 adult females had total lengths of 185 to 238 millimeters (average 212). It is apparent that most young individuals attain adult size quite rapidly. Individuals born early in the season may reach adult proportions by late spring and certainly do so by autumn.

In young males the testes are much smaller than those of males more than one year old (Howard and Childs, 1959:300). Thirty young of the year had testes between three and 10 millimeters in length (average 6.0), and total lengths from 187 to 226 millimeters (average 209). Nineteen adults had testes that measured 11 to 20 millimeters in length (average 15) and total lengths ranging from 187 to 250 (average 223).

Youngman (1958:366) studied museum specimens of *T. bottae* from Colorado, and established three criteria for adulthood: ". . . (a) suture obliterated between supraoccipital and exoccipital, (b) suture at least partly obliterated between basisphenoid and basioccipital, (c) supraorbital crests not widely separated and almost parallel. . . ." I examined 26 skulls from young females, collected in the course of the present study, in order to see if these three criteria are applicable when reproductive condition is known. The skulls were from animals that were unquestionably young of the year. These individuals exhibited no internal or external evidence of reproductive activity, the pubic bar had not been resorbed, and they were among the smaller individuals taken. Females were used because their lack of reproductive activity can be determined with much more certainty than can that of males.

Of the 26 young of the year, 16 met Youngman's first criterion (see above), 18 met the second criterion, and 12 met the third. Because of the rapid rate of growth in young and subadult individuals, developmental characteristics of the skull may be misleading for the establishment of age groupings. I do not consider the above-listed criteria adequate for differentiating young of the year from adult individuals. When studying museum specimens, the investigator must establish arbitrary criteria for separating age groupings. At present there is little known about rates of growth in geomyids, as in other non-game species, and it would be virtually impossible for an investigator to assign accurate age groupings on the basis of skull dimensions alone, without having knowledge of the condition of reproductive organs, and in the case of females, the condition of pubic bones. Many investigators do not dissect female gophers, or if they do, the tendency seems to be to make no notation on the specimen label unless embryos are found. There is more of a tendency to measure and record the size of testes. It is to be hoped that in the future investigators will record lack of embryos as well as their presence; information as to presence or absence of the pubic bar in females also should be recorded.

CLIMATIC CONDITIONS AFFECTING GOPHERS AT PARK POINT

Climatic conditions were studied at Park Point, 8575 feet elevation (see Fig. 8), the highest point in Mesa Verde, as part of an environment measurement program of the Wetherill Mesa Project. As mentioned earlier, one of the largest colonies of pocket gophers in Mesa Verde occurs at Park Point. Thus the choice of this site for a weather station was indeed fortunate. The occurrence of gophers on this rocky ridge was first noticed when the weather station was installed. Gophers later were observed to pile mounds of soil in areas where, because of rocks, I had difficulty in obtaining soil samples at the six- and 12-inch depths. I was surprised to find a sizeable colony of gophers on this ridge where the soil was shallow and rocky and where vegetation, although not in short supply,

FIG. 8. View southward from Park Point, the highest elevation in Mesa Verde (8575 feet). Gophers lived on this ridge from 1961 to 1967 despite the rocky nature of the soil.

seemed to require such an expenditure of effort for gophers to obtain.

A standard U.S. Weather Bureau shelter was installed at this site in September of 1961 and instruments were run through December, 1963. Air temperatures and relative humidities were recorded by means of a Bendix hygrothermograph; soil temperatures were recorded at depths of two, six, and 12 inches by a Kahl three-pen thermograph; and precipitation was measured by means of a standard Weather Bureau rain gauge. Soil moisture was determined gravimetrically at depths of two, six, and 12 inches about twice each month.

Table 4 summarizes the climatic conditions at Park Point. Precipitation at this site is the highest of that at any sites measured in the Mesa Verde. The higher parts of the Mesa Verde land mass are first to receive moisture from ephemeral storms that originate in the nearby La Plata Mountains. Therefore, the higher, northern ends of the mesas are more mesic than the southern ends, and winters are the more severe at the higher elevations. Park Point has the most severe climate of the Mesa Verde as far as cold, persistent snows, and frozen soils are concerned. The growing season at this site is shorter than that at lower elevations.

The range of thermal tolerance of *Thomomys bottae* has not yet been studied, but it is apparent that this species escapes the high surface temperatures and the metabolic stresses that would result from living at such temperatures, by living six or more inches below the surface.

Gophers are active in the winter at Park Point, and in the spring evidence of winter digging is apparent as tubes of soil lying on the surface. In winter, soil temperatures at all levels varied only a few degrees on either side of freezing. Soil temperatures at the lower levels were found to be only slightly above freezing in March when, it is thought, most of the young are born. There is little air movement in tunnels of *Thomomys*; therefore, temperatures in tunnels are the same as those in soils at the same depths (Howard and Childs, 1959:332; Wilks, 1963:272; Kennerly, 1964:408).

The tubes of soil evident on the surface in spring represent tunnels in the snow that were filled with soil. There would seem to be little need for gophers to move soil in order to feed on surface vegetation in the winter, because they could, and do, tunnel in the snow at the surface (see Marshall, 1941). Some of the roots prob-

Table 4.—Soil temperatures at depths of two, six, and 12 inches and precipitation recorded at Park Point, 8500 ft., Mesa Verde National Park. The range represents extreme temperatures for each month; mean temperatures represent a monthly average of daily maximum and minimum readings. An asterisk indicates incomplete data.

Date	Two inches		Six inches		12 inches		Precipitation in inches
	Range	Mean	Range	Mean	Range	Mean	
1962* April	29-72	51.0	36-59	48.5	39-52	46.5	0.39
1962 May	33-79	55.7	39-67	53.0	40-59	50.9	0.93
1962 June	42-103	71.6	47-81	66.4	49-72	62.7	1.03
1962 July	55-104	78.7	63-83	72.9	64-74	69.7	2.02
1962 August	52-105	77.9	60-85	73.2	63-76	70.2	1.97
1962 September	38-96	66.3	45-77	63.4	48-69	61.8	2.13
1962 October	34-76	51.7	38-64	50.2	41-56	48.8	2.94
1962 November	30-64	40.3	31-54	39.9	32-48	39.4	1.50
1962 December	24-41	29.8	26-35	30.4	26-33	30.2	0.90
1963 January	23-31	27.5	25-32	29.1	25-34	29.9	1.30
1963 February	26-34	30.4	28-35	31.4	28-35	32.1	1.20
1963 March	24-64	33.2	27-51	32.6	28-45	33.0	1.00
1963 April	28-73	47.1	32-59	45.2	35-53	44.1	0.55
1963 May	42-95	67.5	46-76	63.1	48-68	60.6	0.16
1963 June	45-111	76.8	55-89	71.2	59-79	69.1	0.07
1963 July	55-110	81.8	61-90	76.7	66-81	75.3	1.97
1963 August	54-110	74.5	58-87	70.7	63-80	70.3	7.62
1963 September	49-99	72.9	56-79	67.8	61-71	66.6	0.45
1963 October	36-100	64.5	43-77	59.9	49-70	59.8	2.70
1963 November	24-66	39.2	32-54	38.8	34-49	40.5	1.04
1963* December	24-44	33.6	29-36	32.7	32-36	34.6	0.75
1964 April	27-70	43.4	32-55	40.6	35-48	40.0	......
1964 May	31-92	60.0	35-74	56.0	38-67	54.0	......
1964 June	40-107	75.0	49-82	68.0	52-75	66.0	......
1964 July	53-112	82.0	61-89	75.0	65-80	74.0	......
1964* August	47-104	74.0	58-83	70.0	63-76	69.0	......

ably are dug and eaten below the surface, even though the first few inches at the surface are frozen. Mounds could not be piled easily in the winter due to the pressure of overlying snow, and tunnels may be dug in the snow to accept this excess dirt. The number of surface tubes indicate that gophers do not dig soil extensively throughout the winter. Soil for surface tubes must come from below the surface, for I have found no evidence of surface gouging that would be expected if gophers were digging shallow trenches to obtain roots at the surface, and then were filling the snow tunnels behind them. I think that food caches and surface feeding are the most likely sources of food in winter months when the ground is frozen. It seems likely that tubes of soil may represent that removed during tunnel cleaning, especially by females preparing to bear young.

Gophers in Mesa Verde have two periods of increased mound production. One period is apparent late in the autumn, especially in

October and November, prior to the onset of cold weather. The other period is in the spring after the ground thaws. In Mesa Verde the ground thaws and the kinds of animals that hibernate begin to appear above ground by about the first of April. The only significant reduction in mound building activity occurs in June and July, when surface temperatures are high. It is not known whether *Thomomys* aestivates during part of the summer, although Howard and Childs (1959) have suggested this possibility. In Mesa Verde there is some mound building throughout all months of spring, summer, and autumn.

Mound building has been thought to be associated with an increase in soil moisture (Miller, 1948). Kennerly (1964) has shown that the period of increased mound building by *Geomys* begins before and subsides later than the period of sustained high soil moisture. He suggested that a basic biologic rhythm is involved and that factors other than soil moisture influence mound building.

In Mesa Verde, the months generally having the most precipitation are July, August, and February. Although the increase of mound building in the spring appears to coincide with an increase in soil moisture, the autumn period of activity comes after the period of increased soil moisture.

PARASITISM

Trap-killed gophers were placed in a plastic bag immediately upon removal from their burrows. Ectoparasites were killed by placing a piece of cotton soaked in carbon tetrachloride in the closed bag with the gopher. After several minutes the parasites could be brushed from the fur and collected on a piece of paper. Endoparasites were recovered from stomachs and intestines, were stored in 70 per cent ethanol, and were later sent to experts for identification.

Gophers in Mesa Verde are heavily parasitized by fleas. Several individuals had more than a dozen fleas each; the most heavily parasitized individual, an old male, had 53 fleas of two species. This male was captured alive, and it was apparent from his frequent scratching that the fleas caused a great deal of discomfort.

Only one tick, an adult *Dermacentor andersoni*, was found on a gopher collected in this study. The tick was found on the cheek, in the middle of a circle about one half inch in diameter where the fur had been rubbed off. Such aggravation by parasites may be linked to the irregular molting patterns seen in *Thomomys*.

It was surprising to find gophers parasitized by larvae of botflies, because these flies lay eggs on the fur of animals, an activity that obviously occurs above ground. The larvae found in gophers appear to me to be identical in appearance with those of *Cuterebra cyanella* Jones found in *Peromyscus* from Mesa Verde (Douglas, 1967a). Judging from larvae found under the skin and from open exit holes made by larvae, infected gophers have from one to three larvae each. The incidence of infestation was highest in September. Some larvae were found in August, but none was observed in gophers collected in spring.

In summary, parasites presently known from *Thomomys bottae* from Mesa Verde are as follows: *Dermacentor andersoni* (Acarina, Ixodidae); *Cuterebra* cf. *cyanella* (Diptera, Cuterebridae); *Trichuris fossor* (Nematoda); *Dactylopsylla (Foxella) ignota, Dactylopsylla rara,* and *Dactylopsylla* sp. (Siphonaptera). In addition, specimens of Cestoda, Mallophaga, and mites currently are being studied and will be reported elsewhere.

PREDATION

Coyotes are the major carnivores in Mesa Verde that are known to prey upon pocket gophers (Howard and Childs, 1959:337; Wilks, 1963:277). Foxes also are common in the area, but appear to rely more upon berries and lizards than do coyotes. I examined a total of 114 coyote scats that were collected at Mesa Verde each month from September, 1963, through August, 1964. Numerous rodents, but no pocket gophers, were present in the 253 food items represented (Douglas, 1967a). Sixteen scats of foxes contained several rodents, but no gophers. Bobcats also are present in Mesa Verde, but scats of bobcats were seen only rarely, and none has been analyzed.

Hawks, owls, and eagles live in Mesa Verde. Red-tailed hawks were seen frequently on the burned area on the northern end of Wetherill Mesa. I have not been successful in locating occupied hawk or owl nests there. Howard and Childs (1959:337) reported that gophers comprise 7.4 per cent of the diet of red-tailed hawks, and 71.4 per cent of the diet of barn owls at the San Joaquin Experimental Range in California. It seems likely that owls may be a significant predator on gophers in Mesa Verde.

There are two species of snakes, the gopher snake, *Pituophis melanoleucus*, and the rattlesnake, *Crotalus viridis*, in Mesa Verde that could be considered as potential predators on gophers (Douglas, 1966). Of the two, the gopher snake is more abundant. I have collected and examined numerous gopher snakes and other snakes in Mesa Verde, but none contained gopher remains.

Gopher remains were not present in the 130 scats of carnivores that I examined, and none was present in 35 scats of coyotes from the area examined by Anderson (1961). Therefore, it seems unlikely that carnivores exert much influence on population dynamics of gophers in Mesa Verde.

ANOMALIES

The following skeletal and dental anomalies were noted in specimens examined.

The lower jaw of an adult male (CLD 810) has a deformed coronoid process, composed of two parts. The ventral part is of normal size in width and depth, but the dorsal part is slender and abnormally close to the articular process. The coronoid process appears to have been broken, then to have ankylosed where the halves touched. The dorsal part of the process barely clears the squamosal when the jaws are articulated in occlusal position with the skull.

Another adult male (KU 75977), taken on November 10, 1957, in Prater Canyon, 7500 ft., by J. R. Alcorn, has several anomalies of the skull. A tumerous growth had deformed the zygomatic plate of the right maxilla, and also involved smaller bones in the area. The right zygomatic plate is abnormally thick, antero-posteriorly; a bulge of bone protrudes from the posterior part of the plate into the orbit. There is a small hole in the maxilla just anterior to the lacrimal. A wormian bone is present at the junction of the right maxilla, lacrimal, and frontal bones. The right jugal is abnormally short and thick, and the zygomatic arch is somewhat displaced medially because of the tumerous growth on the zygomatic plate and a bending of the rostrum to the right. The posterior, ventral margins of the premaxillae appear to have broken, owing to the torsion of the rostrum. A suture occurs in the left premaxilla in line with the posterior border of the nasals, and a suture occurs somewhat posterior to this in the right premaxilla. The torsion of the rostrum has resulted in malocclusion of the upper and lower incisors, but the maxillary and mandibular toothrows appear to be normal.

A young female (CLD 959) has an unusual dental anomaly. The anterior prism of each lower premolar (p4) is unworn and projects dorsally two and three millimeters above the posterior prisms of the respective premolars. The reason for this anomaly appears to be related to the mobility of the jaws. The glenoid fossa in gophers is several millimeters in length and is parallel to the long axis of the skull. This arrangement facilitates propalinal chewing with the cheekteeth, and allows forward movement of the jaws such that the incisors occlude and can be used when the cheekteeth are disengaged. Normally, when the lower jaws are at their posteriormost position and the cheekteeth are occluding, the anterior prism of each lower premolar lies in line with the posterior prism of each upper premolar. In this specimen the jaws cannot move far enough posteriorly for such an overbite to occur. The mobility of the lower jaws is restricted because the distance between rami is not great enough at their posterior ends. Thus, the articular processes bind against the medial sides of the glenoid fossae and against the bullae, before reaching their posteriormost position in the fossa. As a result, the anterior prisms on the lower premolars do not occlude, and remain unworn.

DISCUSSION

In Mesa Verde, pocket gophers live in soils having less than 32 per cent clay and varying amounts of sand and silt. Ten of 18 samples of soil from areas inhabited by gophers contained more silt than sand, whereas the other eight contained more sand than silt. It seems likely that the percentage of clay affects the ability of gophers to use soils more than do varying amounts of silt and sand. Downhower and Hall (1966) found *Geomys* in Kansas living only in soils having less than 30 per cent clay and more than 40 per cent sand. Attempts by these authors to introduce pocket gophers at places where none lived were least successful where soils had a relatively high clay content.

Although the percentage of clay in most of the soils in Mesa Verde was low, it was sufficiently high in most localities to make the setting of traps difficult when the soil was dry. Soils at various localities on the mesa were dry and hard during much of the summer, whereas those in the bottoms of canyons remained friable throughout the year.

The largest sites of concentration of gophers in Mesa Verde occurred in areas having deep soils. Nevertheless, gophers were taken from rocky areas and from places in the woodland where soils were eight inches or less in depth. In such cases, deeper soils generally were within part of the individual's range. When a gopher was taken from a shallow burrow system, it invariably was a young individual. Burrow systems of adults were at varying depths below the surface, depending upon the depth of soil and amount of rock in the habitat. In deep sandy soils, main tunnels of adults generally were eight to 12 inches below the surface; feeding tunnels were shallower.

Gophers live in various vegetational associations in Mesa Verde. In some places grasses are the most abundant plants, but in most places shrubs and various herbaceous species also occur in the ground cover. Gophers eat a variety of roots and aerial parts of plants, as was determined from feeding experiments with captives and by inspecting contents of caches and cheek pouches of gophers.

Most localities at which gophers have been taken in Mesa Verde are on the northern half of the park, at the higher elevations. Gophers are most abundant along the North Rim and in the deep soils of canyons. In general, large colonies do not occur on the mesas at elevations of less than 7000 feet; the lowest canyon elevations at which gophers were taken was at 6200 feet along the Mancos River.

The occurrence of a large colony of gophers on the southern end of Moccasin Mesa is somewhat unusual. Gophers were not found in sandy drainages on the southern ends of other mesas in the park. I think that the deepness of the soil in the meadow on Moccasin Mesa and the persistent moisture of lower depths helps to explain the ability of gophers to live there. This soil moisture is reflected also in the abundance of grasses and herbaceous species in the ground cover; a dense ground cover is not common at lower elevations on the mesas. Apparently the soil in the meadow is deep enough over the underlying bedrock to retain runoff moisture effectively.

Cactus is thought to be an important source of moisture for gophers, especially on the southern end of Moccasin Mesa. Less precipitation occurs at the lower elevations on the southern end of Mesa Verde, thus soils and plants tend to dry out earlier in the summer at these elevations than at higher, more mesic elevations on the north. The roots of cacti were cropped severely during summer months by gophers on Moccasin Mesa. Such a reliance upon cacti was not evident in habitats of higher elevations in the park.

Captive gophers were found to prefer soft, fleshy roots to hard, woody roots. Roots found in food caches and in cheek pouches of gophers were mostly fleshy kinds. Grasses, bushes, and shrubs have numerous soft fleshy roots that apparently can be cropped repeatedly. Plants having only one major tap root, as do many herbaceous species, can be eliminated rather quickly by having their roots cropped. It is thought that *Thomomys* influences the succession of vegetation by a series of events. Initially the soil is disturbed by mound building, thereby providing a seed bed for early successional plants such as globe mallow and other weedy species. Gophers eat roots of the weedy plants that have become established and the evidence indicates that many plants are killed in the process. In about two years time, the earliest-built mounds have become obliterated. Because the disturbed area usually is small, invasion by plants is rapid. The gopher thus changes the habitat temporarily insofar as the vegetation is concerned. On the other hand, gophers turn over large quantities of soil, and their burrows permit percolation of moisture to lower depths; storage of roots, and deposition of fecal material also raises the organic content of the soil.

The two periods of increased activity in mound building, occurring in spring and in late autumn, appear to be related, respectively, to increasing and decreasing temperatures at the 12-inch depth. The causality of this relationship can only be inferred. Gophers also bear young in spring during the period of soil warming, although the earliest breeders must bear young when the soil is still rather cold.

Thomomys apparently forages above ground more extensively than has been supposed. Pine cones found in a food cache suggest that at least one individual may have foraged at a distance of about 30 feet from its burrow. Shrubs, especially rabbit brush, occurring within several feet of fresh mounds showed evidence of browsing. It is assumed that the browsing was done by gophers, owing to the proximity of the shrubs to the mounds and because of the fondness of captives for stems of this shrub.

Various investigators have remarked that gophers, when released near their burrow, do not always seem to be aware of where to enter their tunnels, and often dig new holes. This may be due to individuals being released in daylight; gophers are known to forage above ground at night, and occasionally in the daytime when the sky is overcast. Evidence indicates that gophers forage around the openings of their burrows, and that they move about on the surface and perhaps range for some distance from the openings.

Remains of *Thomomys* have been found in owl pellets (Howard and Child, 1959) and these gophers also have been taken in snap traps set for mice (Williams, 1955:227). Larvae of bot flies were found in gophers taken in Mesa Verde, indicating that they spend enough time above ground for flies to lay eggs on their fur.

The present lack of knowledge about how to accurately determine the age of gophers from skeletal characteristics presents a perplexing problem. Young of the year were found to attain adult size at a rapid rate, and animals several months old could not be differentiated from adults on the basis of skeletal or bodily dimensions. Examination of reproductive organs allows separation of young of the year from adults and this is of some value in studying populations. It would be invaluable to future studies of gopher populations if an accurate method of estimating chronological age could be found. Studies presently are being conducted toward this objective and these will be reported elsewhere.

RELATIONSHIP OF GOPHERS TO ARCHEOLOGICAL SITES

Mesa Verde National Park was formed to protect dwellings of prehistoric Indians who once lived in the area. Park officials are responsible for protecting not only these prehistoric ruins, but also the flora and fauna. Burrowing rodents occasionally cause damage to important archeological sites, and although gophers are less of a problem than rock squirrels, chipmunks, or badgers, they can and do damage sites by burrowing through such things as trash mounds, which would be far more valuable if undisturbed. In Mesa Verde Site 786, a gopher skeleton was recovered from a tunnel that ended on the floor of a kiva, 72 inches below the surface of the ground (Arthur Rohn, personal communication). The digging of a tunnel to this depth undoubtedly was facilitated by the friable nature of the fill in the kiva. Such burrows easily can allow small artifacts to become juxtaposed in the occupational strata, thereby rendering interpretation difficult, if not impossible.

In order to maintain the integrity of archeological sites in Mesa Verde and elsewhere, gophers and other burrowing rodents should be removed as soon as possible after they are noticed in such places. Macabee traps are recommended for pocket gophers and are most effective when used in pairs—one trap being set in each direction in a main underground tunnel. Gophers are important members of the faunal assemblage, however, and should be removed only when they are disturbing archeological sites or underground cables.

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COTTON RATS OF THE SIGMODON FULVIVENTER GROUP

BY

ROLLIN H. BAKER

Cotton rats of the genus *Sigmodon* are dominant grass-eating and runway-making rodents in most grassy habitats of south temperate and tropical North and Middle America. In this region, cotton rats play a role somewhat similar to that of voles of the genus *Microtus* in north temperate and boreal parts of the continent. The genus is known from late Pliocene deposits of North America; one present-day species, *S. hispidus*, is recorded from as far back as Sangamon times in the late Pleistocene. Today, rodents of this genus are widely distributed (see Fig. 1) from southern United States (north to 40° N latitude at the Kansas-Nebraska border) southward to coastal Perú (south to about 8° S latitude). Cotton rats are at home at altitudes ranging from sea level in coastal marshes to more than 3200 meters in the highlands of the Trans-Mexican Volcanic Belt. Ecologically, they are associated with grasses—which may be almost pure stands of perennial bunch grasses, mixed grasses and herbs, or mixed grasses and shrub growth—in a variety of habitats and climates in both xeric areas (where annual rainfall may be no more than 100 millimeters) and mesic situations (where annual rainfall may be more than 500 millimeters).

Cotton rats have been known to science since 1825, when Say and Ord described *Sigmodon hispidus* from Florida. Descriptions of cotton rats from other localities appeared in the literature in the middle and late 1800's, and in 1902 Vernon Bailey reviewed the specific status of North American cotton rats and established the two presently recognized groups: the semi-naked-tailed *S. hispidus* and the hairy-tailed members of the *S. fulviventer* group. Bailey's findings and later taxonomic accounts, mostly by Nelson and Goldman and by Goodwin, form the basis for the synopsis found in Hall and Kelson (1959:671-679). According to the latter, the *fulviventer* group contains 12 species from widely-scattered locations in and along the cordillera from Arizona, New Mexico, and Texas, south to the Mexican state of Oaxaca. It is the purpose of this report to review and revise this present taxonomic arrangement in light of

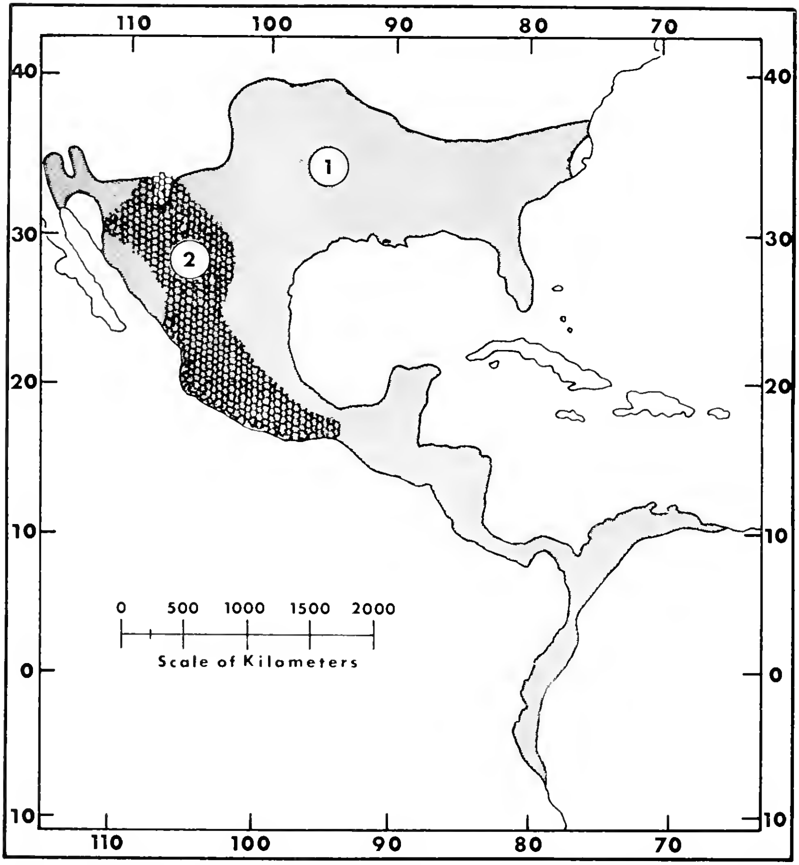

FIG. 1. Geographic distribution of cotton rats. 1. *Sigmodon hispidus.* 2. *Sigmodon fulviventer* group.

additional field and museum studies that have added to our knowledge of the distribution, ecology and systematics of the S. *fulviventer* group.

Specimens examined are listed in the accounts of each taxa discussed. The number from each locality is noted, using abbreviations for the museums listed below to indicate where specimens are on deposit. I am grateful to the persons whose names appear below for allowing me the privilege of examining the specimens: (AM) American Museum of Natural History, G. G. Goodwin, R. G. Van Gelder, and S. Anderson; (CAS) California Academy of Sciences, R. T. Orr; (DMNH) Dallas Museum of Natural History, F. W. Miller; (FM) Field Museum of Natural History, P. Hershkovitz; (KU) University of Kansas, Museum of Natural History, E. R. Hall and J. K. Jones, Jr.; (LA) Los Angeles County Museum, K. Stager and C. A. McLaughlin; (LSU) Louisiana State University, Museum of Zoology, G. H. Lowery, Jr.; (MSU) Michigan State

University, The Museum, R. H. Baker; (MVZ) University of California, Museum of Vertebrate Zoology, S. B. Benson and W. Z. Lidicker; (OC) Occidental College, J. W. Hardy; (TCWC) Texas Cooperative Wildlife Collection, Texas A&M University, W. B. Davis; (TT) Texas Technological College, R. L. Packard; (UI) University of Illinois, Museum of Natural History, D. F. Hoffmeister; (UM) University of Michigan, Museum of Zoology, W. H. Burt and E. T. Hooper; (UNAM) Instituto de Biología, B. Villa-R.; (US) U.S. National Museum including Biological Surveys Collection, R. H. Manville and C. O. Handley, Jr.

Field data and specimens (preserved or brought back alive) have been obtained by summer expeditions from The Museum at Michigan State University, beginning in 1957. Parties, headed by the author, visited known collecting sites for various species of cotton rats and also other likely places located geographically between these localities. Collecting was accomplished each summer from 1957 through 1967, except for 1962. Funds to assist in defraying costs of field work have geen generously provided by the MSU Development Fund, private donors Mrs. E. R. Warren and Mr. Russell Jameson, and the National Science Foundation (GB 2227). In the course of field work 25 persons, including long-time associate Dr. Robert G. Webb, accompanied me and must be recognized as important contributors to the success of the expeditions. These persons, most of them at the time advanced students in biology at Michigan State University, are Bruce R. Baker, Larry P. Bowdre, Daniel E. Boyle, Bernard J. Cripps, Peter L. Dalby, Julian P. Donahue, Leslie C. Drew, James J. Drake, Robert L. Fleming, William C. Gasaway, John Keever Greer, John J. Grost II, James R. Koschmann, David E. Mohrhardt, Michael K. Petersen, Carleton J. Phillips, Rudolph Scheibner, Henry L. Short, Charles E. Smith, Thomas Struhsaker, Donald F. Switzenberg, Charles L. Warner, Jr., Daniel Womochel, Robert G. Webb, and Frances E. Welling.

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All measurements in this report are given in the metric system. Capitalized color terms are those of Ridgway (1912). Those localities printed in Roman type in the lists of specimens examined or of other records are recorded on the distribution maps as either solid circles (specimens examined) or as solid squares (other records). Localities printed in Italic type are not mapped because of their proximity to other places that are mapped. All localities are arranged in the lists from north to south. Measurements of animals of the two sexes are included together since sexual dimorphism in the dimensions used was found to be negligible, although Chipman (1965) noted significant differences between sexes in weight and length of head and body in S. *hispidus* from Louisiana. Unless otherwise credited, all photographs were taken by the author.

DETERMINATION OF AGE IN COTTON RATS

Characteristics of the several species of cotton rats were determined by both gross and microscopic examinations. The selecting of comparative age-classes offered a problem because series of museum specimens include mostly young individuals. This is probably because most of them have been caught in museum special traps, which are not satisfactory for taking animals larger than 60-80 grams. Experience shows that the small- to medium-sized animals also make up a major segment of the trappable cotton rat population, especially in the period of greatest breeding activity in the warm months of the year, during which time most collecting parties are active. Cotton rats of each species, born and reared in captivity in the MSU Museum Live Animal Colony, were killed at intervals and measured. Growth curves, which level out at 250-300 days, are shown in Figures 2 and 3 (see also Hoffmeister, 1963, and Chipman, 1965). In laboratory-raised animals, females produced offspring at 87 days

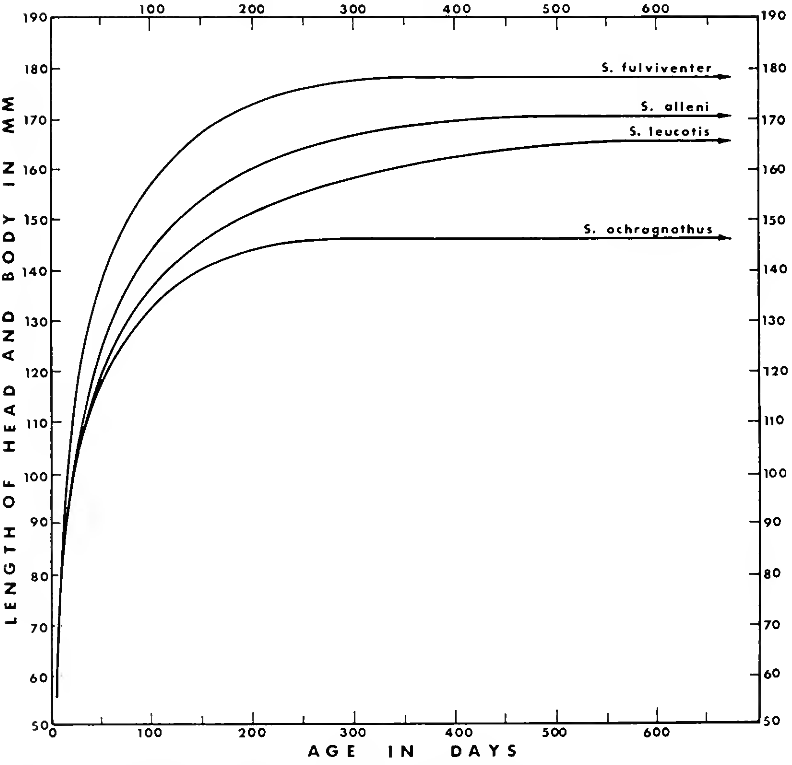

FIG. 2. Growth as judged by length of head and body in cotton rats of the *Sigmodon fulviventer* group. Data from laboratory born and reared animals, the exact ages of which were known at death.

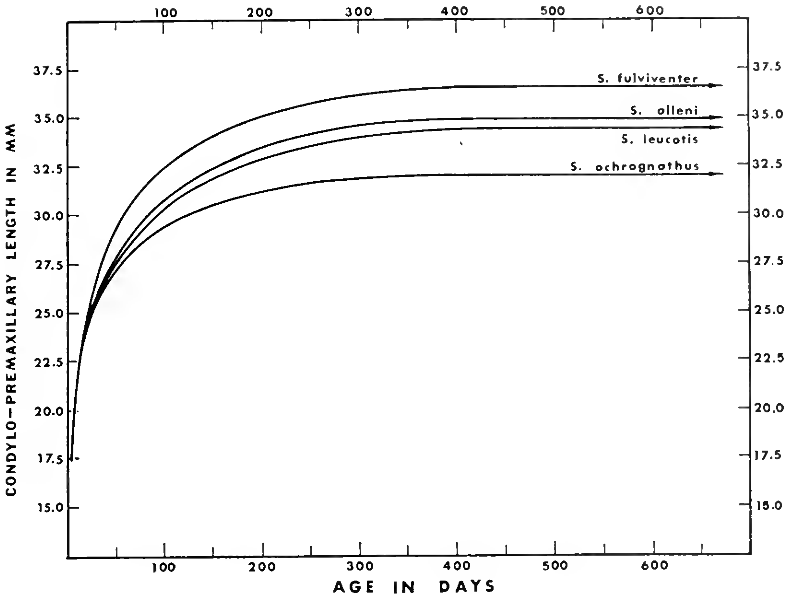

FIG. 3. Cranial growth as judged by condylopremaxillary length in cotton rats of the *Sigmodon fulviventer* group. Data from laboratory born and reared animals, the exact ages of which were known at death.

(*S. alleni*), 77 days (*S. fulviventer*), and 71 days (*S. hispidus* and *S. ochrognathus*) and would have mated approximately 35 days earlier. Cotton rats (*S. hispidus*) in the wild are known to breed at 40-50 days of age (Odum, 1955). It is suspected then that the "normal" life span in nature is no more than six months (Meyer and Meyer, 1944, and Odum, 1955). This would mean that the trappable population would include few truly "full-grown" adult animals (at least 250 days old) and would help account for the scarcity of such animals in population samples preserved in museum collections.

Study specimens of colony-raised animals purposely killed at 100 days and at 200 days were compared with wild-taken specimens with similar age characteristics. It was concluded that a cotton rat less than 75 days old is a juvenile, between 75 and 200 days old is a young adult, between 200 and 300 days old is an adult, and more than 300 days old is an old adult. A detailed study of the characteristics of aging, pelage development, and breeding habits will appear in a later report.

EVOLUTION IN RECENT SPECIES

Grass-eating as an Isolating Mechanism

Probably an important factor in speciation in cotton rats has been the inability of different species to live together in the same habitat. On the few occasions when two species have been collected within the same grassy area, one has been common (seemingly dominant) and the other rare. Field observations lead me to suspect that the local distribution of individual species has fluctuated owing to this competition in changing environments, especially due in the past century to various land-use practices by man, including clearing and lumbering, grazing of livestock, and cultivation. This activity has caused environmental changes that have favored one species over another. Thus, in Michoacán, S. *hispidus* lives in undisturbed bunch grass (sacaton), whereas S. *alleni* lives nearby in heavily-grazed, brushy, fallow fields.

The general negative interspecific reaction of species of cotton rats is not unique but seems typical as well of other grass-eating, runway-making rodents, notably voles of the genus *Microtus* (Findley, 1954; Anderson, 1959; Findley and Jones, 1962). In the Mexican highlands, cotton rats, *M. mexicanus,* and *Neotomodon alstoni* (Davis and Follansbee, 1945) seem to avoid habitats occupied by the others. This relationship can be found also in such places as Kansas, where the aggressive S. *hispidus* probably is replacing *M. ochrogaster*, appearing to have accomplished this already in parts of Louisiana, Texas, and Oklahoma. In short, any given grassy habitat may harbor only one (or one dominant) species of grass-eating, runway-making rodent, but seed-eating species (included in such genera as *Peromyscus*, *Reithrodontomys*, *Baiomys*, *Liomys*, *Perognathus*) appear to experience little evident incompatibility in their own group or with the grass-eater, whose runways they use seemingly without restraint.

That we find several seed-eating rodents but only one grass-eating rodent in a given grassy habitat may be because each seed-eater is adapted to a "smaller" segment of the environment (and thus allows space for several species) than is the grass-eater, whose habitat requirements may be too "broad" to allow for close neighbors with similar food habits. Species segregation and replacement, then, can be an important factor in evolution in *Sigmodon.*

Ancestry

Cotton rats are presumed to be of Neotropical origin, and probably arose in early or middle Pliocene from a yet unknown, grass-eating cricetine ancestor. This ancestor probably had a four-rooted first lower molar (C. W. Hibbard, personal communication) and may have developed as a progressive offshoot of the main line of phyllotine rodent origin (Hershkovitz, 1962:23). It is suspected that cotton rats evolved in a Middle American pastoral habitat, although Hershkovitz (1966) believes it to be South American. Since the

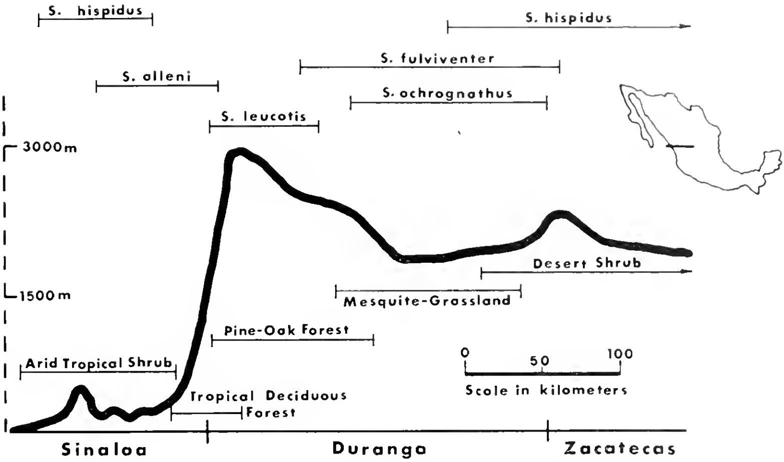

FIG. 4. Distribution of species of *Sigmodon* along an east-west transect in northwestern Mexico between 23° 30′ N and 24° 30′ N.

first terrestrial rodent environments to become established on the Panamanian land bridge after its emergence in late Pliocene were undoubtedly a series of grassland successions leading ultimately to savannas and forests, cotton rats could have easily moved southeastward to populate coastal parts of northern South America where they occur today (see Fig. 1). However, unlike other cricetines such as the rice rats (genus *Oryzomys*), cotton rats appeared unable to spread southward in South America to reach such likely habitats as the Argentine Pampas. Perhaps cotton rats (for which no South American fossils are known) arrived later than rice rats and faced well-entrenched competitors or were blocked by encroaching interior and coastal forests in northern South America. In North America grasslands, which had their beginnings in the late Miocene and their great development in the Pliocene, extended southward into what is now México and offered a broad avenue to northward movements of cotton rats (see Cohn, 1965:138-139). Throughout the Pleistocene this area was subjected to alternating mild and cool periods, and to aridity (Dillon, 1956:173) and subhumid conditions (Hibbard, 1960). Even so, early cotton rats, if possessed of some of the same ubiquitous characteristics as their modern counterparts, should have had no difficulty surviving such changes from the warm climate of their Neotropical home.

The genus is first reported from the Blancan of the late Pliocene (Hibbard, 1960:17) with the modern species, *S. hispidus,* known from what is now Texas as early as Sangamon times (third interglacial) in the Pleistocene (Moore Pit local fauna, Slaughter, 1966: 90). From the south-central United States, S. *hispidus* was presumed to have been displaced southward and laterally during Wisconsin glaciation into refugia in peninsula Florida and the Southwest (alluded to by Blair, 1958:460). Following the melt of the glaciation, S. *hispidus* appeared again in the southern Great Plains and seems still to be on the move northward (to the southern border of Nebraska in 1958—Jones, 1964:212). As mentioned previously, S. *hispidus* is replacing *Microtus ochrogaster* as the dominant grass-eating, runway-making rodent in Oklahoma and parts of Kansas.

Perhaps it was as late as Wisconsin times that conditions occurred to account for the evolution from S. *hispidus* of the distinctive S. *fulviventer* group. Today, these species generally replace (ecologic segregation) one another in and along the cordillera from Arizona and Texas southeastward to Oaxaca. Although there is some overlap (see profile, Fig. 4), one species dominates in each suitable montane environment: S. *fulviventer* in open, elevated grasslands; S. *ochrognathus* in bunch grasses on arid, rocky slopes; S. *leucotis* in mesic, boreal grass-shrub; and S. *alleni* in mesic, boreal-tropical grass-shrub. Presumably, basic stocks of S. *hispidus* occupied some of these habitats in the late Pleistocene with climatic, vegetational, and edaphic selective forces operating so as to produce the generally allopatric Recent species (see Fig. 5).

Of the species of the S. *fulviventer* group, S. *alleni* might have been derived most recently from a stock of S. *hispidus* (from the westward in the Pacific coastal lowlands), whereas the other three species could have been derived from stocks of S. *hispidus* found on the Mexican Plateau. It is thought that S. *fulviventer* and S. *alleni* are less differentiated from S. *hispidus* than are S. *ochrognathus* and S. *leucotis*. The latter species seems most remote and could have branched off even earlier than the others, being set apart by unique features including rostral depressions and a reduced or absent lingual root on the first molar (see also Dalby and Lillevik, 1969).

In summary, *Sigmodon* consists of one wide-spread, ubiquitous species, S. *hispidus*, and four derived species that occupy comparatively small, allopatric ranges, mostly in western México. Speciation in and along the cordillera in southwestern North America may have come about through ecologic segregation and morphologic divergence resulting from the availability of arid uplands, rocky slopes, and mesic boreal and mesic tropical-boreal habitats (presumably

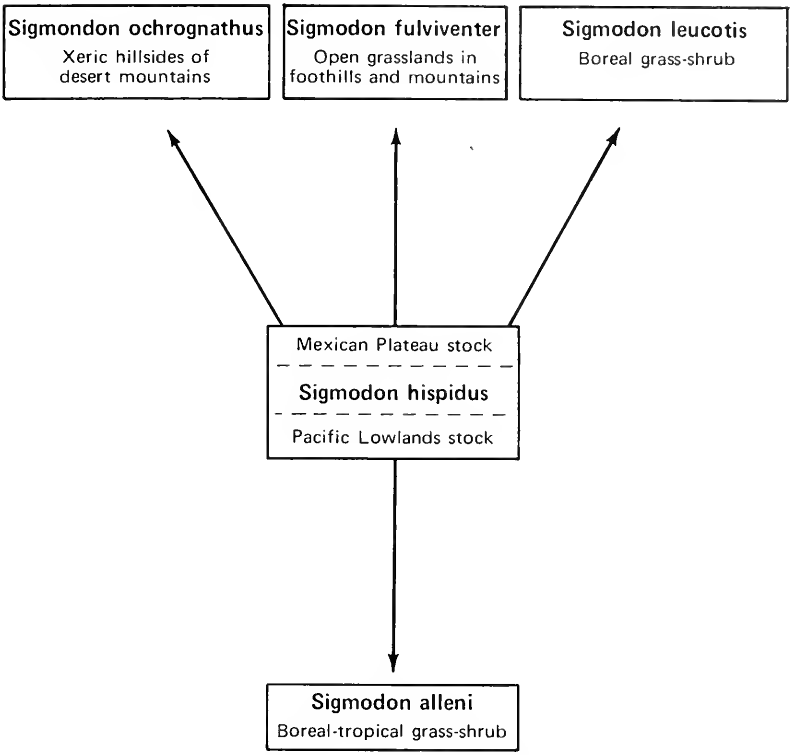

FIG. 5. Adaptive relationships of Recent cotton rats.

unoccupied by grass-eating rodents) in which the parent hispid species lacked survival ability. Selection for characters found in the species occurring in these habitats today was the result. Segregation and character displacement probably were intensified because of the general incompatibility of different kinds of cotton rats in the same living places.

KEY TO SPECIES OF COTTON RATS (GENUS SIGMODON)

1\. Tail sparsely haired and scaly in appearance, individual scales broad, 0.75 mm. wide; skull generally long and narrow, basioccipital long and broad, palatal pits shallow .... *Sigmodon hispidus*

1′. Tail heavily haired and not scaly in appearance, individual scales narrow, 0.50 mm. wide; skull generally short and broad, basioccipital either long and narrow or short and broad, palatal pits deeply marked .... *Sigmodon fulviventer* group, 2

2\. Ears (inside of pinnae) whitish, in marked contrast to color of dorsum; interparietal generally less than 2.0 mm. in length at midline; upper part of each premaxillary with pronounced rostral depression;

mesopterygoid fossa generally parallel-sided at anterior end; lingual root of first lower molar reduced in size and sometimes absent .... S. *leucotis*

2′. Color of ears not conspicuously different from color of dorsum; interparietal usually 2.0 mm. or more in length at midline; upper part of premaxillary with slight or no rostral depression; mesopterygoid fossa generally not parallel-sided anteriorly; lingual root of first lower molar not reduced in size 3

3. Buff coloring on nose and around eye conspicuous; adult size small, length of head and body averaging 143 mm. and condylopremaxillary length averaging 32.0; auditory bullae small and elongate; median keel on basioccipital developed; lateral bulge of capsular projections of upper incisors pronounced; interparietal with slight to marked median posterior notch; paraoccipital process curved (when viewed from below) and notched on the anterior base .... S. *ochrognathus*

3′. Buff color on nose and around eye usually not in marked contrast with rest of dorsum; adult size large, length of head and body averaging at least 168 mm. and condylopremaxillary length averaging at least 34.5; auditory bullae large and broad (relative to length of skull); lateral bulge of capsular projections of upper incisors slight to moderate; interparietal usually lacking any indication of a median posterior notch; paraoccipital process (when viewed from below) generally straight or slightly hooked 4

4. Color of dorsum always brownish, underparts washed with whitish or pale buff; adult size medium, length of head and body averaging 168 mm. and condylopremaxillary length averaging 34.5; skull flattened in appearance, long and narrow; incisive foramina not extending to line drawn between anterior ends of first upper molars; basioccipital short and wide; mesopterygoid fossa broad anteriorly; median keel on palate slightly developed; palatal pits moderately deep; incisors usually markedly recurved (opisthodont) .... S. *alleni*

4′. Dorsum "pepper and salt" in color, underparts washed with buff; adult size large, length of head and body averaging 179 mm. and condylopremaxillary length averaging 36.5; skull arched, short and broad; incisive foramina extending to or beyond a line drawn between anterior surfaces of the first upper molars; foramen ovale large, at least three-fourths diameter of third upper molar; basioccipital long and narrow; mesopterygoid fossa narrow anteriorly; median keel on palate well developed; palatal pits markedly deep; incisors not highly recurved .... S. *fulviventer*

Sigmodon alleni

Sigmodon alleni, the brown cotton rat, is the most tropical-adapted member of the S. *fulviventer* group. Its preferred living places are in mixed grass-herbs-shrub areas in the Pacific coastal lowlands and extending up to the mesic boreal-tropical ecotone on the Pacific-facing slopes of the Sierra Madre Occidental, the Sierra Madre del Sur, and where these mountain chains join at the western end of the Trans-Mexican Volcanic Belt (see Fig. 6.) It is recorded from near sea level in Nayarit, Colima, and Oaxaca to as high as 3050 meters in Jalisco.

Habitat and Habits

The brown cotton rat seems to prefer moist, vine- and shrub-covered slopes in tropical or mixed tropical-boreal situations, and thereby occupies parts of the Tropical Deciduous Forest and humid Pine-Oak Forest (vegetation zones of Leopold, 1959). My acquaintance with this species is from only four localities, although I spent time during each of several summers trying to find S. *alleni* at places where it had been previously taken in Sinaloa, Nayarit, Jalisco, Michoacán, Guerrero, and Oaxaca. At one locality (in Michoacán) S. *alleni* was common, but at three others (in Sinaloa and Oaxaca) it was uncommon. As yet the habitat requirements of this species are poorly known, although it is surely more adapted to shrub habitat than to open grasslands. Specific trapping localities are discussed below.

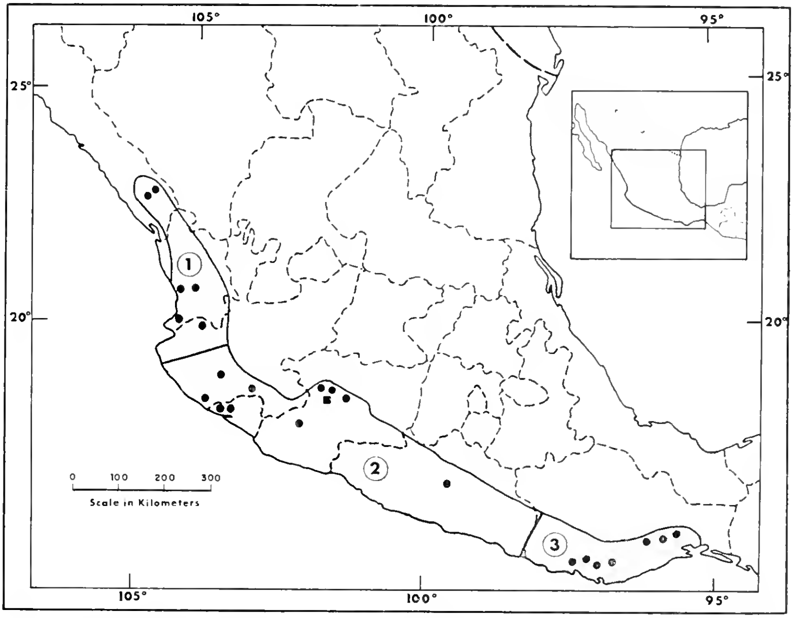

FIG. 6. Geographic distribution of the brown cotton rat. 1. *Sigmodon alleni alleni*. 2. *Sigmodon alleni vulcani*. 3. *Sigmodon alleni planifrons*.

Sinaloa.—At 1.7 km. E Santa Lucía, 1720 m., two brown cotton rats were trapped on June 23, 1955. This locality is on a Pacific-facing slope in the upper foothills of the Sierra Madre Occidental in tropical deciduous vegetation, just below the pine-oak belt. Cotton rats were caught in a narrow canyon in dense second-growth shrub of a fallow corn field. The writer visited this place on several other occasions but caught no other *S. alleni,* although one *S. hispidus* was lived-trapped there in the summer of 1967. Small mammal associates at this place included *Liomys pictus, Reithrodontomys fulvescens, Peromyscus boylii* and *Neotoma mexicana.*

Michoacán.—Twenty-five *S. alleni* (12 males and 13 females) were taken 10 km. W Capácuaro, 2360 m., in grazed and logged pasture with scattered oaks and pines as the prominent woody vegetation. The cotton rats lived in short, closely-grazed, grassy areas with scattered forbs covering the dark volcanic soil. Some evidence of runways were found under shrubs and immediately adjacent to rock walls (see Fig. 7). The animals were active both at night and during daylight hours in this sparse habitat. Because it rained during most of our successful trapping period at this locality, I judge that cotton rat movements were not curtailed by precipitation. Several were seen moving across open, grazed turf between clumps of forbs or shrubs. Nests, presumed to be constructed by cotton rats, were found in rotting pine logs, under volcanic rocks, beneath a pile of pine bark, and in a rotted pine stump, out of which a cotton rat was flushed. Grass used as nest material and also found as cuttings along runways was identified as *Eragrostis limbata.* Owing to heavy grazing by cattle, this grass was able to mature only in protected clumps of shrubs or adjacent to rock fences. Other plants collected were species of the genera *Hyptis* and *Lupinus,* and *Solanum elaeagnifolium.* Of interest here is that 25 *S. alleni* were live-trapped in two nights (July 20-21, 1967) in a sparsely-vegetated area of mixed pasture and fallow fields of less than 25 hectares. The

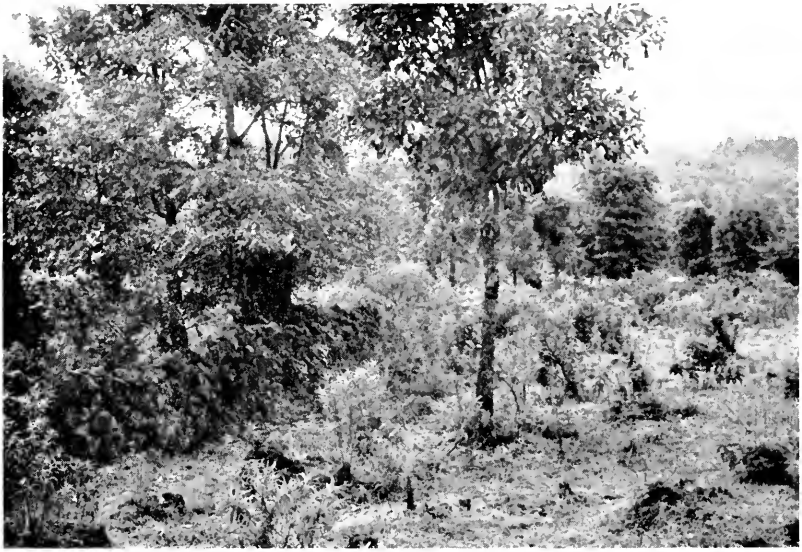

FIG. 7. Habitat of the brown cotton rat, *Sigmodon alleni,* near Capácuaro, 2360 m., Michoacán. Photograph taken on July 22, 1967.

only other small mammal captured in the live-traps was *Peromyscus boylii*. This ability of S. *alleni* to live in an open area with vegetative cover consisting of forbs and shrubs is in marked contrast to the little-disturbed grassy situations required as living places by S. *fulviventer* and S. *ochrognathus*.

At Dos Aguas, 2135 m., Hooper (1961, 1962) found S. *alleni* in growths of grass, poison ivy, other herbs, and shrubs in an area of pine forest mixed with some broad-leafed oaks, alder, and madrone. Tree trunks and branches were draped with lichens, bromeliads, and orchids.

Jalisco.—J. H. Batty collected 29 brown cotton rats on Volcán de Fuego ". . . at an altitude of about 10,000 feet, July 10 to 28, 1905" (Allen, 1906: 248). The exact habitat from which these rodents were taken is unknown. Previously in 1892, Nelson and Goldman (Goldman, 1951:180) had ascended adjacent Sierra Nevada de Colima without taking this cotton rat; a field party from the Michigan State University in 1963 (Baker and Phillips, 1965) also climbed to the fir belt on this mountain without finding S. *alleni*, although S. *hispidus* was taken along grassy fence rows on the lower, southeastern slope. J. Knox Jones, Jr. (personal communication) reported that a field party from the University of Kansas Museum of Natural History ascended the Volcán de Fuego in 1966 without finding brown cotton rats.

Guerrero.—Nelson and Goldman (Goldman, 1951:152) obtained the brown cotton rat at Omilteme and subsequently named it S. *guerrerensis*. In 1964, a field party from Michigan State University failed to reach this place owing to rains in the mountains but did collect, without finding brown cotton rats, in "similar" montane country near Xochipila, somewhat to the north of Omilteme. After spending several summers having little success in finding cotton rats at localities visited more than 60 years earlier by Nelson and Goldman, I have concluded that the scarcity or absence of this species is because many of the habitats in which it lived have been altered by man's land uses since the turn of the century. This change has presumably "eliminated" some of the preferred living places of these cotton rats.

Oaxaca.—The brown cotton rat was live-trapped on the Pacific side of the Sierra Madre del Sur at approximately 13 km. SSW Juchatengo, 1920 m. This locality, on the road between Oaxaca and Puerto Escondido, is approximately 200 meters below the seawardmost crest of the mountains and 18 kilometers east of Juquila, the type locality of S. *planifrons*. The collecting site was in a transition between the pine-oak montane forests and the tropical semi-deciduous forests, the latter being mostly in protected, well-watered canyons (see Baker and Womochel, 1966). Cotton rats were live-trapped in second-growth vegetation, often thick and tangled, in fallow, hillside cornfields. Plants growing on these abandoned fields belong to species in such genera as *Rubus*, *Lupinus*, *Adiantum*, *Castilleia*, *Solanum*, *Acalypha*, *Valeriana*, *Geranium*, *Cerastium*, *Cyperus*, *Hedyotis*, *Bomarea*, *Arbutus*, and *Tradescantia*, and the species *Phytolacca decandra*, *Zeugites mexicana*, *Toxidendron radicans*, and *Ostrya virginiana*. Small mammal associates obtained were *Marmosa mexicana*, *Liomys irroratus*, *Oryzomys alfaroi*, *Reithrodontomys sumichrasti*, *Peromyscus megalops*, *Peromyscus evides*, and *Neotoma mexicana*. On returning to the same locality three years later (in 1967), I was unable to catch any more cotton rats. Nowhere in Oaxaca have collectors obtained a large series of this rodent; George Goodwin (personal communication) reported six specimens taken at

Santa Lucía as the largest number. I took four brown cotton rats near Juchatengo; near Capácuaro, Michoacán, we caught 25 specimens of S. *alleni* along with one small mammal associate, *Peromyscus boylii.*

Two young S. *alleni* were captured alive in a grassy roadside ditch next to a poorly-drained palm jungle 8 km. ESE Río Grande, elevation less than 30 m., in July, 1967. This low, moist area adjoined a coastal mangrove swamp. Taken at the same place were *Liomys pictus, Tylomys nudicaudus, Peromyscus mexicanus,* and *Neotoma mexicana.*

Association of brown cotton rats with other species of the genus.—There is no report of S. *alleni* living in ecological association with S. *fulviventer,* S. *leucotis,* or S. *ochrognathus.* On the western slopes of the Sierra Madre Occidental in Durango (see Fig. 4) and southeastward, the ranges of S. *alleni* and S. *leucotis* might meet at the junction of the pine-oak belt and the tropical habitat. It is also possible that S. *alleni* and S. *fulviventer* may occupy somewhat the same areas in the vicinity of Pátzcuaro in Michoacán, where Nelson and Goldman caught a large series of the latter in the 1890's and Hall and Villa-R. (1949:465) took the former species, which they erroneously identified as S. *melanotis.* The latter authors also took S. *hispidus* at the same place. It is suspected that in the Pátzcuaro area S. *alleni* occupies brushy areas, and S. *fulviventer* and S. *hispidus* occupy grassy situations. I failed to obtain any of the species directly west of Pátzcuaro in the summer of 1963. Near Santa Lucía in Sinaloa, S. *hispidus* was captured in a runway under a dense tangle of *Acacia* and *Mimosa* on a moist, tropical hillside. This place is not unlike that where S. *alleni* was taken nearby a few years previously. Near Carapán in Michoacán, S. *hispidus* was trapped in open sacaton meadows, whereas S. *alleni* was caught in overgrazed shrubs not many kilometers away near Capácuaro. Since S. *hispidus* has proved to be an aggressive species elsewhere, such as extending its range northward from the Oklahoma-Kansas line to Nebraska in a space of about 56 years (Cockrum, 1948, and Jones, 1964:212), there is good reason to believe that S. *hispidus* may usurp habitat (possibly altered by man) formerly inhabited by other species of cotton rats.

Specific Characters and Comparisons

A rich, brownish dorsum together with medium size (for captive animals, maximum weights are 178 grams for a male and 180 for a non-pregnant female; maximum lengths of head and body are 173 mm. and 183, respectively) and strongly recurved incisors (opisthodont) distinguish S. *alleni* from other species in the S. *fulviventer* group. Other unique characters include skull with flattened appearance when viewed laterally, bulge of capsular projections for the upper incisors slight, and paraoccipital processes, when viewed from below, slightly hooked rather than straight or curved.

From S. *fulviventer,* S. *alleni* differs further in having underparts washed with whitish or pale buff rather than tawny; skull long and narrow instead of short and broad; auditory bullae smaller in relation to breadth; basioccipital short and wide instead of long and narrow; posterior ends of incisive foramina usually not extending (rather than extending) to a line drawn between the anterior surfaces of the first upper molars; anterior end of mesopterygoid fossa broad instead of narrow; anterior lip of foramen magnum obviously (rather than slightly) notched; foramen ovale small (no more than half width of M3) instead of large (at least three-fourths width of M3); palatal pits shallow rather than deep; and median keel of palate slightly developed instead of well developed.

From S. *leucotis*, S. *alleni* is further distinguished by hairs of inside of ear not whitish in contrast to rest of dorsum; skull long and narrow instead of short and broad; auditory bullae smaller in relation to breadth; basioccipital short and wide instead of long and narrow; posterior ends of incisive foramina usually not extending (rather than extending) to a line drawn between the anterior surfaces of the first upper molars; anterior end of mesopterygoid fossa broad rather than parallel-sided; length at midline of interparietal more (instead of less) than 2 mm.; anterior lip of foramen magnum obviously (rather than slightly) notched; rostral depressions on sides of premaxillae slight instead of deep and pronounced; angular process of lower jaw rounded instead of slightly hooked; lingual root of first lower molar large rather than reduced or absent.

From S. *ochrognathus*, S. *alleni* differs further in nose lacking extensive and contrasting yellow coloring; skull long and narrow instead of short and broad; auditory bullae larger and broader; median keel on basioccipital slight instead of obvious; bulges of capsular projections for upper incisors slight rather than pronounced; median-posterior area of interparietal lacking distinct notch; and paraoccipital process (from ventral view) slightly hooked rather than curved with a basal notch.

From S. *hispidus*, S. *alleni* is distinguished by small size of tail scales (0.5 mm. wide rather than 0.75 mm. wide); tail heavily haired instead of sparsely haired; incisors usually more strongly recurved (opisthodont); basioccipital short in relation to breadth rather than long; paraoccipital processes (from ventral view) slightly hooked instead of generally straight; and palatal pits moderately deep rather than shallow.

Geographic Variation

Brown cotton rats occur along the Pacific-facing mountains and foothills from southern Sinaloa southeastward to eastern Oaxaca at the Isthmus of Tehuantepec. Probably their systematic relationships have remained unclear because of the availability of only a few scattered specimens in museum collections. These have been given an assortment of no less than six specific names since 1902, when

Vernon Bailey named S. *alleni* (see Hall and Kelson, 1959:676-679). Like S. *leucotis*, S. *alleni* seems to occupy a disjunct range with field collectors being especially lucky to pick up more than one or two individuals at any locality. Field parties from the Michigan State University worked the Pacific slopes from Sinaloa to Oaxaca attempting to gather specimens from heretofore unreported and intermediate localities. Little additional material was obtained, although live animals from near Capácuaro, Michoacán, and from near Juchatengo, Oaxaca, were successfully bred as well as crossed in the live colony (the findings from this study will appear in a later report).

Herein, cotton rats previously assigned to the specific names S. *guerrerensis*, S. *macdougalli*, S. *macrodon*, S. *planifrons*, and S. *vulcani* all are arranged as a single species under S. *alleni*, the oldest available name. All share the common specific characteristics as presented in the previous section and may differ from one another in minor ways that demonstrate intraspecific geographic variation.

In general, these cotton rats are larger and darker in the montane areas and smaller and paler in coastal situations. However, populations in the northwestern part (assigned to S. *a. alleni*) and in the southeastern part (assigned to S. *a. planifrons*) of the range of the species are both smaller and paler than populations from the central sector (assigned to S. *a. vulcani*) of the species distribution. To determine the degree of size difference, measurements of the condylopremaxillary lengths of the wild-taken animals listed in Table 1 were evaluated by analysis of variance. The overall differences between the means of this cranial dimension are just significant at the five per cent level ($F=3.72$). The degree of difference between the individual means of the four samples was then determined by the new multiple range test (see Table 2). Population means underscored by a common line in the table are not significantly different. As suggested above, the smaller animals representing S. *a. alleni* from the northwestern part of the range (Sinaloa, Nayarit, and northern Jalisco) and representing S. *a. planifrons* from the southeastern part of the range (Oaxaca) are not significantly different from each other, but are significantly different from the two samples from the central part of the range (southern Jalisco and Michoacán) that represent S. *a. vulcani*.

Sigmodon alleni alleni Bailey

Sigmodon alleni Bailey, Proc. Biol. Soc. Washington, 15:112, June 2, 1902.

Type.—Young adult male, skin and skull; no. 88227 U.S. National Museum; from San Sebastián, Mascota, Jalisco; obtained on March 15, 1897, by E. W. Nelson and E. A. Goldman, original no. 10708.

Table 1.—Selected measurements (averages and extremes) of young adult brown cotton rats, *Sigmodon alleni*.

Locality of capture (sample size[1] in parentheses)	Length of head and body	Length of hind foot	Height of ear from notch	Condylo-premaxillary length	Zygomatic breadth	Least interorbital constriction	Depth of cranium[2]	Length of nasals	Alveolar length of maxillary toothrow
Sigmodon alleni alleni									
Sinaloa, Nayarit, northern Jalisco (8)	145 139-152	30 27-32	21 20-22	31.2 30.3-31.9	18.3 17.4-19.5	5.1 4.9-5.3	9.3 8.6-9.7	12.6 12.3-13.1	6.1 5.9-6.4
Sigmodon alleni vulcani									
Volcán de Fuego, Jalisco (7)	---- ----	---- ----	---- ----	32.2 31.5-33.9	19.0 18.5-19.5	5.3 5.2-5.4	10.5 10.0-10.8	12.8 12.6-13.7	6.5 6.3-6.7
Michoacán (8)	150 140-159	32 30-33	21 20-24	32.5 30.7-34.1	18.9 18.3-19.8	5.3 5.1-5.7	10.4 9.7-10.9	13.2 12.2-13.9	6.2 6.0-6.6
Omiltemi, Guerrero (3)	160 150-169	32 31-33	20 ----	32.8 32.0-33.7	19.1 18.9-19.3	5.4 5.2-5.6	---- ----	13.3 13.2-13.4	6.2 6.0-6.3
Sigmodon alleni planifrons									
Juchatengo, Oaxaca (6, 100 days old)[3]	154 143-160	32 30-33	20 19-23	31.6 30.5-32.8	18.1 17.5-18.8	5.1 4.9-5.3	10.3 9.0-9.7	12.9 12.3-13.8	6.3 6.2-6.4
Tehuantepec, Oaxaca (5)	136 130-140	33 32-34	---- ----	30.8 30.3-31.1	18.3 17.8-18.7	5.3 5.2-5.6	10.0 9.6-10.1	12.6 12.3-13.1	6.4 6.2-6.5

[1] All measurements not available for some specimens in samples.

[2] Measurement taken as described by Findley and Jones (1963:308).

[3] Born and raised in laboratory.

Range.—Mixed grass-forb-shrub areas on western slopes of the Sierra Madre Occidental and adjacent Pacific coastal lowlands from southern Sinaloa southward to northwestern Jalisco (see Fig. 6).

Diagnosis.—Size small for the species (see Table 1); dorsum intermixed with black hairs and agouti-banded hairs of Ochraceous-Tawny; underparts and upper surfaces of feet whitish or pale buff; base of tail slightly darker than dorsum; skull short and broad with short rostrum and small auditory bullae.

Comparisons.—From *S. a. vulcani, S. a. alleni* differs in size smaller (see Table 1); color paler (upperparts Ochraceous-Tawny rather than Clay Color); skull smaller with flatter cranium, shorter rostrum, and less expanded auditory bullae.

Remarks.—This northernmost subspecies of *S. alleni* is characteristically pale in color and smaller than adjoining *S. a. vulcani.* Specimens have been taken at elevations from near sea level at San Blas up to 1723 meters near Santa Lucía. In its coastal habitat, *S. a. alleni* probably comes into some contact with *S. hispidus.* At Santa Lucía, *alleni* was caught in hillside fallow-field habitat in 1955 and *hispidus* was taken in 1967 in approximately the same place.

Specimens examined (20).—SINALOA: 2 km. E Santa Lucía, 1723 m., 2 (KU); Copalá, 4 (LACM). NAYARIT: San Blas, 1 (US); Tepic, 2 (US); Valle de Banderas, 1 (US). JALISCO: San Sebastián, 10 (US).

Sigmodon alleni vulcani J. A. Allen

Sigmodon vulcani J. A. Allen, Bull. Amer. Mus. Nat. Hist., 22:247, July 25, 1906.

Sigmodon guerrerensis Nelson and Goldman, Proc. Biol. Soc. Washington, 46: 196, October 26, 1933, type from Omilteme, 2440 m., Guerrero.

Type.—Young adult female, skin and skull; no. 26310 American Museum of Natural History; from Volcán de Fuego, 3050 m., Jalisco; obtained on July 25, 1905, by J. H. Batty, original no. 2330.

Range.—Western slopes of Sierra Madre Occidental and Sierra Madre del Sur and coastal plain from southwestern Jalisco southeastward to southern Guerrero (see Fig. 6).

Diagnosis.—Size large for the species (see Table 1); dorsum intermixed with black hairs and agouti-banded hairs of Clay Color; underparts and upper surfaces of feet whitish or pale buff; base of tail slightly darker than dorsum; skull large and broad with cranium abruptly expanding posteriorly; auditory bullae large.

TABLE 2.—RESULT OF NEW MULTIPLE RANGE TEST ON CONDYLOPREMAXILLARY LENGTHS OF CRANIA OF SAMPLES OF *Sigmodon alleni.* POPULATION MEANS UNDERSCORED BY A COMMON LINE ARE NOT SIGNIFICANTLY DIFFERENT.

	S. a. planifrons	*S. a. alleni*	*S. a. vulcani*	
Locality	Tehuantepec, Oaxaca	Sinaloa, Nayarit, northern Jalisco	Volcán de Fuego, Jalisco	Michoacán
Means of condylopremaxillary lengths	30.80	31.10	32.18	32.53

Comparisons.—For comparison with *S. a. alleni*, see account of that subspecies. From *S. a. planifrons*, *S. a. vulcani* differs in size larger; color of upperparts darker (near Clay Color rather than Cinnamon-Buff); skull larger and broader; skull flatter; nasals longer; incisors less recurved.

Remarks.—This large, dark subspecies occurs from near sea level in Colima to above 3000 meters in Guerrero. It occupies a variety of habitats from mesic, boreal-tropical, montane forest-shrub to coastal shrub-vine areas. In many places its distribution seems to be interdigitated with populations of *S. hispidus*.

Specimens examined (67).—JALISCO: 10 km. SSW Autlán, 1372 m., 2 (UM); 9 km. NNW Barro de Navidad, 2 (KU); Volcán de Fuego, 3050 m., 36 (AMNH). COLIMA: 3 km. E Santiago, 1 (KU). MICHOACAN: 3 km. W Pátzcuaro, 2380 m., 2 (MVZ); *6 km. S Pátzcuaro, 2350 m.*, 2 (MVZ); 14 km. E on road from Angahuan, 2300 m., 2 (UM); *15 km. E on road from Angahuan*, 2300 m., 2 (UM); 10 km. W Capácuaro, 2059 m., 3 (MSU); *9 km. N Uruapan*, 1 (UM); *7 km. N and 2 km. W Uruapan, 1937 m.*, 1 (KU); *Uruapan, Cupatitzio National Park*, 1 (UM); 23 km. W Dos Aguas, 2135 m., 5 (UM); *Dos Aguas, 2135 m.*, 3 (UM). GUERRERO: Omilteme, 2440 m., 1 (UM), 2 (US).

Other record.—MICHOACAN: Tancitaro, 1830 m. (Hall and Villa-R., 1949: 465).

Sigmodon alleni planifrons Nelson and Goldman

Sigmodon planifrons Nelson and Goldman, Proc. Biol. Soc. Washington, 46:197, October 26, 1933.

Sigmodon planifrons minor Goodwin, Amer. Mus. Novit., 1705:1, February 4, 1955, type from Santa Lucía, 1220 m., 12 km. NE Tenango, Tehuantepec, Oaxaca. Not *Sigmodon minor* Gidley, 1922.

Sigmodon macdougalli Goodwin, Amer. Mus. Novit., 1705:3, February 4, 1955, type from Santo Tomás Teipán (rain forest above village), 2135 m., 12 km. S San Bartolo Yautepec, Yautepec, Oaxaca.

Sigmodon macrodon Goodwin, Amer. Mus. Novit., 1705:4, February 4, 1955, type from Cerro San Pedro (rocky summit), 1098 m., 20 km. W Mixtequilla, Tehuantepec, Oaxaca.

Sigmodon planifrons setzeri Goodwin, Jour. Mamm., 40:447, August 20, 1959, a renaming of *S. p. minor* Goodwin.

Type.—Young adult female, skin and skull; no. 71918 U.S. National Museum; from Juquila, 1525 m., Oaxaca; obtained on February 28, 1895, by E. W. Nelson and E. A. Goldman, original no. 7569.

Range.—Western slopes of the Sierra Madre del Sur and adjacent Pacific coastal lowlands of southern Oaxaca eastward to the Isthmus of Tehuanatepec (see Fig. 6).

Diagnosis.—Size small for the species (see Table 1); dorsum intermixed with black hairs and agouti-banded hairs of near (a) Cinnamon-Buff; underparts and upper surfaces of feet whitish or pale buff; base of tail slightly darker than dorsum; skull small and flat; rostrum depressed; incisors markedly recurved.

Comparisons.—For comparison with *S. a. vulcani*, see account of that subspecies.

Remarks.—This subspecies is smaller (especially those from Tehuantepec) and slightly less richly colored than *S. a. vulcani*, its relative directly to the northwest. Although much of the available study material consists of young animals, the few adults present show that there is considerable variation between populations in coastal Oaxaca. Animals from lower elevations are smaller and those from mesic tropical situations on the higher slopes seem larger. Goodwin (1955) detected some of this variation and quite reasonably named three taxa from the area of Tehuanatepec. However, a comparison of his material with the recently-obtained and laboratory-raised animals from near Juchatengo shows that the differences are not of sufficient magnitude to warrant retention of these taxa and that all of the populations should be arranged under the oldest name, *S. a. planifrons.*

The arid tropical shrub habitat in coastal areas of Oaxaca is chiefly the home of *S. hispidus,* with grayish *S. h. mascotensis* to the westward and brownish *S. h. ischyrus* to the eastward. The distributional relationship between *S. alleni* and *S. hispidus* in this area is obscure, although *S. alleni* in the lowlands can be expected in highly mesic situations, such as palm forests near mangrove. The brownish *S. h. ischyrus* resembles *S. alleni* in color and in tail hair, but is larger with a longer tail and shorter, thinner pelage.

Specimens examined (29).—Oaxaca: Santo Tomás Teipán, 2135 m., 12 km. S San Bartolo Yautepec, Yautepec, 1 (AMNH); *Arroyo Palmar (Tequisistlán), Tehuantepec,* 3 (AMNH); *Arroyo Arenal, Tehuantepec,* 3 (AMNH); *Cerro Pollé, Tehuantepec,* 3 (AMNH); *Cerro del Chorro, Tehuantepec,* 1 (AMNH); *Cerro de Pastle, Tenango, Tehuantepec,* 1 (AMNH); *Cerro Ocate, Tenango, Tehuantepec,* 1 (AMNH); *Llano de Ocate, Tehuantepec,* 2 (AMNH); *Tres Cruces, Tehuantepec,* 5 (AMNH); Santa Lucía, 1220 m., 1 (AMNH); Cerro San Pedro, 1921 m., 20 km. W Mixtequilla, 1 (AMNH); 40 km. SSE Miahuatlán, 1647 m., 1 (CAS); 2 km. NNW Soledad, 1433 m., 2 (KU); 13 km. SSW Juchatengo, 1921 m., 1 (MSU); Juquila, 1525 m., 2 (US); 8 km. ESE Río Grande, 30 m., 1 (MSU).

Sigmodon fulviventer

Habitat and Habits

The tawny-bellied cotton rat (Fig. 8) is an inhabitant of the mesquite-grassland that occurs in a north-northwest to south-southeast direction along the eastern base of the Sierra Madre Occidental (see Leopold, 1959:27-28). This range extends northward to central New Mexico and Arizona and southward to the northern base of the Transverse Volcanic Belt in Jalisco and northern Michoacán (see Fig. 15). To the westward, the mesquite-grassland merges with the pine-oak of the higher elevations of the mountains at approximately 2000-3000 meters. To the eastward the growing aridity of the lower elevations causes a gradual change to the desert. Leopold *(loc. cit.)* noted that the mesquite-grassland has been the major Mexican habitat for the pronghorn *(Antilocapra americana),* the mule or burro deer *(Odocoileus hemionus),* the white-sided jackrabbit *(Lepus callo-*

FIG. 8. A tawny-bellied cotton rat, *Sigmodon fulviventer*, captured near Boquilla, Durango, on July 10, 1965. Photograph taken in October, 1965, by Robert Brown.

tis), and for such rodents as the banner-tailed kangaroo rat *(Dipodomys spectabilis)*, the grasshopper mouse *(Onychomys torridus)*, the northern pygmy mouse *(Baiomys taylori)*, the spiny pocket mouse *(Liomys irroratus)*, the hispid pocket mouse *(Perognathus hispidus)*, and the tawny-bellied cotton rat *(S. fulviventer)*. However, as Leopold stated, much of this fine grassland, interspersed with mesquite, acacias, cacti, agaves, and herbaceous plants, has been depleted by overgrazing. Today, habitats suitable for cotton rats consist of scattered plots, which have been protected from heavy grazing by cattle, goats and sheep, along fence lines, at edges of cultivated fields, along rights-of-way of highways and railroads, and in situations where low thorny shrubs protect grasses underneath. The reduction in the quality of the habitat for cotton rats and other grassland mammals is not a recent development; E. A. Goldman (1951:291), who went to Zacatecas in December, 1902, hoping to collect topotypes of *S. fulviventer*, wrote: "The season had been a dry one and at the time of my visit the hills, overgrazed

FIG. 9. Runway of the tawny-bellied cotton rat, *Sigmodon fulviventer,* in grass belonging to species of the genera *Bouteloua* and *Muhlenbergia.* Photograph taken near Atotonilco, 2040 m., Durango, on July 11, 1967.

by goats, were nearly bare, leaving no local habitat suitable for the cotton rat."

Tawny-bellied cotton rats have been found in association with bunch grasses. Their well-worn runways may be completely hidden in thick, grassy cover or may be periodically exposed (see Fig. 9) with segments of trails covering distances over bare ground of as much as a third of a meter between grassy clumps. Plant and animal associates are described in the following paragraphs.

Chihuahua.—Tawny-bellied cotton rats were found in open, moderately-grazed grasslands. One such place (2 km. N Gallego, 1610 m.) had heavy grass (*Muhlenbergia* sp.) in poorly-drained areas with numerous runways paralleling roadside or railside ditches (see Fig. 10). Other plants collected were *Kuhnia chlorolepis, Engelmannia pinnatifida, Aphanostephus ramosissimus, Allionia* sp., *Baileya multiradiata, Jatropha macrohiza, Hedyotis rubra,* and *Evolvulus sericeus.* Small mammals obtained in association with S. *fulviventer* at the Gallego locality were *Dipodomys spectabilis, Perognathus hispidus, Perognathus flavus, Perognathus nelsoni, Baiomys taylori, Onychomys torridus, Reithrodontomys megalotis, Reithrodontomys montanus, Peromyscus maniculatus,* and *Neotoma albigula.* Although this locality was visited on two occasions (in 1965 and 1967), only one S. *hispidus* was captured. This indicates that at least two cotton rats were present, but S. *hispidus* was scarce and S. *fulviventer* was common, based on trap success.

FIG. 10. Elevated grasslands near Gallego, 1610 m., Chihuahua. The dry bunch grass is inhabited by the tawny-bellied cotton rat, *Sigmodon fulviventer*. Photograph taken on July 4, 1965.

Durango.—At 3.3 km. NE Boquilla, 1952 m., tawny-bellied cotton rats were caught in the level part of a mountain valley floor in mixed grassland, mesquite, acacia, juniper, and oaks (see Fig. 11). Grasses were mostly *Muhlenbergia* sp. and *Aristida* sp. Composites present were *Erigeron* sp., *Leucolene ericoides*, and *Sanvitalia* sp. Nightshade (*Solanum* sp.) also was present in the vicinity of runways. Small mammal associates included *Perognathus nelsoni* and, on adjacent hillsides, *S. ochrognathus*. At 12 km. NNE Boquilla, 1890 m., a locality just above the Durangan grassland plains to the eastward but within a scattered stand of juniper, acacia, *Mahonia trifoliata*, and mesquite, *S. fulviventer* was captured in runways in clumps of grass (*Muhlenbergia* sp.) and scattered composites, *Baileya* sp. and *Haplopappus spinulosus*. Small mammal associates included *Notiosorex crawfordi* (see Baker, 1966:345), *Perognathus flavus, Perognathus nelsoni, Perognathus hispidus, Reithrodontomys megalotis, Onychomys torridus, Baiomys taylori*, and (on adjacent hillsides) *S. ochrognathus*. At 9 km. NNW Canatlán, 1952 m., *S. fulviventer* was caught in runways in a dense stand of grasses, *Bouteloua gracilis* and *Muhlenbergia* sp., which were protected from intense grazing by an overhead growth of low acacia. Also present were *Verbena* sp., *Perymenium* sp., and *Haplopappus spinulosus*. Runways led from one clump of grass to another, through bunches of prickly pear (*Opuntia* sp.), among rocks, and between roots of huisache and acacia. One *S. fulviventer* was dug out of a burrow, which was approximately three-fourths of a meter long with a tunnel diameter of 45 mm. Other mammals caught in these runways were *Liomys irroratus*, *Perognathus nelsoni*, *Reithro-*

FIG. 11. Field camp in oak grove near Boquilla, 1952 m., Durango. The sparsely-vegetated hillsides are occupied by the yellow-nosed cotton rat, *Sigmodon ochrognathus*, and the valley floor by the tawny-bellied cotton rat, *Sigmodon fulviventer*. Photograph taken on July 1, 1965.

dontomys megalotis, *Peromyscus pectoralis*, *Baiomys taylori*, and, on adjacent hillsides, *S. ochrognathus*.

In the vicinity of Hacienda Coyotes, 2475 m., tawny-bellied cotton rats were trapped in open grassy meadows surrounded by pine-oak vegetation characteristic of the higher parts of the Sierra Madre Occidental. These rodents and their runways were most common in bunch grasses adjacent to rock fences, and seemed to avoid stands of tall sacaton grass, in which *Microtus mexicanus* was the only grass-eating rodent captured. The meadow was dotted with plants belonging to species of the genera *Verbena*, *Gnaphalium*, *Achaetogeron*, *Commelina*, *Heterotheca*, and *Ranunculus*, and to *Achillae lanulosa* and *Taraxacum officinale*. Other small mammals caught in cotton rat runways were *Reithrodontomys megalotis*, *Peromyscus melanotis*, and *Peromyscus boylii*. *Sigmodon leucotis* and *Microtus mexicanus* were present, but not trapped in the same areas, and were presumably ecologically segregated.

At 5 km. SE Tepehuanes, 1789 m., one *S. fulviventer* was trapped in a small patch of Johnson grass, *Sorghum halepense*, in an apple orchard that was protected from grazing by a rock fence. This patch also produced a catch of

FIG. 12. Mixed desert shrub and mesquite grassland near Atotonilco, 2040 m., Durango. Here, the tawny-bellied cotton rat, *Sigmodon fulviventer*, is the dominant grass-eating rodent and the hispid cotton rat, *Sigmodon hispidus*, is less common. Photograph taken on August 11, 1967.

Liomys irroratus, *Perognathus flavus*, *Reithrodontomys megalotis*, *Peromyscus boylii*, and *Peromyscus truei*. The latter two species were taken adjacent to a high canyon wall that bordered the orchard on one side.

At Hacienda Atotonilco, 2040 m., tawny-bellied cotton rats were found in distinct, well-used runways (see Figs. 9 and 12) in mixed grass, weeds, and shrubs along an arroyo. Clumps of grass were identified as blue gramma, *Bouteloua gracilis*, and *Muhlenbergia* sp. Runways also led through tall weeds of the genus *Viguiera*. *Verbena bipinnatifida* also was collected in the cotton rat area. Thorn shrubs of the genus *Mimosa* made up the woody cover along the arroyo; pods emptied of the beans were found in small piles along runways. It was supposed that S. *fulviventer* or other rodents used this food. Other small mammals captured in runways and adjacent habitats included *Notiosorex crawfordi*, *Liomys irroratus*, *Perognathus flavus*, *Perognathus hispidus*, *Reithrodontomys fulvescens*, *Baiomys taylori*, and *Sigmodon hispidus*. S. *hispidus* was uncommon, and S. *fulviventer* seemed to dominate as the grass-eating rodent in the community.

Zacatecas.—One S. *fulviventer* was hand-caught in mid-afternoon in a runway in tall grass, *Muhlenbergia* sp., at 13 km. S Villanueva, 2090 m.

Guanajuato.—Runways of S. *fulviventer* were noted in elevated grassland surrounded by oak-covered valleys in the mountains of extreme northwestern Guanajuato at 8 km. SW Ibarra, 2500 m. (see Fig. 13). This cotton rat was taken in runways in open country and near the edge of the oak timber in mixed grass and low-growing scrub oak, *Quercus* sp. Most runways were through grasses belonging to species of the genera *Muhlenbergia*, *Stipa* and *Bouteloua*.

Fig. 13. Open grassland and oak-filled canyons near Ibarra, 2500 m., Guanajuato. The mixed grass, forbs, and scrub oak clumps in the foreground are occupied by the tawny-bellied cotton rat, *Sigmodon fulviventer*; the rocky canyon slide in the background is the habitat of the white-eared cotton rat, *Sigmodon leucotis*. Photograph taken on July 19, 1966.

Moderate grazing by cattle seemed not to be a limiting factor on cotton rat distribution over this broad grassland. Other plants identified were *Euphorbia* sp., *Oenothera* sp., *Milla biflora*, *Dahlia coccinea*, *Oxalis* sp., *Sisyrinchium* sp., *Verbesina* sp., *Calochartus* sp., *Zemenia* sp., *Hypoxis* sp., *Castilleia* sp., *Achaetogeron* sp., *Baccharis glutinosa*, *Linum* sp., *Bouvardia* sp., and *Gutierrezia glutinosa*. Other small mammals taken in runways were *Peromyscus maniculatus* and, on adjacent hillsides, S. *leucotis*. The skull of a cotton rat, disgorged by a gopher snake, *Pituophis* sp., was obtained at this locality. A nest containing four young S. *fulviventer* (with eyes not yet open) was found on July 21 under a large rock (30 by 60 centimeters), adjacent to a rock wall in an abandoned corral (see Fig. 14). The nest was of shredded grass about 75 mm. in circumference and 50 mm. high, and situated in a shallow depression about 25 mm. deep and 100 mm. across.

Jalisco.—Tawny-bellied cotton rats were captured (mostly by hand) in mixed vegetation in a fence row bordering a field of carrots at 2 km. NW La Barca, 1525 m. Grass and weeds were growing in piles of mesquite branches, which had been placed over the vegetation on the field side of the barbed-wire fence. The runways, mostly directly under the fence wire, led through thick Bermuda grass (*Cynodon dactylon*), with some morning glory (*Ipomoea* sp.) growing on the fence. Cuttings of both morning glory and Bermuda grass were found in rodent trails; a nest constructed entirely of Bermuda grass was found along one runway. The field party visited this place between 2:00 and 4:00 p.m. on July 14, 1966, set Sherman live-traps in runways at one end of the fence line and, starting at the other end, drove any animals using the runways toward the traps. This action was repeated several times. Either captured or observed were the amphibians, *Rana pipiens* and *Hyla eximia*, the reptiles, *Sceloporus torquatus*, *Cnemidophorus scalaris*, and *Thamnophis* sp, and *Baiomys taylori*. *Sigmodon hispidus* was captured nearby, within the vegetable field but not in the fence row.

At 2½ km. W Mazamitla, Hooper (1955:21) captured one tawny-bellied cotton rat in a plant community consisting of grass, weeds, cactus, scrub oak, and a few shrubs. This place was in the oak belt, altitudinally just below the pine forest. Less than two kilometers away he captured S. *hispidus* in understory plants including grass, blackberry, and *Salvia*.

FIG. 14. Nest of young of the tawny-bellied cotton rat, *Sigmodon fulviventer*, found under a rock near Ibarra, 2500 m., Guanajuato. Photograph taken on July 19, 1966.

New Mexico.—Mohlhenrich (1961) found tawny-bellied cotton rats at elevations of 1200 to 1920 meters, mostly associated with piñon, oak, and juniper, and often found in swales containing thick grasses such as *Hilaria jamesii*.

Association of tawny-bellied cotton rats with other species of the genus.—*Sigmodon fulviventer* has been taken in association with or immediately adjacent to S. *hispidus*, S. *leucotis*, and S. *ochrognathus* (see Fig. 4). Probably S. *ful-*

viventer and *S. alleni* do not co-exist because of their differing ecological preferences. In the grasslands on deep alluvial soils along the eastern base of the Sierra Madre Occidental, *S. fulviventer* dominates or presumably excludes other cotton rats. When found in the vicinity of either *S. leucotis* or *S. ochrognathus*, *S. fulviventer* occupies the level, open areas leaving the peripheral rocky, sparsely-vegetated slopes to the former. However, where *S. fulviventer* is absent, *S. leucotis* (in Durango west of San Luis and southwest of Vicente Guerrero) and *S. ochrognathus* (in Coahuila in the Sierra del Carmen and southwest of Ocampo and in Texas in the Chisos and the Davis mountains) may take over all available grassy habitats. Whereas *S. fulviventer* comes in contact with *S. leucotis* and *S. ochrognathus* in the higher foothills and in mountain meadows of the Sierra Madre Occidental, *S. fulviventer* is more apt to live in some degree of association with *S. hispidus* in the lower, eastern parts of its range, especially where the mesquite grasslands and the desert habitat interdigitate. In New Mexico, Mohlhenrich (1961) found hispid cotton rats more common in plant communities containing cottonwood trees, joint-fir, cattail, saltbush, mesquite, creosote-bush, cholla, and prickly pear and tawny-bellied cotton rats more common in communities containing piñon, juniper, evergreen oak, and grasses such as *Hilaria jamesii*. In areas where both species occur in New Mexico, *S. fulviventer* is found at higher elevations with lower temperatures and more vegetative cover, whereas *S. hispidus* occurs at lower elevations with higher temperatures and more sparse vegetative cover. This same situation seems to prevail where the distribution of these species adjoin along the western border of the Mexican Plateau. In the northern part (in Chihuahua near Gallego and in Durango at Atotonilco) *S. fulviventer* appeared, at least from our trapping records, to be more abundant than *S. hispidus*. In more humid Jalisco (near La Barca), however, we captured almost equal numbers of each (five *S. fulviventer* and four *S. hispidus*), although each species was from a different part of a cultivated field. It would seem that the *fulviventer* group of cotton rats saturates most suitable habitats in the western part of the Mexican Plateau, in the adjacent Sierra Madre Occidental, and in montane grasslands from Trans-Pecos Texas and Coahuila westward to Arizona, Chihuahua, and northern Durango. In southern Zacatecas, Jalisco, and Michoacán, where rainfall increases markedly, *S. hispidus* takes over more of the available grassland habitat, apparently restricting greatly the areas used by *S. fulviventer* and *S. leucotis*. In these states, grassy places that in Durango might ordinarily harbor *S. fulviventer* contain only *S. hispidus*.

Elevated grasslands in eastern Chihuahua, western Texas, and western Coahuila seem entirely suitable for occupancy by *S. fulviventer*, although now are included in the ranges of *S. ochrognathus* (in the higher areas) and *S. hispidus* (in the lower areas). It would appear that *S. fulviventer* has been unable to "cross" desert country in the vicinity of the Río Grande in New Mexico and Texas and in the Bolson de Mapimí in Chihuahua and Coahuila to reach these areas to the eastward. The success of *S. ochrognathus* and the ubiquitous *S. hispidus* in occupying these desert mountains suggests that they, as species, can survive more xeric conditions than *S. fulviventer*.

Parasites.—Dr. Robert Traub identified from *S. fulviventer* the fleas, *Polygenis martinez-baezi* Vargas, 1951, and *Archopeas leucopus* ssp. from near

Boquilla, and *Pleochaetis* sp. from near Hda. Coyotes. Doran (1955:164) recorded the nematode, *Litomosoides carinii* (Travassos, 1919), from *S. f. melanotis*.

Specific Characters and Comparisons

The "pepper and salt" colored upper parts and the tawny underparts, coupled with large size (for captive animals, maximum weights are 222 grams for a male and 206 for a non-pregnant female; maximum lengths of head and body are 197 mm. and 200, respectively) distinguishes *S. fulviventer* from other members of the *S. fulviventer* group. Other unique characters include: anterior end of mesopterygoid fossa narrow; foramen ovale large (at least three-fourths width of M3); palatal pits markedly deep; and median keel on palate well developed.

From *S. alleni*, *S. fulviventer* is further distinguished by skull more arched, short and broad rather than long and narrow; incisors less recurved; basioccipital more elongate in comparison to width; auditory bullae, in relation to size of skull, larger; posterior ends of incisive foramina extending (instead of not) to or beyond a line drawn between the anterior surfaces of the first upper molars; and paraoccipital process, when viewed from below, straight instead of hooked.

From *S. leucotis*, *S. fulviventer* differs further in interparietal more than (instead of less than) 2 mm. long; rostral depressions on upper premaxillary slight instead of pronounced; angular process of lower jaw more rounded and less hooked; and lingual root of first lower molar normal, not reduced or absent.

From *S. ochrognathus*, *S. fulviventer* is further distinguished by whitish tips of hairs on inner side of pinnae that do not contrast with color of pelage of rest of head; auditory bullae large and broad rather than small and elongate; median keel on basioccipital slight instead of obvious; anterior lip of foramen magnum not obviously notched; bulge of capsular projections of upper incisors moderate rather than pronounced; median-posterior notch in interparietal absent instead of present; and paraoccipital process (in ventral view) straight instead of curved with basal notch.

From *S. hispidus*, *S. fulviventer* differs in small size of tail scales (0.5 mm. wide rather than 0.75 wide); tail heavily haired instead of sparsely haired; posterior ends of incisive foramina extending (instead of usually not) to or beyond a line drawn between the anterior surfaces of the first upper molars; foramen ovale larger, at least three-fourths instead of one-half the width of M3; palatal pits more deeply marked; and median keel on palate better developed.

Geographic Variation

Tawny-bellied cotton rats were recognized by Bailey (1902) as belonging to three distinct species: S. *minimus* Mearns 1894, with type locality on the Mexican-New Mexico boundary and southernmost collecting locality at Casas Grandes, Chihuahua; S. *fulviventer* Allen, 1889, with type locality at Zacatecas and northernmost collecting locality at Durango, about 800 kilometers southward of Casas Grandes; and S. *melanotis* Bailey 1902, with type locality at Pátzcuaro, 400 kilometers to the south of Zacatecas. Hall and Kelson (1959:676-677) retained Bailey's arrangement and noted that S. *minimus* was polytypic by listing subspecies named for New Mexican populations (also see Findley and Jones, 1963) and citing records for S. *m. minimus* from northern Durango, thus bridging the gap considerably between known collecting stations of S. *minimus* and S. *fulviventer* (to about 300 kilometers—Rosario to Durango). They also reported additional collecting localities to shorten the gap between S. *fulviventer* and S. *melanotis* to about 325 kilometers (Zacatecas to Mazamitlá, Jalisco).

Baker and Greer (1962:121-123) concluded that S. *minimus* and S. *fulviventer* were conspecific and arranged taxa previously designated as S. *minimus* under the older name, S. *fulviventer*. My own field work in southern Zacatecas, northwestern Guanajuato, and in the vicinity of Lago de Chapala in Jalisco has provided specimens from additional collecting stations to reduce the gap between S. *fulviventer and* S. *melanotis* to less than 175 kilometers and to demonstrate that tawny-bellied cotton rats live in grassy upland habitats in more or less continuous fashion all the way south to the northern foothills of the Trans-Mexican Volcanic Belt. Since characters distinguishing S. *melanotis* from S. *fulviventer* (see accounts of subspecies) are, in magnitude, no greater than those distinguishing one subspecies of S. *fulviventer* from another, S. *melanotis* is arranged as a subspecies with the older name, S. *fulviventer*, being used to designate all of these tawny-bellied cotton rats. Subspecies now recognized are: *Sigmodon fulviventer fulviventer* J. A. Allen, *Sigmodon fulviventer goldmani* Bailey, *Sigmodon fulviventer minimus* Mearns, and *Sigmodon fulviventer melanotis* Bailey. S. *f. goldmani* is not treated in the accounts beyond.

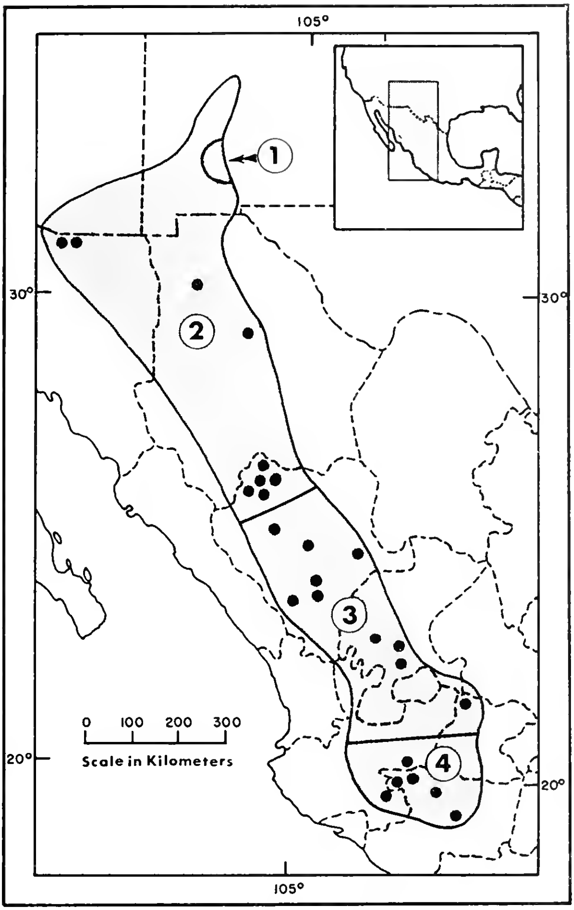

FIG. 15. Geographic distribution of tawny-bellied cotton rats. 1. *Sigmodon fulviventer goldmani.* 2. *Sigmodon fulviventer minimus.* 3. *Sigmodon fulviventer fulviventer.* 4. *Sigmodon fulviventer melanotis.*

In their study of this species (listed as the least cotton rat, *Sigmodon minimus*) in New Mexico, Findley and Jones (1963) found a slight cline in color in at least the population inhabiting the upper Río Grande valley but no definite patterns in the southern part of the state. Along the eastern face of the Sierra Madre Occidental from Chihuahua and northeastern Sonora southeastward to Michoacán, there is a conspicuous color cline with pale, buff-colored populations in the arid grasslands of the north grading into rich, tawny-colored populations in the more humid country in the northern foothills of the Trans-Mexican Volcanic Belt. Logical breaks in the color pattern in northern Durango and northern Guanajuato-Jalisco are aligned with changes in other external and cranial characteristics.

There is no attempt here to compare cranial characters of the various wild-taken Mexican specimens of S. *fulviventer*. The few museum specimens of sufficient maturity to show wear, as illustrated in figure 8 of Findley and Jones (1963:313), present a similar discordance in the geographically varying features, as found for New Mexican cotton rats of this species by Findley and Jones. It is likely that their specimens included some of the same variations due to differences in age as does the Mexican material. In Table 3 are presented average and extreme measurements of selected external and cranial dimensions of 100-day-old, laboratory-born S. *fulviventer*, whose parents were wild-caught at localities in each of four Mexican states (from north to south—Chihuahua, Durango, Guanajuato, and Jalisco). These animals were raised in the same room and in similar cages and fed similar amounts and the same kind of food (Purina Mouse Chow). Even though it might be argued that cotton rats whose ancestors came from an arid grassland plain north of the Tropic of Cancer (at 29° 17′ N in Chihuahua) might develop, as individuals, more slowly than cotton rats whose ancestors came from a much more humid situation, south of the Tropic of Cancer (at 20° 17′ N in Jalisco), the dimensions of these 100-day-old animals are used in this taxonomic comparison along with those of offspring of similar age resulting from a cross between parents from Chihuahua and from Jalisco. Laboratory-raised cotton rats 200-210 days old whose parents came from Gallego and who were the offspring of the above-mentioned cross also were available in sufficient numbers to be inserted in the table for growth comparisons. It will be noted that 200-day-old cotton rats are considerably larger than 100-day-old specimens. There is no attempt to compare laboratory-raised animals with animals snap-trapped in nature, but it is possible from this demonstrated growth that the comparison of dimensions (except for alveolar length of maxillary toothrow) of "adult" wild-taken animals may not be highly meaningful from a taxonomic point of view. Because of this, comparisons of the dimensions of laboratory-raised cotton rats of known ages are made to assist in appraising geographic variation in S. *fulviventer*.

A study of Table 3 shows that 100-day-old samples of S. *fulviventer* range in size both externally and cranially from small in Chihuahua to large in Jalisco. To evaluate the extent of the variation

TABLE 3.—SELECTED MEASUREMENTS (AVERAGES AND EXTREMES) OF KNOWN-AGE, LABORATORY-RAISED *Sigmodon fulviventer*.

Age and size of sample (in parentheses)	Length of head and body	Length of hind foot	Height of ear from notch	Condylo-premaxillary length	Zygomatic breadth	Least interorbital constriction	Depth of cranium*	Length of nasals	Alveolar length of maxillary toothrow
Gallego, Chihuahua									
100 days (5)	143 (138-155)	31 (30-31)	19 (18-19)	30.7 (29.8-31.1)	18.9 (18.1-19.7)	4.7 (4.3-5.1)	10.3 (9.9-10.8)	11.8 (11.2-12.7)	6.4 (6.3-6.6)
200 days (10)	157 (142-176)	30 (27-32)	19 (17-21)	34.0 (32.7-36.2)	20.5 (19.8-21.0)	5.0 (4.6-5.6)	11.1 (10.3-12.4)	13.1 (12.5-13.9)	6.6 (6.4-6.8)
Coyotes, Durango									
100 days (5)	158 (154-160)	32 (31-33)	20 (19-21)	32.5 (31.3-33.5)	20.0 (19.0-20.7)	4.7 (4.2-4.9)	10.5 (10.1-10.8)	12.3 (11.9-13.0)	6.4 (6.3-6.5)
Ibarra, Guanajuato									
100 days (6)	164 (149-176)	34 (32-36)	20 (18-21)	34.1 (32.2-36.1)	20.3 (19.9-20.8)	5.1 (4.5-4.9)	11.0 (10.5-11.0)	12.5 (11.4-14.3)	6.4 (6.1-6.6)
La Barca, Jalisco									
100 days (5)	178 (172-188)	35 (34-36)	21 (20-22)	34.8 (33.6-36.0)	20.4 (19.2-21.2)	4.9 (4.6-5.3)	10.6 (10.4-11.1)	12.8 (12.0-13.5)	6.5 (6.3-6.9)
Cross between stocks from Gallego, Chihuahua, and La Barca, Jalisco									
100 days (10)	162 (150-177)	33 (31-35)	21 (19-23)	34.1 (33.2-36.2)	20.1 (19.3-21.3)	5.0 (4.8-5.3)	10.8 (10.2-11.4)	13.2 (12.4-14.2)	6.8 (6.6-7.2)
200 days (9)	171 (156-203)	33 (31-35)	21 (19-24)	36.5 (35.6-37.7)	20.7 (20.1-21.3)	5.0 (4.6-5.6)	11.4 (11.0-11.8)	14.5 (14.1-15.1)	6.8 (6.7-6.9)

* Measurement taken as described by Findley and Jones (1963:308).

TABLE 4.—RESULT OF NEW MULTIPLE RANGE TEST ON CONDYLOPREMAXILLARY LENGTHS OF CRANIA OF SAMPLES OF *Sigmodon fulviventer*. POPULATION MEANS UNDERSCORED BY A COMMON LINE ARE NOT SIGNIFICANTLY DIFFERENT.

Subspecies	*S. f. minimus*	*S. f. fulviventer*		*S. f. melanotis*	*S. f. minimus-S. f. melanotis*
Locality	Gallego, Chihuahua	Coyotes, Durango	Ibarra, Guanajuato	La Barca, Jalisco	Cross Chihuahua-Jalisco
Means of condylopremaxillary lengths	30.7	32.5	34.0	34.8	33.9

between the samples, analysis of variance was applied to the condylopremaxillary lengths. The overall differences between the means of this dimension are highly significant ($F=18.36$). A new multiple range test was then made to determine the degree of difference between the means from the selected localities (see Table 4). Population means underscored by a common line are not significantly different. As expected, the sample from Chihuahua (representing *S. f. minimus*) is significantly different from all other samples; the samples from Durango and Guanajuato (representing *S. f. fulviventer*) are not significantly different from each other; the samples from Guanajuato, from Jalisco (representing *S. f. melanotis*) and from a cross between animals from Chihuahua and from Jalisco also are not significantly different from one another. This test demonstrates that there are subspecific differences between these Mexican populations of tawny-bellied cotton rats and there is logic for arranging them under three subspecific designations.

Sigmodon fulviventer minimus Mearns

Sigmodon minima Mearns, Proc. U.S. Nat. Mus., 17:130, July 19, 1894.

Sigmodon fulviventer minimus Baker and Greer, Michigan State Univ., Publ. Mus., Biol. Ser., 2:123, August 27, 1962.

Type.—Young adult male, skin and skull; no. 21187/37291 U.S. National Museum; from near Monument no. 40, 1500 m., Hidalgo Co., New Mexico, on the Mexican boundary line, 166 km. W initial monument on west bank of Río Grande; obtained on April 26, 1892, by Edgar A. Mearns and Frank X. Holzner, original no. 1704.

Range.—Elevated grasslands of southeastern Arizona, central and southwestern New Mexico, northeastern Sonora, westcentral Chihuahua and northcentral Durango (see Fig. 15).

Diagnosis.—Size small for the species; dorsum intermixed with black hairs and agouti-banded hairs near (c) Pinkish Buff; underparts and upper surfaces of feet and tail with this same pale coloring; base of tail slightly darker, hairs dark Pinkish Buff. No measurements of wild-taken specimens are given; consult Table 3 for listing of selected measurements of laboratory-raised animals from north-central Chihuahua (Gallego).

Comparisons.—To compare S. *f. goldmani* of New Mexico with S. *f. minimus*, the reader may refer to the account by Findley and Jones (1963). From S. *f. fulviventer*, found directly to the southward, S. *f. minimus* differs in size smaller (see Table 3); color paler (near Pinkish Buff rather than Cinnamon-Buff) both above and below; zygomatic arches noticeably wider in relation to length of skull.

Remarks.—Sigmodon fulviventer minimus is the smallest and palest of the Mexican tawny-bellied cotton rats. This subspecies is identifiable as far southward as north-central Durango where the color of specimens from near Boquillas is almost identical to that of animals from Gallego. Specimens from near Canatlán in west-central Durango show an intermediate coloring between the paler S. *f. minimus* and the darker S. *f. fulviventer*, but are assigned to the latter subspecies.

Specimens examined (42).—SONORA: Los Nogales, 1 (US); Santa Cruz River, near Monument no. 111, 6 (US). CHIHUAHUA: Casas Grandes, 2135 m., 1 (US); 2 km. N Gallego, 1366 m., 2 (MSU). DURANGO: Rosario, 9 (AMNH); Río Sestín, 10 (AMNH); Guanaceví, 1 (AMNH); Rancho Bailon, 5 (AMNH); 11 km. NNE Boquilla, 1952 m., 7 (MSU).

Sigmodon fulviventer fulviventer J. A. Allen

Sigmodon fulviventer J. A. Allen, Bull. Amer. Mus. Nat. Hist., 2:180, October 21, 1889.

Type.—Young adult male, skin and skull: no. 1975/1244 American Museum of Natural History; from Zacatecas, Zacatecas; obtained on August 17, 1889, by Audley Buller, original no. 59.

Range.—Grasslands on eastern foothills of the Sierra Madre Occidental from central Durango southeastward to western Guanajuato and southern Zacatecas (see Fig. 15).

Diagnosis.—Size medium for the species; dorsum intermixed with black hairs and agouti-banded hairs of Cinnamon Buff; underparts and upper surfaces of feet and tail washed with similar coloring; base of tail darker, near (a) Clay Color. Average and extreme external and cranial measurements of nine wild-trapped adults (measurements compare closely with those of 100-day-old, laboratory-raised animals from the same locality, see Table 3) from Hda. Coyotes, Durango, are as follows: length of head and body, 150 (138-164); length of hind foot, 28 (26-30); height of ear from notch, 21.6 (20-22); condylopremaxillary length, 32.5 (31.2-33.7); zygomatic breadth, 19.7 (18.8-20.6); least interorbital constriction, 4.9 (4.6-5.3); interparietal breadth, 10.8 (10.0-11.4); depth of cranium, 10.9 (10.7-11.1); length of nasals, 12.1 (10.6-12.7); and alveolar length of maxillary toothrow, 6.5 (6.2-6.9).

Comparisons.—For comparison with S. *f. minimus,* see account of that subspecies. From S. *f. melanotis,* S. *f. fulviventer* differs in size smaller (see Table 3); color less rich (Cinnamon-Buff rather than near (a) Clay Color) both above and below; skull less massive in appearance and less arched in the interorbital area.

Remarks.—Sigmodon fulviventer fulviventer is intermediate in both size and coloration between S. *f. minimus* to the northward and S. *f. melanotis* to the southward. There is evidence of intergradation with the former subspecies in specimens taken near Canatlán in Durango. These are more or less intermediate in color but allocated to S. *f. fulviventer.* Specimens from an elevated grassland near Ibarra in Guanajuato are paler than typical S. *f. fulviventer,* but in terms of size show a tendency toward the larger S. *f. melanotis* of nearby Jalisco. As Table 3 shows, the laboratory-raised animals from Ibarra also are more or less intermediate in size between animals from Hda. Coyotes in Durango and from near La Barca in Jalisco.

Specimens examined (42).—DURANGO: 5 km. SE Tepehuanes, 1780 m., 1 (MSU); 9 km. NNW Canatlán, 1950 m., 2 (MSU); 4 km. SE Atotonilco, 2037 m., 1 (MSU); *5.5 km. SE Atotonilco, 2037 m.,* 1 (MSU); 10 km. N Durango, 2 (UI); *Durango,* 2 (US); Hda. Coyotes, 2475 m., 1 (CAS), 12 (MSU). ZACATECAS: Laguna Valderama, 67 km. W Fresnillo, 2380 m., 5 (CAS); Zacatecas, 3 (AMNH); 13 km. S Villanueva, 2090 m., 1 (MSU). GUANAJUATO: 8 km. SW Ibarra, 2500 m., 9 (MSU); *12 km. SW Ibarra, 2623 m.,* 3 (MSU).

Sigmodon fulviventer melanotis Bailey

Sigmodon melanotis Bailey, Proc. Biol. Soc. Washington, 15:114, June 2, 1902.

Type.—Adult female, skin and skull; no. 50190 U.S. National Museum; from Pátzcuaro, 2135 m., Michoacán; obtained on July 15, 1892, by E. W. Nelson, original no. 2834.

Range.—Mesic grasslands of the southwestern part of the Mesa Central (southern part of the Mexican Plateau) bordering and in the foothills of the northwestern slopes of the Trans-Mexican Volcanic Belt (see Fig. 15). Distribution in grasslands and mixed agricultural country spotty, presumably because of competition with S. *hispidus.*

Diagnosis.—Size large for the species; dorsum intermixed with black hairs and agouti-banded hairs near (a) Clay Color; underparts, upper surfaces of feet and tail washed with similar rich coloring; base of tail slightly darker. No measurements of wild-taken specimens are given; consult Table 3 for selected measurements of laboratory-raised animals from Jalisco.

Comparisons.—From S. *f. fulviventer,* which occurs directly to the northward, S. *f. melanotis* is larger and more richly colored as indicated in the account of the former subspecies.

Remarks.—Until now, the systematic status of S. *melanotis* has remained unchanged since first described by Bailey in 1902. Its rich coloring (especially conspicuous on the underparts of the specimens from Pátzcuaro, Michoacán) and its characteristic "pepper and salt" dorsal appearance set it apart from other cotton rats. Moreover, its seemingly spotty distribution has been a deterrent to collectors. Aside from the extensive type series taken in the 1890's, from the vicinity of Pátzcuaro, there were no sizeable series assigned to this taxa extant, until members of a Michigan State University Museum field party saw a tawny-bellied cotton rat cross the road near La Barca, Jalisco, in July of 1966, and subsequently caught it and four others. In other cases (see specimens examined), only a few examples of these rats from localities in Michoacán and Jalisco occur in Mexican and American museums. The Pátzcuaro series is the richest in color; specimens from near Zamora and in the vicinity of Lago de Chapala are slightly paler (tending in color to be closer to Cinnamon-Buff than to Clay Color), which shows evident relationship with the more northward and paler *S. f. fulviventer.* Specimens assigned to the latter from Ibarra in Guanajuato also are somewhat intermediate in size between the larger *S. f. melanotis* and its smaller relatives to the northward.

Specimens examined (18).—Jalisco: 2 km. NW La Barca, 1525 m., 1 (MSU); 2 km. N Mazamitlá, 1 (UM). Michoacan: 5 km. S Cumuato, 1 (UNAM); 3 km. E La Palma, SE side Lago de Chapala, 1 (MSU); 18 km. E Zamora, 1 (TCWC); Pátzcuaro, 2135 m., 12 (US).

Sigmodon leucotis

Sigmodon leucotis, the white-eared cotton rat, occupies montane habitats in a Y-shaped distributional pattern (see Fig. 16) from approximately 25° N latitude in the Sierra Madre Occidental (in the west) and the Sierra Madre Oriental (in the east) southeastward into the central part of the Trans-Mexican Volcanic Belt and culminating in the Sierra Madre del Sur in Oaxaca. This cotton rat lives in a comparable, but more mesic, habitat than does *S. ochrognathus,* which occupies montane areas generally northward of 25° N latitude.

Habitat and Habits

The white-eared cotton rat is strictly a montane species and associated chiefly with mesic pine-oak habitat. In such areas the species seems most adapted to mixed grass and shrub cover on shallow, rocky soils, although animals also have been taken in grassy meadows, adjacent to streams, in "sacaton" meadows, and in scattered clumps of bunch grass on dry, rocky slopes. The latter situation is much like that preferred by *S. ochrognathus,* although these species have never been found together where their ranges overlap (in latitude) in the Sierra Madre Occidental of central Durango. In grassy patches, *S. leucotis* can be taken in well-used runways, typical of other cotton rats. In low, shrub cover, runways are obscure or absent; little or no sign may be present and the detection of the presence of the species in such areas can be difficult. Such places, with exposed rocky ledges and shallow soils, often appear to be more suitable for species of *Peromyscus* and *Neotoma* than for *Sigmodon.* Like *S. ochrognathus, S. leucotis* does not seem to exist in such dense populations as does *S. hispidus* or *S. fulviventer.* Descriptions of collection stations are given below.

Durango.—In boreal, mesic, pine-oak forest 30 km. SSW of Tepehuanes, 2500 m., two white-eared cotton rats were trapped in dense shrubs on a hillside covered with mixed pine, oak, manzanita, and juniper. The catches were made under clumps of *Ceanothus fendleri* and scrub oak, *Quercus* sp. Other plants in this thicket included bunch grass (*Muhlenbergia* sp.), *Senecio*

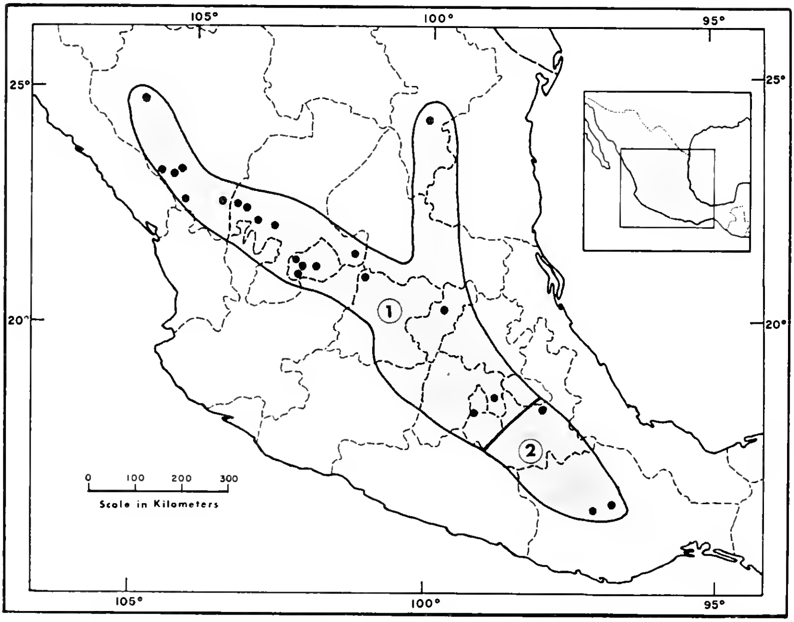

FIG. 16. Geographic distribution of the white-eared cotton rat. 1. *Sigmodon leucotis leucotis*. 2. *Sigmodon leucotis alticola*.

actinella, and species of the genera, *Geranium, Cosmos, Valeriana, Castilleia, Achaetogeron, Lupinus, Tradescantia* and *Cologania*. At ground level there was no evidence of runways among the woody stems of the shrubs or at the bases of grass clumps. No burrows were found although one surface nest of grass, thought to be that of a cotton rat, was located at the base of a manzanita bush, *Arctostaphylos*. The nest measured 130 mm. in circumference and 80 mm. in depth. Although no other small mammals were captured in this bushy habitat, *Peromyscus boylii* and *Peromyscus melanotis* were taken in adjacent woody cover and *Thomomys umbrinus, Reithrodontomys megalotis*, and *Microtus mexicanus* in wet montane meadows dotted with clumps of sacaton grass.

Within 3 km. of San Luis, 2300 m., S. *leucotis* was found in an open meadow along a cold, mountain tributary of the Río Piaxtlá (see Fig. 17). This area was surrounded by boreal pine-oak, fir-aspen forest. Traps set in runways also captured *Reithrodontomys megalotis* and *Peromyscus melanotis*. *Microtus mexicanus* was present, but only in the open grass, whereas S. *leucotis* occupied the shrub zone.

At Hacienda Coyotes, 2475 m., white-eared cotton rats lived on partly bare, rocky slopes under patches of low vaccinium and manzanita, just at the edge of dense pine-oak forest. No runways or cuttings were evident, but holes under rock ledges were conspicuous. Traps placed in front of these holes captured most of the animals. No other small mammals were taken in association with S. *leucotis*, although *Reithrodontomys megalotis, Sigmodon fulviventer*, and *Microtus mexicanus* occupied adjacent wet meadows in bunch grasses and sacaton.

FIG. 17. Riparian grass-shrub habitat surrounded by pine-fir boreal forest near San Luis, 2300 m., Durango. The Mexican vole, *Microtus mexicanus,* uses the open grass, whereas the white-eared cotton rat, *Sigmodon leucotis,* seems to prefer the areas of mixed shrubs. Photograph taken on July 17, 1957.

On a canyon side, approximately 3.3 km. N of Pueblo Nuevo, 1830 m., a white-eared cotton rat was shot (by headlight at night) in an area of large rocks in an abandoned weedy and brushy peach orchard (see description in Webb and Baker, 1962:328). This locality is situated on the west side of the Sierra Madre Occidental in mixed boreal-tropical habitat. Intensive trapping in the place where the one cotton rat was shot produced no more individuals. Other mammals taken there were *Thomomys umbrinus, Peromyscus boylii,* and *Neotoma mexicana.* This is the most "tropical" habitat in which S. *leucotis* has been found.

In southern Durango on the Rancho Las Margaritas (47 km. S and 28 km. W Vicente Guerrero, 2545 m.), S. *leucotis* was captured in pine-oak habitat in a narrow valley in obscure runways in scattered bunch grasses (see Drake, 1958). Other small mammals in this association were *Thomomys umbrinus, Eutamias bulleri, Reithrodontomys megalotis,* and *Peromyscus boylii.* In nearby canyon-side habitat our field party caught *Peromyscus difficilis, Peromyscus truei, Neotoma mexicana,* and *Nelsonia neotomodon.*

Zacatecas.—At approximately 13 km. W of Milpillas, 2530 m., J. Dan Webster (personal communication) reported catching S. *leucotis* in a wet meadow surrounded by boreal pine-oak forest. At 15 km. W Zacatecas, 2135 m., white-eared cotton rats were found at a creek border in willow trees and baccharus bushes.

Guanajuato.—At the Rancho La Puerta Guadalupe (8 km. SW Ibarra, 2500 m.) S. *leucotis* occupied obscure runways in grass leading between rocks and clumps of low-growing (40 centimeters high) scrub oak (see Fig. 13). The

FIG. 18. Open valley meadow surrounded by oak forest near Ibarra, 2590 m., Guanajuato. The sacaton, *Briza rotundata*, is occupied by the white-eared cotton rat, *Sigmodon leucotis*, and three species of *Peromyscus*. Photograph taken on July 22, 1966.

bunch grasses included representatives of the genera *Muhlenbergia*, *Stipa*, and *Bouteloua*. This location was on a sloping hillside with large oaks and manzanita in the shallow valley below. Above the slope the level open grasslands were occupied by *Sigmodon fulviventer*. In runways used by *S. leucotis*, we found grass cuttings, the husks of acorns and manzanita berries, and small piles of lily bulbs. These foods might have been used by the white-eared cotton rat or by other small mammals found in the runways (*Peromyscus boylii*, *Peromyscus maniculatus*, and *Peromyscus truei*).

At 13 km. S Ibarra, 2590 m., *S. leucotis* was captured in a small meadow of about two hectares along a cold stream and surrounded entirely by an oak forest (see Fig. 18). This opening contained short grass, *Piptochaetium* sp., with scattered clumps of bunch grass, *Muhlenbergia* sp., and sacaton, *Briza rotundata*. Eaten-out areas at the bases of these grasses plus a few leaf cuttings were the only evidences of sign attributable to cotton rats. One cotton rat was taken in front of a hole beneath a prickly pear plant, in mixed oak and manzanita. There was no evidence that either *S. fulviventer* or *Microtus mexicanus* were present, although the moist meadow seemed ideal for the Mexican vole. Small mammal associates in the sacaton area were *Thomomys umbrinus*, *Peromyscus difficilis*, *Peromyscus boylii*, and *Peromyscus truei*.

Morelos.—In a moist, open meadow 6.5 km. NW Huitzilac, 2800 m., one white-eared cotton rat was captured in an eaten-out area at the base of a large clump of sacaton, *Muhlenbergia macroura* (see Fig. 19). This clump was one of a large number that surrounded an open meadow containing such plants as *Senecio pinnatisectus*, *Ranunculus* sp., and *Taraxacum officinale*. Surrounding the meadow was a boreal forest of pine, oak, fir, and other montane vegetation. Small mammal associates were *Reithrodontomys megalotis*, *Peromyscus melanotis*, *Neotomodon alstoni*, and *Microtus mexicanus*. In the case of the latter two, both grass-eating "competitors" of the cotton rat, *M. mexicanus* was most abundant in the short grass-herb meadow and *N. alstoni* (see Davis and Follansbee, 1945) dominated the sacaton clumps. On the basis of these observations, *S. leucotis* evidently was rare and perhaps at an ecological disadvantage. This same locality was visited again three years later (in 1967) and the entire area was intensely live-trapped for three days, without obtaining other *S. leucotis*. Davis (1944:399), caught five animals in a meadow with *Microtus* at Monte Río Frío in the state of México, but subsequently failed to catch others. Field parties from the Michigan State University Museum also failed to find cotton rats in montane habitats in the vicinity of Oaxaca in the state of Oaxaca and in the vicinity of Pinal de Amoles in Queretaro; specimens were obtained at both places by E. W. Nelson and E. A. Goldman in the 1890's (Bailey, 1902:116). The fact that *S. leucotis* may live in shrub vegetation, especially where bunch grass habitat is grazed off, makes the presence of the species difficult to determine.

FIG. 19. Open valley meadow surrounded by pine-fir boreal forest near Huitzilac, 2800 m., Morelos. The open meadow is occupied by the Mexican vole, *Microtus mexicanus*; the volcano mouse, *Neotomodon alstoni*, is the dominant grass-eating rodent in the large clumps of sacaton where the white-eared cotton rat, *Sigmodon leucotis*, is uncommon. Photograph taken on July 24, 1964.

Association of white-eared cotton rats with other species of the genus.—*Sigmodon leucotis* has not been taken in company with *S. alleni*, *S. hispidus*, or *S. ochrognathus*. Perhaps *S. leucotis* and *S. alleni* might associate in such situations as found in the vicinity of Pueblo Nuevo in Durango where the former species has been taken in a mixed boreal-tropical habitat, not unlike some of the places in Michoacán and Oaxaca where S. *alleni* occurs. In the mountains of west-central Durango, S. *leucotis* and S. *ochrognathus* occur in the same latitude (see Fig. 4) but at different elevations, with the former in higher more mesic areas and the latter on the lower slopes and foothills in arid oak-juniper areas.

The two species, S. *leucotis* and S. *fulviventer*, were found in the same areas in Durango (vicinity of Hacienda Coyotes) and in Guanajuato (8 km. SW Ibarra). At both of these places, S. *fulviventer* dominates the open grasslands whereas S. *leucotis* lives on the rocky, brushy, well-drained slopes. The meeting ground of these two species appears to be at the junction of these two environments. In somewhat similar situations, where S. *fulviventer* is absent (as at San Luis and the Rancho Las Margaritas in Durango), S. *leucotis* takes over both habitats. Also, S. *leucotis* seems to avoid extensive association with other grasseaters, *Microtus mexicanus* and *Neotomodon alstoni,* when S. *fulviventer* is absent (as at Huitzilac in Morelos). When S. *leucotis, S. fulviventer* and *M. mexicanus* are in the same area (as at Hacienda Coyotes in Durango), S. *leucotis* occupies the forest-meadow ecotone (mixed brush on rocky slopes). S. *fulviventer* occupies the bunch grass flats, and *Microtus mexicanus,* although occasionally taken in runways with S. *fulviventer*, occupies exclusively the poorly-drained parts of the montane meadow that is covered with clumps of sacaton.

Parasites.—Dr. Robert Traub identified the flea, *Polygenis martinez-baezi* Vargas, 1951, from S. *leucotis* from near Hda. Coyotes. Dr. Richard B. Loomis identified the chiggers, *Hyponeocula argenicola* and *Fonsecia* sp., from S. *leucotis* from the same area.

Specific Characters and Comparisons

Conspicuous whitish ears in contrast to a brownish-gray head and body together with small to medium size (for captive animals, maximum weights are 131 grams for a male and 140 for a non-pregnant female; maximum lengths of head and body are 160 mm. and 169, respectively), pronounced premaxillary depressions on each side of the rostrum, and highly reduced or absent lingual root on the first lower molar distinguish S. *leucotis* from other species in the S. *fulviventer* group, and, with the exception of size, from S. *hispidus* as well. Other unique characters are: anterior portion of mesopterygoid fossa parallel-sided; interparietal short, length at midline less than 2 mm.; angular process of lower jaw slightly hooked rather than rounded. The reduction or absence of the lingual root on the first lower molar is possibly the most distinctive character and sets this species apart as perhaps the most highly evolved in the genus (see also Dalby and Lillevik, 1969).

From S. *alleni*, S. *leucotis* is further distinguished by skull short and broad rather than long and narrow; dorsal profile of skull more arched than flattened; upper incisors less instead of more recurved (opisthodont); auditory bullae large instead of small in relation to size of skull; basioccipital long and narrow rather than short and wide; posterior ends of incisive foramina extending (rather than not extending) to a line drawn between the anterior surfaces of the first upper molars; anterior lip of foramen magnum slightly instead of obviously notched; and paraoccipital process (from ventral view) straight rather than slightly hooked.

From S. *fulviventer*, S. *leucotis* differs in color of under parts (usually whitish not buff), and in that the foramen ovale is small (no more than half width of M3) instead of large (at least three-fourths width of M3).

From S. *ochrognathus*, S. *leucotis* is further distinguished by nose usually lacking extensive, contrasting yellow coloring; auditory bullae large and broad instead of small and elongate; basioccipital long and narrow instead of short and wide; median keel on basioccipital slight rather than obvious; posterior ends of incisive foramina extending (rather than not extending) to a line drawn between the anterior surfaces of the first upper molars; notch on anterior lip of foramen magnum slight instead of obvious; bulge of capsular projections for upper incisors moderate rather than pronounced; interparietal without (instead of having) medium-posterior notch; and paraoccipital process (from ventral view) straight rather than curved with a basal notch.

From S. *hispidus*, S. *leucotis* differs in small size of tail scales (0.5 mm. wide rather than 0.75 mm. wide); tail heavily haired instead of sparsely haired; skull short rather than long; palatal pits deep as opposed to shallow; and median keel on palate conspicuous rather than slight.

Geographic Variation

Although certain cranial and dental characters seem to set S. *leucotis* apart as the most distinctive Recent species in the genus, the apparent lack of geographic variation in this montane species is surprising and can be compared with the condition found in monotypic *Peromyscus melanotis*, which occupies some of the same habitat in the same Y-shaped distributional pattern in the Sierra Madre Occidental, the Trans-Mexican Volcanic Belt (part), and the Sierra Madre Oriental. On the southward side of the watershed of the Río Balsas, the more richly-colored S. *leucotis* in Puebla and Oaxaca can be easily distinguished at the subspecific level.

Herein, cotton rats previously assigned to S. *leucotis* and to S. *alticola* are arranged as belonging to the same species, with the former name being adopted as the specific name because of page priority. Both species were named by Vernon Bailey in his 1902 paper with the description of S. *leucotis* appearing on page 115 and that of S. *alticola* on page 116. After examining and comparing recently-obtained material from localities in Aguascalientes and Guanajuato, which are intermediate between places from where S. *leucotis* and S. *alticola* were previously reported (see Hall and Kelson, 1959:678), it was readily evident that these montane cotton rats in central and southern México belong to one species.

Cotton rats of this species were obtained in abundance (as based on series in museum collections) only at a few places: in Durango near San Luis, at Hda. Coyotes, and southwest of Vicente Guerrero; in Zacatecas in the Valparaiso Mountains; in Aguascalientes near Cerro del Jagüey; in Guanajuato near Ibarra; in the state of México at Monte Río Frío; and in Morelos near Huitzilac. Field parties from the Michigan State University Museum either failed to obtain any or could not get adequate series of animals in numerous "likely" montane localities from west-central Durango and central Nuevo León south to Oaxaca, including such out-of-the-way places as Pinal de Amoles in Querétaro. Furthermore, live animals (from Hda. Coyotes and Ibarra) brought back to the MSU Museum Live Animal Colony, unlike the other species of cotton rats, produced few offspring under captive conditions. It is my opinion that this animal may be highly adapted to certain montane mixed grass and brush areas, but presumably in many such situations gives way to other grass-eating "competitors" including *Microtus mexicanus* and possibly *Neotomodon alstoni* and S. *fulviventer*. At least this is one way to explain the disjunct distribution, because on many occasions S. *leucotis* was not taken in places that looked almost "identical" to other sites where the animals were easily obtained.

Sigmodon leucotis leucotis Bailey

Sigmodon leucotis Bailey, Proc. Biol. Soc. Washington, 15:115, June 2, 1902.

Sigmodon alticola amoles Bailey, Proc. Biol. Soc. Washington, 15:116, June 2, 1902, type from Pinal de Amoles, Querétaro.

Type.—Young adult female, skin and skull; no. 92001 U.S. National Museum; from Valparaiso Mountains, 2653 m., Zacatecas; obtained on December 2, 1897, by E. W. Nelson and E. A. Goldman, original no. 11812.

Range.—Montane grass-brush habitats from approximately 25° N latitude in the Sierra Madre Occidental and Sierra Madre Oriental southward to the Trans-Mexican Volcanic Belt in the states of Morelos and México (see Fig. 16).

Diagnosis.—Size large for the species; dorsum intermixed with black hairs and agouti-banded hairs, Pinkish Buff or slightly darker, near (c) Cinnamon-

TABLE 5.—SELECTED MEASUREMENTS (AVERAGES AND EXTREMES) OF YOUNG ADULT WHITE-EARED COTTON RATS, *Sigmodon leucotis*.

Locality of capture (sample size[1] in parentheses)	Length of head and body	Length of hind foot	Height of ear from notch	Condylo-premaxillary length	Zygomatic breadth	Least interorbital constriction	Depth of cranium[2]	Length of nasals	Alveolar length of maxillary toothrow
				Sigmodon leucotis leucotis					
Durango (10)	143 132-157	28 26-31	21 19-23	32.5 31.4-34.1	20.1 19.7-20.6	5.1 4.7-5.3	11.2 10.9-12.0	11.8 11.1-12.9	6.4 6.1-6.8
Zacatecas (3)	145 143-147	30 29-30	---- -------	31.5 31.1-32.0	19.3 18.8-19.5	5.1 5.0-5.4	10.5 10.4-10.6	11.5 11.5-11.6	6.4 6.4-6.5
Aguascalientes (6)	148 144-155	26 25-27	18 16-19	32.2 31.1-33.0	19.7 18.5-20.4	5.0 4.6-5.1	10.6 10.1-11.0	11.1 10.6-11.5	6.5 6.4-6.8
Querétaro (1)	147	29	----	31.6	19.8	5.4	10.7	10.9	6.6
Guanajuato (1)	153	29	22	32.4	19.4	5.1	9.9	------	6.2
Estado de México (1)	148	27	20	31.1	19.7	4.9	10.1	12.2	6.4
Morelos (2)	144, 160	28, 29	18, 19	32.4, 33.6	19.7, 20.0	5.3, 5.5	11.1, 11.2	11.8, 12.9	6.0, 6.4
				Sigmodon leucotis alticola					
Oaxaca (2)	152, 129	30, 29	--------	32.2, 30.6	19.1, 17.8	4.8, 5.1	10.0, 9.7	11.5, 10.8	6.1, 6.5

[1] All measurements not available for some specimens in samples.

[2] Measurement taken as described by Findley and Jones (1963:308).

Buff; base of tail darker; under parts whitish but sometimes washed with buff; skull wide in interorbital area, heavily ridged, and with noticeably large auditory bullae. Selected external and cranial measurements are given in Table 5.

Comparisons.—From S. *l. alticola*, S. *l. leucotis* differs in: size larger (see Table 5); color paler (near Pinkish Buff rather than Clay Color); under parts usually not washed with pale buff; skull more massive, with greater width in interorbital area; auditory bullae larger; nasals broader; palatal pits deeper.

Remarks.—*Sigmodon leucotis leucotis* is slightly larger and much paler in color than S. *l. alticola* from the Sierra Madre del Sur, southward of the Río Balsas, whose watershed seems to have effectively barred the north-south passage of many mammalian species (see Baker, 1963:245). Specimens of S. *l. leucotis* from the northern limits of its range (Durango, Zacatecas, Querétaro, and Nuevo León) are palest (Pinkish Buff), whereas specimens from further to the south are slightly more richly colored (near Cinnamon-Buff).

Specimens examined (112).—Nuevo Leon: 20 km. SSW Galeana, 1891 m., 1 (CAS). Durango: 30 km. SSW Tepehuanes, 2500 m., 2 (MSU); 2.5 km. W San Luis, 2303 m., 2 (MSU); *San Luis*, 1 (AMNH); *1 km. E San Luis, 2348 m.*, 6 (UM), 1 (UNAM); 25 km. ENE Coyotes, 2544 m., 1 (MSU); *7 km. N from highway on road to San Luis via Coyotes*, 2 (CAS); 92 km. W Durango, on road to El Salto, *2407 m.*, 7 (CAS); Hda. Coyotes, 2477-2501 m., 4 (CAS), 8 (MSU); *El Salto, 2318-2440 m.*, 15 (FM), 2 (US); 3 km. N Pueblo Nuevo, 1830 m., 1 (MSU); 43 km. S and 30 km. W Vicente Guerrero, 2547 m., 9 (MSU). Zacatecas: 13 km. S Chalchuites, 2623 m., 4 (CAS); 13 km. W Milpillas (or 100 km. W Fresnillo), 2531 m., 1 (CAS); *27 km. W Milpillas (or 112 km. W Fresnillo), 2531 m.*, 1 (CAS); Valparaiso Mountains, 2653 m., 10 (US); 15 km. W Zacatecas, 2135 m., 1 (CAS); 17 km. S Pinos, 2165 m., 1 (UNAM). Aguascalientes: 5 km. N Cerro del Jagüey, 2501 m., Sierra Fría, 15 (MVZ); Río de San Pedro, NW side San Antonio, 1 (MVZ); 1 km. S La Labor, 1830 m., 1 (MVZ); 7.5 km. NW Calvillo, 1830 m., 1 (MVZ). Guanajuato: Puerta de Guadalupe, 2196 m., 8 km. W Ibarra, 1 (OC); *13 km. SW Ibarra, 2592 m.*, 1 (MSU). Querétaro: Pinal de Amoles, 2 (US). México: Monte Río Frío, 45 km. ESE México, 5 (TCWC); *Hda. Cordoba*, 2600 m., 1 (UM). Morelos: 4 km. N Tres Cumbres, 3202 m., 2 (TCWC); *3 km.* W Huitzilac, 3050 m., 4 (TCWC); *7 km. W Huitzilac, 2806 m.*, 1 (MSU).

Sigmodon leucotis alticola Bailey

Sigmodon alticola Bailey, Proc. Biol. Soc. Washington, 15:116, June 2, 1902.

Type.—Young adult male, skin and skull; no. 68231 U.S. National Museum; from Cerro San Felipe, 3050 m., Oaxaca; obtained on March 15, 1894, by E. W. Nelson and E. A. Goldman, original no. 6624.

Range.—Montane grass-shrub areas in parts of the Sierra Madre del Sur of Puebla and Oaxaca (see Fig. 16).

Diagnosis.—Size medium; dorsum intermixed with black hairs and agouti-banded hairs, Clay Color becoming more Sayal Brown on rump and at base of tail; under parts, tops of hind feet, and tail faintly washed with buff (Pale Pinkish Buff); skull slender, lightly constructed, and with narrow interorbital space; small auditory bullae; and shallow palatal pits. Measurements are given in Table 5.

Comparisons.—For comparison with *S. l leucotis*, see account of that subspecies.

Remarks.—Again the paucity of study material made an analysis of geographic variation difficult, but this subspecies is much more richly colored than *S. l. leucotis.* A subadult from near Acatzingo, Puebla, is less richly colored above but has the distinctive buffy wash on the underparts. The widespread occurrence and abundance of voles (genus *Microtus*) in boreal grassy areas in Oaxaca lead me to wonder if the white-eared cotton rat in Oaxaca plays a secondary role and is highly restricted ecologically.

Specimens examined (6).—PUEBLA: 15 km. NE Acatzingo, 1 (KU). OAXACA: 25 km. W Oaxaca, 2897 m., 2 (US); Cerro San Felipe, 2200 m., 2 (UM), 1 (US).

Sigmodon ochrognathus

Sigmodon ochrognathus, the yellow-nosed cotton rat, is the most xerophilous species in the genus. It is adapted to the dry, rocky slopes (oak-piñon-juniper habitat) of the eastern side of the Sierra Madre Occidental from Arizona and New Mexico south to central Durango and in the widely-scattered desert ranges of the Mesa del Norte (northern part of the Mexican Plateau) in Trans-Pecos Texas, western Coahuila, northeastern Durango, and probably eastern Chihuahua (see Fig. 20).

Habitat and Habits

The yellow-nosed cotton rat is an inhabitant of the desert mountains of the American Southwest. It lives chiefly on rocky slopes with scattered clumps of grasses, mostly in oak-juniper habitat (see Figs. 11 and 21), although it occupies grassy montane flats in localities where other species of *Sigmodon* are not present. Undoubtedly, the preferred habitat of *S. ochrognathus* has been altered where grazing by livestock, especially goats, has been severe. However, this cotton rat will persist on rocky hillsides where only sparse grass occurs. Its runways are often well-marked in thick grass but are rarely visible on bare hillsides, where the animals dart from one rock shelter to another. On several occasions animals were observed (especially in the vicinity of Boquilla, Durango) moving across such open spaces of as much as one meter in distance. Cuttings of grass blades and piles of fecal droppings are generally conspicuous; openings into burrows, many being excavated by pocket gophers *(Thomomys umbrinus)*, may be obscured behind or at the sides of rocks. These cotton rats will often feed at the base of a clump of grass. Since the grass droops down, it is necessary for one to raise up the dead grass to find the rat's secluded chamber, circling around the base of the clump.

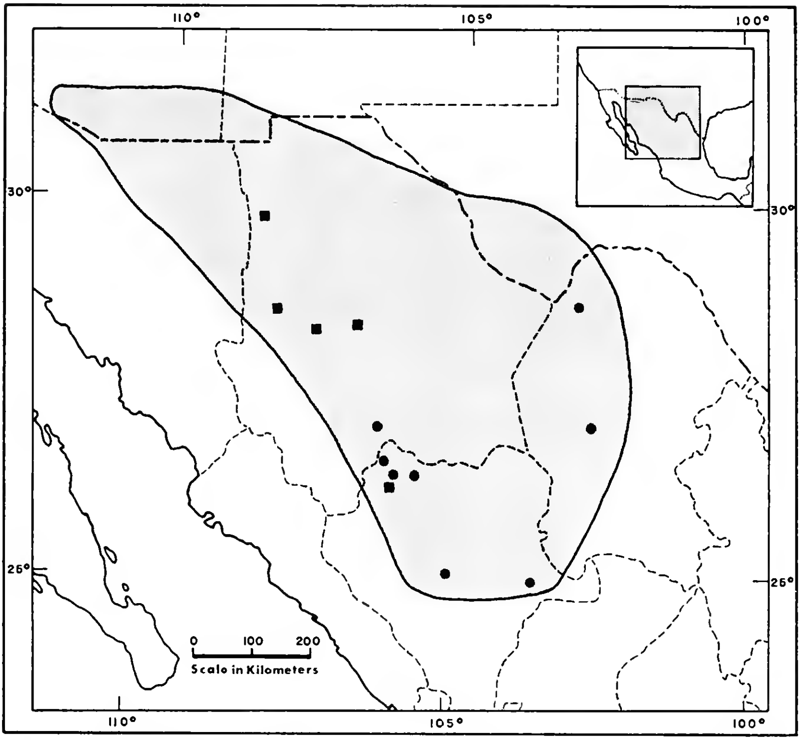

FIG. 20. Geographic distribution of the yellow-nosed cotton rat, *Sigmodon ochrognathus.*

As a species, this cotton rat lives under more xeric conditions than any of the other species in the genus. Succulent plants may provide necessary moisture on dry hillsides, because it is doubtful that S. *ochrognathus* has much opportunity to find surface water in such well-drained situations, even if rain were more prevalent than is actually the rule in these foothills. Although no quantitative data are available, one obtains the impression that S. *ochrognathus* occurs in less concentrated numbers than do other species of cotton rats. Perhaps the food supply is generally less abundant on the rocky hillsides than on deep alluvial valley soils where S. *fulviventer* and S. *hispidus* live. The seemingly lower carrying capacity of the hillside habitat may cause yellow-nosed cotton rats to be more widely spaced in nature than other cotton rats. This suggestion is based on the fact that it is unusual to catch more than one yellow-nosed cotton rat at any one trap station, although there was no reason to indicate that the rodents did not share common runways. Hoffmeis-

FIG. 21. Hillside occupied by the yellow-nosed cotton rat, *Sigmodon ochrognathus*, near Fort Davis, 1610 m., Jeff Davis Co., Texas. The vegetative cover consists of scattered shrubs of species belonging to the genera *Juniperus, Rhus,* and *Mimosa* and grasses of the genera *Andropogon, Bouteloua, Muhlenbergia, Elyonurus, Aragrostis, Setaria,* and *Panicum.* Photograph taken on August 17, 1967.

ter (1963), who described the habits of *S. ochrognathus* in Arizona, found nests, usually of grass, in thickets of grasses or drooping *Nolina* and *Agave.* Captive rats sometimes made nests of cotton either inside or outside of refuge cans placed in their cages. Hoffmeister as well as Baker and Greer (1962:125) have given dimensions of runway systems and burrows. Descriptions of several collecting localities are given below.

Durango.—At 12 km. NNE Boquilla, 1890-1965 m., yellow-nosed cotton rats were captured on two occasions (10 July 1965 and 8 July 1967). Most animals were taken on a north-facing slope on the eastern foothills of the Sierra Madre Occidental (see Fig. 11). The slope was rocky and covered with scattered shrubs—algerita *(Mahonia trifoliata),* cliff rose *(Cowania mexicana),* and catclaw (*Mimosa* sp.). Moderately-grazed clumps of tall grass of the genus *Muhlenbergia,* and composites, *Haplopappus spinulosus* and *Baileya* sp., were scattered on this hillside. Small mammal associates taken with *S. ochrognathus* include *Perognathus nelsoni, Reithrodontomys fulvescens, Reithrodontomys megalotis,* and *Baiomys taylori. Sigmodon fulviventer* lived on the grassy valley floor which adjoins the hillsides.

At 9 km. NNW Canatlán, 1950 m., yellow-nosed cotton rats were taken on a rocky hillside in runways through clumps of grasses, *Bouteloua gracilis* and *Muhlenbergia* sp., mostly protected from grazing by thick over-head cover of *Acacia, Mimosa* and prickly pear *(Opuntia).* Associated small mammals obtained in the area were *Perognathus nelsoni, Liomys irroratus, Thomomys um-*

brinus, Reithrodontomys fulvescens, Peromyscus pectoralis, Baiomys taylori, and, on adjacent flats, *Sigmodon fulviventer.*

Coahuila.—Baker (1956:278) found yellow-nosed cotton rats in runways in bunch grass, prickly pear, and scrub oak at 1616 meters in elevation (in the Sierra de la Madera), and in thick grass in a narrow valley floor with runs leading to burrows under small oaks at 2135 meters in elevation (in the Cañon del Hillcoat in the Sierra de la Encantada). Taylor *et al.* (1945:26) found cuttings, burrows, and piles of earth in grass in the Sierra del Carmen.

Texas.—A north-facing, rocky hillside 3 km. NW Fort Davis, 1610 m., in Jeff Davis County (see Fig. 21) was covered with seattered cedars, *Juniperus* sp., and shrubs, *Rhus trilobata, Rhus microphylla,* and *Mimosa* sp. Yellow-nosed cotton rats were caught in obscure runways in clumps of grasses including *Bouteloua gracilis, Bouteloua curtipendula, Andropogon saccharoides, Muhlenbergia* spp., *Elyonurus barbiculmis, Aragrostis pilosa,* and *Setaria macrostachya.* Leaf cuttings, presumed to have been left in the runways by *S. ochrognathus,* of *Andropogon saccharoides, Setaria macrostachya,* and *Panicum* sp. were identified. Small mammal associates were *Perognathus nelsoni* and *Peromyscus pectoralis.* In Brewster County, Denyes (1956) found *S. ochrognathus* in such plant associations as sotol-sachuiste, oak chaparral, gramma-bluestem, and feathergrass-grama.

New Mexico.—Findley and Jones (1960) found *S. ochrognathus* in an altitudinal range from 1160 to 2560 meters, from the upper limits of the grassland into the pine-oak forests on rocky slopes. In higher areas this cotton rat is associated with pines, juniper and oaks; at lower elevations it lives in bunch grass, *Yucca, Agave, Opuntia,* and beargrass *(Nolina).* These authors also observed the rodents in association with plants belonging to such genera as *Dasylirion, Fouquieria, Prosopis, Mimosa, Acacia, Arctostaphylos,* and *Cercocarpus.*

Arizona.—Hoffmeister (1963) recorded the yellow-nosed cotton rat on grassy, rocky slopes near or within the oak belt. He listed plant associates as *Quercus, Agave, Nolina, Cowania mexicana, Mimosa biuncifera, Opuntia, Yucca, Rhus ovata,* and *Dasylirion wheeleri.* The sparse cover used by *S. ochrognathus* included *Bouteloua gracilis, Bouteloua curtipendula, Aristida* sp., *Heteropogon contortus, Muhlenbergia* sp., *Senecio longilobus, Grindelia aphanactis,* and *Eleocharis* sp. Small mammal associates, according to Hoffmeister, were *Thomomys umbrinus, Reithrodontomys fulvescens, Peromyscus boylii, Peromyscus eremicus,* and *Neotoma albigula.*

Association of yellow-nosed cotton rats with other species of the genus.—The yellow-nosed cotton rat occupies rocky, bunch-grass slopes from just below to within the pink-oak-juniper belt. Where it is the only cotton rat present (as in southwestern Texas and western Coahuila), *S. ochrognathus* also occurs on grassy montane "flats" or alluvial fans where deep soils and few rocks occur. In most of its range in New Mexico, Arizona, Chihuahua, and Durango, however, this cotton rat is absent or occurs only peripherally in the latter habitats because these areas are occupied by *S. fulviventer,* although Hoffmeister *(loc. cit.)* found *S. ochrognathus* and *S. hispidus* at one place in Arizona. Near Canatlán, Durango, *S. ochrognathus* was captured in bunch grass and shrubs on a hillside slope of approximately 20 degrees, whereas *S. fulviventer* was trapped in more or less identical, but less rocky, cover at the base of the slope where the alluvial fan began to level out. Here, the two species were not taken at the same trap stations and according to field notes, were not trapped closer together than 18 meters. At this locality, in July of 1965, 17 S. *ochrognathus* and three S. *fulviventer* were caught. The larger catch of S. *ochrognathus* probably is the result of trap placement, more on the rocky slopes than on the level base. In the vicinity of Boquilla, Durango, we also caught both species of cotton rats; S. *ochrognathus* was taken on rocky, bunch-grass slopes and S. *fulviventer* in grassy areas on "flat" hilltops and in the deep soils of valley floors. In one narrow intermontane valley (3.3 km. NE Boquilla) containing bunch-grass, a few scattered rocks and reddish "clay" soil, I caught in one live-trap set in a runway, one S. *fulviventer* on the night of 8 July 1965 and one S. *ochrognathus* the following day. Here was one instance where both species "occupied" the same runway and were caught at the same trap station. At 12 km. NNE Boquilla tawny-bellied cotton rats seemed entirely restricted to a grassy, hilltop flat, and yellow-nosed cotton rats occupied the rocky slopes almost entirely around the hill.

Although the ranges of S. *ochrognathus* and S. *leucotis* "overlapped" in latitude in the Canatlán-Tepehuanes area of west-central Durango (see Fig. 4), the yellow-nosed cotton rat seemed confined to the lower, dry slopes of the foothills (no higher than 1950 meters in elevation), whereas S. *leucotis* occupied higher mesic areas of mixed grass, brush and rocks (at an elevation of 2500 meters), well within the montane boreal forest of the Sierra Madre Occidental. It would appear that as a species, S. *ochrognathus* is the cotton rat mostly highly adapted to the extreme aridity of the lower slopes of the "desert" mountains of the northern part (Mesa del Norte) of the Mexican Plateau. This kind of habitat, in the more mesic southern part (Mesa Central) of the Mexican Plateau in such states as Aguascalientes and Guanajuato is occupied by S. *leucotis*.

Parasite.—Dr. Robert Traub identified the flea, *Polygenis martinez-baezi* Vargas, 1951, from S. *ochrognathus* from near Canatlán, Durango.

Specific Characters and Comparisons

The drab gray dorsum contrasting with an ochraceous-colored nose and eye-ring together with small size (for captive animals, maximum weights are 130 grams for a male and 133 for a non-pregnant female; maximum lengths of head and body are 154 mm. and 149, respectively) distinguish S. *ochrognathus* from other species in the S. *fulviventer* group. Other unique characters include: small and elongate auditory bullae; an obvious median keel on the basioccipital; pronounced lateral bulges of the capsular projections of the upper incisors; a median-posterior notch on the interparietal, and curved paraoccipital processes with distinctive basal notches.

From S. *alleni*, S. *ochrognathus* further differs in having a short and broad skull rather than a long narrow one, and slightly recurved incisors rather than pronounced recurved (opisthodont) incisors.

From *S. fulviventer*, *S. ochrognathus* is further distinguished by whitish instead of tawny underparts; less-arched skull; short rather than long (in relation to width) basioccipital; posterior ends of incisive foramina not extending (rather than extending) to a line drawn between the anterior surfaces of the first upper molars; anterior end of mesopterygoid fossa broad instead of narrow; anterior lip of foramen magnum obviously notched rather than not; and foramen ovale small (no more than half width of M3) instead of large (at least three-fourths width of M3).

From *S. leucotis*, *S. ochrognathus* is further distinguished by less-arched skull; short and broad rather than long and narrow basioccipital; posterior ends of incisive foramina not extending (rather than extending) to a line drawn between interior surfaces of the first upper molars; anterior end of mesopterygoid fossa expanded instead of parallel-sided; anterior lip of foramen magnum obviously notched rather than not; length at midline of interparietal more instead of less than 2 mm.; rostral depressions on sides of premaxillaries slight rather than pronounced; angular process of lower jaw rounded instead of slightly hooked; and lingual root of first lower molar large instead of reduced or absent.

From *S. hispidus, S. ochrognathus* differs in narrower tail scales, 0.50 mm. rather than 0.75; heavily haired instead of sparsely haired tail; short and broad rather than long and narrow skull; short instead of long (in relation with width) basioccipital; less arched skull; deep rather than shallow palatal pits; and conspicuous instead of slight median keel on the palate.

Geographic Variation

Yellow-nosed cotton rats have been considered as being separable into three subspecies (Hall and Kelson, 1959:677-678): *S. o. madrensis* Goldman and Gardner, *S. o. montanus* Benson, and *S. o. ochrognathus* Bailey. Later *S. o. madrensis* was placed in synonymy under *S. o. baileyi* J. A. Allen, which had been previously regarded as a subspecies of *S. hispidus* (Baker and Greer, 1962:125). The presence of distinctive geographic variation in this species with its isolated desert-mountain populations seems at first logical, although Findley and Jones (1960), after a thorough examination of most museum specimens then extant, came to the conclusion that no significant geographic variation was discernible. They thought that the presently disjunct environment in which *S. ochrognathus* lives has not long been separated. This is in line with the findings of

Wells (1966) that xerophilus woodland (oak-piñon-juniper) vegetation, in which associations S. *ochrognathus* lives today, occurred as much as 800 meters lower in elevation perhaps 11,560 to more than 40,000 years B. P. (during the Wisconsin pluvial) than today. This would then mean that these disjunct populations have not been separated for much more than 10,000 years. Furthermore, it is likely that this xerophilus woodland maintained its continuity in the Mesa del Norte up to a postglacial period of heavy rains, perhaps between 6210 and 7756 B.P. (Findley and Jones, 1960:468), and that the present disjunct montane distribution may have resulted from ensuing desiccation after the above dates. Findley and Jones felt that the disjunct habitat of S. *ochrognathus* may be so newly developed that isolation has not been long enough to allow for a discernible degree of geographic variation. Relying in part on the findings mentioned above and in part on study of material from Durangan localities from which S. *ochrognathus* has not been reported previously, I am inclined to consider yellow-nosed cotton rats, for the present, as belonging to a monotypic species.

Sigmodon ochrognathus Bailey

Sigmodon ochrognathus Bailey, Proc. Biol. Soc. Washington, 15:115, June 2, 1902.

Sigmodon baileyi J. A. Allen, Bull. Amer. Mus. Nat. Hist., 19:601, November 12, 1903, type from La Ciénega de las Vacas, 2990 m., Durango.

Sigmodon ochrognathus montanus Benson, Proc. Biol. Soc. Washington, 53:157, December 19, 1940, type from Peterson's Ranch "Sylvania"), 1860 m., 3 km. N Sunnyside, Huachuca Mts., Cochise Co., Arizona.

Sigmodon ochrognathus madrensis Goldman and Gardner, Jour. Mamm., 28:58, February 17, 1947, type from foothills of Sierra Madre Occidental, 50 km. NW Parral, 1890 m., Chihuahua.

TABLE 6.—SELECTED MEASUREMENTS (AVERAGES AND EXTREMES) OF WILD-CAUGHT AND OF LABORATORY-RAISED (100 DAYS OLD) *Sigmodon ochrognathus*.

Measurement	9 km. NNW Canatlán, Durango (8 specimens, wild-taken)	3 km. NE Boquilla, Durango (6 specimens, laboratory-raised)
Length of head and body	139 (132-144)	138 (130-144)
Length of hind foot	28 (25-29)	29 (29-30)
Height of ear from notch	21 (20-22)	19 (18-19)
Condylopremaxillary length	31.2 (30.2-32.0)	29.4 (28.6-30.1)
Zygomatic breadth	18.7 (18.3-19.4)	18.1 (17.6-18.4)
Least interorbital constriction	4.8 (4.6-4.9)	4.8 (4.6-5.1)
Depth of cranium*	10.0 (9.6-10.3)	9.5 (9.4-9.7)
Length of nasals	11.7 (11.0-12.5)	11.5 (11.2-12.1)
Alveolar length of max. toothrow	6.3 (6.1-6.4)	6.1 (6.0-6.2)

* Measurement taken as described by Findley and Jones (1963:308).

Type.—Young adult female, skin and skull; no. 110333 U.S. National Museum; from Chisos Mountains, 2840 m., Brewster Co., Texas; obtained on June 13, 1901, by Vernon Bailey, original no. 7681.

Range.—Montane habitats, mostly arid, rocky, bunch-grass-covered slopes in piñon-oak-juniper in southern Arizona, southwestern New Mexico, Trans-Pecos Texas, Chihuahua, Coahuila, and Durango (see Fig. 20).

Diagnosis.—See account of specific characters and comparisons.

Remarks.—In Table 6 are presented selected external and cranial measurements of young adult, wild-taken specimens and of laboratory-raised, 100-day-old specimens, all from Durango. The two samples originated from localities approximately 175 km. apart. The 100-day-old individuals are smaller and less mature than the wild-taken sample, the latter judged to be almost adult.

Specimens examined (41).—Chihuahua: near Parral, 1890 m., 1 (US). Coahuila: Tinaja de Telles, 1464 m., El Jardin Ranch, Sierra del Carmen, 1 (TCWC); *Juarez Cañon, 1464 m., Sierra del Carmen,* 16 (DMNH), 3 (US); 33 km. S and 7 km. W Ocampo, 1616 m., 3 (KU). Durango: Rancho Santuario, 4 (AMNH); La Ciénega de las Vacas, 1 (AMNH); *Arroyo de Bucy*, 1 (AMNH); 11 km. NNE Boquilla, 1952 m., 2 (MSU); *2 km. NE Boquilla, 1890 m.*, 1 (MSU); *3 km. NE Boquilla, 1952 m.,* 2 (MSU); 9 km. NNW Canatlán, 1950 m., 11 (MSU); 2 km. ESE Atotonilco, 2043 m., 1 (MSU).

Other records.—Chihuahua: 5 km. SW Pacheco; 13 km. NE Laguna, 2211 m.; 3 km. W Minaca, 2104 m.; Cherry Ranch, 18 km. NW Cocomorachi (Findley and Jones, 1960:468). Durango: Guanaceví (Baker and Greer, 1962:126).

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CONE CACHES AND MIDDENS OF TAMIASCIURUS IN THE ROCKY MOUNTAIN REGION

BY

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The red squirrel *(Tamiasciurus hudsonicus)* of the Rocky Mountain region is an animal of the coniferous forests. Its conspicuous middens of cone debris are easily recognized throughout the Rocky Mountains from Alaska to Arizona. In this vast region deciduous hardwood forests are of minor extent and little importance as producers of food for squirrels. *Tamiasciurus* is well adapted to these conditions and is able to subsist on almost any of the conifer seed crops that may be available. In the West, red squirrels are able to survive a winter of complete cone crop failure (M. C. Smith, 1968) but rarely, if ever, occupy hardwood stands without conifers.

In the eastern United States and adjacent Canada red squirrels are likewise primarily dependent on conifer seed crops, but they also make considerable use of hardwood mast where available and are able to exist in some deciduous forests without conifers (Hatt, 1929:43).

As to be expected of a species so wide ranging, the red squirrel has a wide adaptability to different habitats and food supplies. It is not known to what extent this adaptability represents genetic differences between populations and to what extent it is behavioral response to one environmental condition or another. Much information has been published on the life history and behavior of red squirrels of the northeastern (Klugh, 1927; Hatt, 1929; Layne, 1954) and northwestern (Shaw, 1936; C. C. Smith, 1968) United States. Because much less has been reported for the Rocky Mountain region, a contribution to knowledge of red squirrel habitat relations is presented here.

The caching habit of red squirrels has long been known and exploited in the West by foresters and nurserymen as a source of conifer seeds for planting (Cox, 1911:17). It is usually the cheapest source for large quantities of seed of the commercially and horticulturally desirable spruce, fir, and pine trees, and the seeds thus harvested have high viability (Lavender and Engstrom, 1956). However, some timber managers accuse the squirrels of harvesting such a high percentage of cones of certain species as to prevent adequate natural forest regeneration. Inasmuch as there seems to be little information in the literature on the economic status of *Tamiasciurus* in the Rocky Mountains, some observations on this aspect are also given.

This paper is based on examination of several hundred middens and caches of *Tamiasciurus hudsonicus fremontii*, *T. h. mogollonensis*, and *T. h. richardsoni* in Colorado, northern Arizona, and western Montana in the period 1963 to 1968. Approximately 60 of these were excavated for cone caches, and 34 of the more noteworthy middens were described in some detail. Many of the middens in the Front Range of Colorado were examined repeatedly in different years.

Much general information was gained from Harry M. Swift, nurseryman and owner of Colorado Evergreens, Inc., of Golden, Colorado, who has had many years of experience collecting and marketing conifer seeds from squirrel caches in Colorado. I am indebted to Curtis H. Halvorson for many stimulating discussions of his red squirrel studies in Montana and for reviewing a draft of this paper. William B. Finley, U.S. Forest Service, first acquainted me with the remarkably productive cone caches on the Kaibab Plateau.

CHARACTERISTICS AND VARIATION OF MIDDENS AND CACHES

The importance of conifer seed in the diet of the red squirrel is strikingly evident to anyone who examines one of the great midden heaps under a dense, shady stand of blue spruce *(Picea pungens)* alongside a mountain stream in Colorado. The larger middens are frequently 20 to 30 feet across, one to one and a half feet deep in the center, and carpet the ground to the exclusion of all living plants. The surface is usually littered with fresh cone scales and cores dropped by the squirrels. The material below is loose and damp, easily dug into with the bare hands. As one digs into the deeper deposits the material at lower levels is found to be older and more decomposed, forming a rich mulch in contact with the mineral soil. Large middens must be decades old and represent the accumulations of many successive generations of red squirrels. Such a midden is an example of ecological homeostasis, for its owner can easily store in it a much larger supply of food in good condition than a squirrel could store under a similar tree stand not previously occupied by red squirrels. Cache holes are much harder to dig in soil and the cones dry out quicker if not covered with cone litter.

The continuing utility of such a long-used midden is illustrated by a medium-sized one I saw in 1963 under a recently dead spruce tree 57 feet tall near Corral Park, 8600 feet, in the Rio Grande National Forest, Colorado. The midden was exposed in the sunlight but still in use by the squirrel chattering from a dead limb above. Almost five years later the midden was still active, as evidenced by an accumulation of fresh cone scales and cores of blue spruce around the base of the dead tree. The midden, on a north-facing slope, was still damp below a depth of three inches in mid-June. Sparse grasses and blooming red columbines *(Aquilegia elegantula)* were growing on its outer portion. There was a grass nest about 30 feet high in a live blue spruce standing 20 feet upslope from the dead tree.

Active middens remain fairly loose, with fresh or discolored cone scales and cores on the surface, but old inactive middens become mixed with needle litter, compacted, weathered, and decomposed. Abandoned middens eventually become covered with a layer of forest duff; if exposed to some sunlight, they gradually become covered over with encroaching grasses, forbs, mosses, kinnikinnick *(Arctostaphylos uva-ursi)*, or low shrubs.

Kinds of Cones Cached

Although cones of nearly all species of needle-leaved trees in Colorado are cached for food, there are differences in preference. In general, red squirrels seem to prefer cones of blue and Engelmann spruce *(Picea engelmanni)* and Douglas-fir *(Pseudotsuga menziesii)*. Cones of ponderosa, limber, and bristlecone pines *(Pinus ponderosa, P. flexilis,* and *P. aristata)* are also abundantly cached at times, but seem to be somewhat less preferred. Cones of lodgepole pine *(Pinus contorta)* provide a staple food supply when other cone crops fail, but are often passed over when one or more of the above-named cone crops is good.

Use of Engelmann spruce and lodgepole pine by squirrels enables them to occupy thousands of square miles of montane forest in which other cone supplies are absent or erratic. Two reasons for this are the great extent of these two forest types in the Canadian Life-Zone and the relatively high reliability of their cone crops. Lodgepole pines produce cones almost every year, and in this region a high percentage of the cones are serotinous (persist on the branches unopened throughout the year), thus providing an excellent reserve food supply. Engelmann spruce in Colorado produces a good or moderate cone crop two out of three years, on the average.

Douglas-fir, limber pine, and bristlecone pine are much more limited in distribution and produce a good cone crop in Colorado only one year out of four or five. But when cones of these species are produced at all, they are invariably cached, perhaps because of their unusually large seeds. The ponderosa pine is a somewhat erratic cone producer. Its cones are usually cached to some extent when available, but may be ignored if a good crop of spruce or Douglas-fir is at hand.

There is one other species of pine native to Colorado, the pinyon *(Pinus edulis)*, but I have no knowledge of the use of its cones by *Tamiasciurus.* Although the pinyon usually occurs zonally below the red squirrel and on dry sites, in some places it grows rather high on south slopes and in contact with other forest types on north slopes occupied by the squirrels.

Although the pinyon produces a good seed crop only once in several years, its seeds in these years are large and heavily consumed by mice, chipmunks, and other animals. Failure of red squirrels to utilize pinyon seed crops is probably explained primarily by the dryness of the pinyon-juniper woodland type. It would be almost impossible to find a damp caching site under pinyon trees except under water in the few permanent streams.

According to H. M. Swift, cones of all three kinds of true fir in Colorado are cached—the white fir, subalpine fir, and corkbark fir *(Abies concolor, A. lasiocarpa,* and *A. lasiocarpa* var. *arizonica).* I have seen a few caches of subalpine fir cones, which were stored in somewhat smaller amounts than cones of the Engelmann spruce in the same stand. White fir cones are heavily cached by red squirrels on the Kaibab Plateau, Arizona, according to W. B. Finley.

Junipers (*Juniperus* sp.) are present in most of the forest types of Colorado, up to elevations of 10,000 to 12,000 feet, but I have not found any juniper seeds or berries in midden caches, nor has Mr. Swift seen any use of juniper seed.

In spite of the importance of conifer seeds as winter food, the red squirrel is able to survive a year of complete cone crop failure. In Colorado there are few forests in which this is likely to occur, because of the wide availability of Engelmann spruce and lodgepole pine. However, in southern Colorado red squirrels occur in forests 40 miles or more from the nearest lodgepoles. When cones failed there, Mr. Swift found the squirrels had cached small piles of kinnikinnick berries, bird cherries *(Prunus pennsylvanicus)*, and squaw currants *(Ribes cereum).*

Kinds of Midden Sites Used for Caches

Earlier observers have described the cache sites of red squirrels on or in the ground in various kinds of situations. Nearly all agree that caches are characteristically in damp, shady locations, such as beneath a dense tree canopy or in a spring or boggy area. The importance of moisture for preserving the cones in closed condition was briefly mentioned by Grinnell and Storer (1924:206). Shaw (1936) demonstrated the ability of cones of white fir *(Abies concolor)* and white pine *(Pinus monticola)*, after storage for two years in water, to open and begin to shed their seeds after eight days of exposure to dry air. The high adaptive value of this caching habit is illustrated by the varying degrees to which red squirrels in different climatic regimes and site situations restrict their choice of cone caching sites.

Caches on the high plateaus of the Colorado Rockies often cover extensive level ground under stands of spruce, fir, and lodgepole pine. Cones are buried in shallow cone litter, duff, or soft soil, or stuffed under the edges of logs and roots of stumps. Such sites remain damp most of the summer and autumn because of high rainfall and the early arrival of snow cover.

At lower elevations (below 9000 feet) on the east side of the Continental Divide the squirrels rarely cache cones in soil or thin duff, but almost solely in the deeper, looser cone debris of the middens left by their own feeding activities.

Mountain slope in relation to insolation and density of tree canopy are also vital factors at lower elevation, severely restricting the sites that are utilized by red squirrels for cone caching. Middens are almost totally absent from the ponderosa pine stands on south-facing slopes, and are sparse and small under Douglas-fir and spruce stands on north-facing slopes. They are largest and closest together under blue spruces along drainage bottoms at the foot of north-facing slopes (see Fig. 1). Protection against the sun, either by tree crowns or topographic exposure, seems to be of great importance below 9000 feet in Colorado, except where hillside drainage brings water directly into the midden.

The life form of a tree has an important bearing on its suitability for providing a good midden site. Spruces retain their lower branches almost to the ground, thus shading the ground beneath the tree through almost all hours of the day. In dense stands, the lower branches are lost, but on such sites the ground is shaded any-

FIG. 1. Blue spruce stand by Redskin Creek, Pike National Forest, Colorado. This low, dense tree crown provides maximum shade for red squirrel caches in the Transition Life-Zone below 9000 feet.

way by the closed crown canopy. Spruces provide ideal midden sites.

Douglas-firs retain a fairly dense crown well down the trunk in open stands, but the ground level is usually fairly open and exposed to sunlight unless the trees are in a closed stand. In closed stands, these trees provide adequate midden sites, but a single tree rarely shelters a midden in Colorado.

Ponderosa pines have few limbs on the lower portion of the trunk. In Colorado they nearly always occur in fairly open stands, or are mixed with Douglas-fir. The ground under these pines is nearly always open to sunlight most of the day. This growth form, combined with the dry sites occupied, makes the ponderosa pine quite unsuitable as cover for squirrel caches (see Fig. 2). Consequently they can provide a winter food supply only at the edges of the pine forest where they grow close to other trees that produce better shade.

Lodgepole pines replace ponderosa pines in the Canadian Life-Zone at higher elevations. Lodgepoles likewise have few branches on the lower trunk, but they usually occur in dense even-age stands

FIG. 2. Ponderosa pine stand on dry open slope with southerly exposure near Redskin Creek, Pike National Forest. This type of tree form does not provide enough shade and soil moisture for cone caching in the Colorado Transition Zone.

with a closed canopy that provides a moderate amount of shade. The sites, however, are usually dry, and middens in lodgepole pine stands are usually small and dry. Because the cones are commonly serotinous, their seeds remain available throughout the year.

Oddly enough, red squirrels seem to know that lodgepole cones do not have to be cached in wet places to remain closed, for the squirrels commonly leave them on, or close to, the surface of a midden, or pile them in little heaps against logs, stumps, or tree trunks (see Fig. 5). Because of the greater and more continuous snow cover at higher elevations, middens in lodgepole stands may remain damp near the bottom, but such levels are not much used to cache lodgepole cones.

Bristlecone pines and limber pines also occur at high elevations and on usually poorer sites than lodgepoles, growing even up to timberline. In Colorado, the high precipitation and nearly continuous winter snow cover at these elevations allow middens to remain fairly damp under moderately dense limber and bristlecone stands.

Fig. 3. Part of a large complex *Tamiasciurus* midden in an Engelmann spruce forest near Arapaho Basin, Summit County, Colorado. A bed of spruce cone litter covers the entire forest floor in the foreground.

The true firs *(Abies)*, like the spruces, retain branches close to the ground and provide ample shade for middens. In addition, they occur on moist sites and at high elevation where middens and caches under them have little opportunity to dry out. *Abies* cones may be found piled under the edges of logs, inside rotten logs, or even piled on the surface. Though they are usually buried in the wet midden, those left exposed to the air soon become covered under snow and are thus protected against drying.

In view of the wide variety of middens and cone-caching situations used, I have selected a few examples illustrating this diversity from among the 34 studied in detail. Descriptions of these are given in the following paragraphs. Tree measurements were made with a clinometer and a tree tape. Timber stand densities were estimated from three stem counts by angle gauge, expressed in square feet of basal area per acre.

Engelmann spruce—subalpine fir forest.—One of the largest middens I have seen was characteristic of those found at higher elevations in the spruce-fir forests (see Fig. 3). It was under a stand of Engelmann spruce in a small swale at 10,000 feet elevation on a lower south-facing slope 3 mi. W Arapaho Basin, Summit County, Colorado. The midden was roughly triangular in shape, measuring 60, 58, and 54 feet along the three sides, with 1440 square feet of surface area. Outside this area there were several other small middens and feeding stations covered with cone scales around individual trees. When I first examined the midden in October of 1963, it was crammed full of Engelmann cones stuffed in little pits two to three inches in diameter that riddled a layer of cone debris covering the ground. The midden was about 10 to 15 inches deep over the western half of the area, decreasing in depth toward the east side. I dug six bushels of cones out of it without exhausting the supply. On August 3, 1968, the same midden had changed considerably in appearance, the west side being nearly inactive and having become more compacted and reduced to depths of only three to 10 inches. The area of greatest activity had shifted toward the east and south sides where most of the recent cone debris was accumulating. The cone crop of 1968 promised to be almost a complete failure, and the only cached Engelmann spruce cones I found in the midden were a few wet, black, but still sound cones of the 1967 crop. The midden was still damp at depths below six or seven inches, but dry in the upper 6-inch layer, except in open areas where the top two to three inches were wet from recent rains. Most of the fresh cone debris on the surface was dry, light brown scales of 1967 cones, many of which still could be seen in the tree tops. They probably retained only a small percentage of the original seed content. A further indication of food shortage in 1968 was the large number of lodgepole pine cones and cone debris in (and on) the topmost layer of the active midden. Almost no lodgepole cones were cached in this midden in 1963, a good seed year for spruce.

Sometime in the winter or spring of 1968 an Engelmann spruce 18 inches d.b.h. (diameter at breast height) and 89 feet tall blew over on the south side of the midden downslope from the area of principal activity of the squirrel in 1963. This event may have influenced the squirrel to shift its center of feeding activity, for the deepest piles of fresh cone scales in August of 1968 were around the stump and under the butt end of the tree. The lower 10 feet of the log was much used as a feeding area. The foliage was still fairly green and the top branches still held many open and partly open cones.

The spruce stand was fairly open over the midden, averaging 140 square feet basal area per acre. It enclosed 14 dominant and codominant trees from seven to 19 inches d.b.h., the largest being 81 feet tall, and eight trees of pole and sapling size. Two of the codominant trees were subalpine firs with eight and nine inches d.b.h. Many small lodgepole pines stood on a low ridge beyond the east end of the midden. The light coming through the tree canopy over the midden was sufficient for a thin ground cover of *Arnica*, *Rosa*, *Salix*, and *Lonicera involucrata*. Green foliage cuttings of spruce lay scattered over the midden. The southwest half of the midden was littered with hundreds of slender dead willow branches from dead willow clumps.

In August of 1968, I counted 13 grass nests in trees within the periphery of the midden, the largest number I have seen at any single midden. There were five in a large spruce standing directly over the middle of the fallen tree. The highest nest was 34 feet up in a subalpine fir. The lowest was 58 inches above the ground in drooping branches of a small spruce located six feet from the fallen spruce stump. This nest measured 13 inches wide and 16 inches deep. It was a nearly solid ball of dry grass with a few forb leaves, strands of willow bark, and some fine dusty debris in the center.

Many similar, but smaller, middens were scattered through the spruce-fir forest on adjacent mountainsides. Crown canopy closure and shade on the ground seemed to be adequate for some caching almost anywhere in the forest. Presence of good seed-producing trees and logs or stumps for feeding posts may have been factors initiating the accumulation of middens at certain sites. Engelmann spruce cones had been cached abundantly in most of these middens in previous years, but were scarce in August, 1968, whereas some lodgepole cones were commonly seen on the middens or piled against logs. One large midden (50 by 47 feet) among many rotten logs contained some 1967 cones of subalpine fir in addition to those of lodgepole pine. It was the only midden at which I have seen a grass ball nest on the ground, nearly hidden under a large rotten log.

Blue spruce in valley bottoms.—A large midden in a typical situation for the lower elevations east of the Continental Divide was first examined in October of 1963, and examined again in June of 1968. It was under a dense stand of large blue spruce trees on the south side of Beaver Creek, 8300 feet elevation, below Beaver Creek Campground, Rio Grande County, Colorado. The spruces stood on an alluvial flat in a ravine about 40 feet deep, cut by the creek through volcanic rock. The creek was about 20 feet wide where it passed the spruce flat. The steep slope north of the creek as well as the upper flats both north and south of the ravine were grassy, with scattered mature ponderosa pines. A few Douglas-firs and ponderosa pines as well as spruces grew on the 50 degree north-facing slope of the ravine.

The squirrel midden was a low, oval mound of cone litter under and around three blue spruce trees, two of which were among the tallest in the stand, which extended about 50 yards along the creek. There were 52 trees of about 10 or more inches d.b.h. in this stand. The basal area at three sample points in the stand averaged 167 square feet per acre. This density of timber was enough to exclude almost all understory vegetation, there being little ground cover except needle litter and cone debris. The dominant and co-dominant trees were 75 to 90 feet tall.

The midden was 34 feet long and 27 feet wide, covering an area of approximately 722 square feet, with a maximum depth of 16 inches. The contents were a mixture of cone debris of blue spruce and ponderosa pine.

The largest blue spruce, under which recent cone debris was piled highest, measured 22 inches d.b.h. and 105 feet high. The second tree on the midden was nearly as large, and the third was 12 inches d.b.h. and 85 feet tall. Two spruces of even larger diameter (25 and 29 inches) stood on the creek bank about 15 feet north of the midden. There were also two cut 10-inch stumps in the midden that were used as feeding posts, and a tangle of dead branches between the trees and the steep ravine bank. Two grass nests could be seen in the trees over the midden. One was at a height of 23 feet and the other at 43 feet in the foliage of the main blue spruce in the center of the midden.

There was much cone litter scattered elsewhere on the flat and fairly recent accumulations under a few other spruce trees in the stand, but there were no middens deep enough to provide good cone caching sites.

In October, 1963, I dug about two bushels of ponderosa pine and blue spruce cones (mostly the former) out of the midden on the east and south sides. Much of the rest of the midden had already been excavated, probably having yielded at least six more bushels. In June of 1968, some sound blue

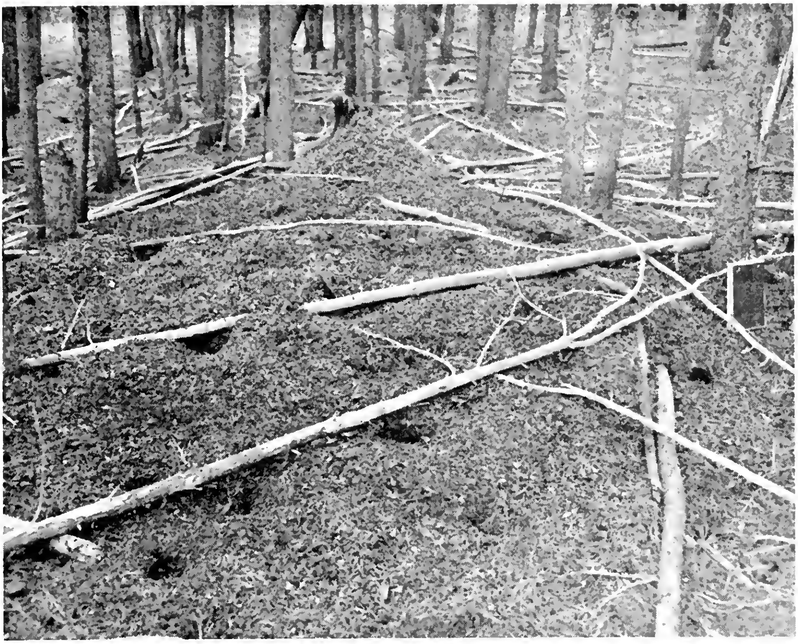

FIG. 4. A large midden of lodgepole cone debris in a dense stand of lodgepole pine, Gilpin County, Colorado. A stump at the peak of the midden served as the principal squirrel feeding station.

spruce cones of the 1967 crop were still cached in the midden, and a few sound 1967 pine cones. Most pine cones found were rotting, from years previous to 1967, indicating a poor pine cone crop in 1967. Nearly all of the recent midden material consisted of cone scales and cores of blue spruce. In June, the top two to four inches of midden were dry, but material below that level was still damp enough to keep cones closed.

A few feet east of the midden I found a water cache of ponderosa pine cones described below under a separate heading.

Lodgepole pine forest.—Cone caches in a pure stand of lodgepole pine bear little resemblance to those described above. Shade and moisture are not required, and piles of closed lodgepole cones lie exposed on the surface of the midden. I have seen many such caches and middens on a fairly open south-facing slope northeast of Blackhawk, at 9300 feet, Gilpin County, Colorado. In October, 1965, two rather large mounds of cone debris were heaped around an old stump and an uprooted snag. These feeding posts had more than a bushel of closed lodgepole cones piled under and around the snag and buried in the top layer of fresh cone scales. The cones covered by cone scales were found not concentrated in cache holes, but scattered or loosely aggregated through the material as though incidentally covered by accumulation of newly dropped cone debris.

A much larger midden nearby was centered around another stump and formed a low mound of lodgepole cone scales and cores 18 feet long and 15 feet across. Extending out from this on the lower side was a tail of older, more weathered cone debris and needle litter reaching as a carpet for another 18 feet from the active mound.

The lodgepole stand was of closely-spaced, predominantly pole-sized trees from two to 11 inches d.b.h. and nearly all of about the same height, estimated to be approximately 30 feet. Few other kinds of trees were seen within 100 yards of the midden—only a single ponderosa pine, widely scattered Douglas-firs, and a small group of blue spruces in a wet spring area perhaps farther away. On and around the big midden, the tree spacing varied from four to 54 inches measured from any tree to its nearest neighbor. There were 11 lodgepoles of three to five and a half inches d.b.h. standing in the midden, as well as two dead poles still standing. The largest opening between tree stems on the midden was seven and a half feet across. The crown canopy was mostly closed, and lower branches and understory vegetation were almost totally absent.

The midden material, consisting almost entirely of the scales and cores of lodgepole cones, was heaped up around and almost covering the stump (see Fig. 4), the tip of which stood 22 inches above the ground and served as the primary feeding perch on the midden. Six poles lay across the mound and others were partly buried in it. When the midden was examined and measured in June of 1968, stored cones were few, and there were tunnels into the cone scales under the stump and between its root snags. I counted 72 open cache holes in the midden. The material was mostly damp or wet below the top layer of two or three inches, but I found no cones cached in the wet material. There were a few closed lodgepole cones lying on the midden, mainly on the higher parts and near the main feeding post; few were buried in the debris. A few green lodgepole needle cuttings lay on the edges of the midden and on the ground nearby. Ground cover outside the midden consisted almost entirely of dry needle litter with a few low clumps of *Juniperus communis* and many patches of the mat-forming kinnikinnick.

Numerous smaller middens in the vicinity were centered around single trees that served as the main feeding stations. Carpets of kinnikinnick grew around several of these trees, encroaching a foot or two over the outer layer of old decomposing midden. One small midden had accumulated so rapidly that a patch of kinnikinnick with bright green leaves was covered completely by fresh cone scales.

About a quarter mile away on a north-facing slope I found the largest lodgepole midden measured. It was 39 feet long and 18 feet across and was shaded by more widely spaced and larger trees, up to 12 inches d.b.h. A noteworthy feature was two piles of closed lodgepole cones heaped up under trees on the lower end of the midden (see Fig. 5). The larger pile contained 1072 cones (approximately two-thirds of a bushel). Within a radius of 25 yards of the center of this midden were seven smaller middens, five of which had cones piled on the surface. Because of their close spacing, it is likely that all these cone piles were made by the same squirrel.

On the alluvial flat of Gold Creek, 4300 feet elevation, 25 mi. NE Missoula, Montana, there were numerous small middens under lodgepole pines in August 1963. Such creek valley bottoms in Colorado are usually occupied by spruce stands. The pine cone litter was dry on the surface but wet below, from the frequent summer thundershowers. There were a few closed cones on the

FIG. 5. A surface cache of lodgepole cones (half bushel) on a midden of cone scales and cores against the base of a lodgepole pine.

middens, but no piles were in evidence. I trapped red squirrels on some of these middens and saw others in the larch—Douglas-fir forests on adjacent slopes.

Ponderosa pine forest, Kaibab Plateau.—Although I have never seen a substantial midden or cache solely under ponderosa pines in Colorado, sizable ones occur on the Kaibab Plateau in northern Arizona. I examined such a midden in August of 1968 under two pines on a south-facing slope at 8700 feet, about 12 mi. S Jacob Lake. It was in an open ponderosa forest bordered on the lower side with aspen. The stand density was 110 square feet per acre, basal area. White fir and Douglas-fir grew at the foot of the slope about 100 yards away from the midden. Both pines on the midden were infested with mistletoe in the lower branches, which induced the heavier-than-normal foliage on branches near the ground. The two pines were 21 and 16 inches d.b.h., the larger one 57 feet tall, with two secondary stems arising from a mutilated mid-section.

The midden measured 31 by 19 feet, encompassing a stump and rotten wood as well as the two trees. Moisture distribution in the midden was erratic. At different points the dry surface layer of cone debris varied from one to five inches in depth. Below that it was more or less wet, depending on the degree of shade or shelter. Pine needles were mixed in the midden, and in some parts layered, probably indicating a period of abandonment when no squirrel dug into it and mixed the needle fall with the cone litter. All cone debris seen was of ponderosa pine, mostly old but with a few fresh green scales and cores on the surface. I dug about 30 green closed pine cones out of some of the many cache holes scattered over the midden, plus one old closed pine cone and several of Douglas-fir from the previous year's crop. One grass nest was about halfway up in the smaller pine.

About 2 mi. SE Jacob Lake, at 8100 feet elevation in a ponderosa pine forest, there were a few widely scattered middens under single large pines and around logs and stumps on a north-facing slope. The largest and most active midden, measuring 23 by 11 feet, was around a pine 22 inches d.b.h. and 91 feet tall, and extended under nearby logs and large limbs. The greatest depth of the midden was about one foot. It contained no cone debris other than of ponderosa pine, and no cached cones. The top two-inch layer was dry; below that it was wet. The density of trees around the midden was 137 square feet per acre. Large aspens were scattered through the pines, but I saw no other species of conifer within a mile or more of the site. Because the new pine seed crop was light at best, the squirrels were facing a tight winter.

Near Jacob Lake, I dug into two mounds of duff around the bases of large pines. They were wet below two inches and had six to eight inches of loose, wet bark litter, needles, and decaying cones and twigs. They were ideal sites for cone caching but contained no squirrel food litter of any kind. Elsewhere in the pine forest, I saw a few inactive, deteriorated middens in seemingly suitable habitat.

Water Caches

Since middens must remain damp to be of value for cone storage, it is not uncommon to find them extending into springs, boggy areas, and creek bottoms. Shaw (1936:340) described and illustrated such wet cache sites in the Pacific Northwest. He made little mention of caching in midden material, possibly because soil and leaf mulch were soft and easy to cache in. In Colorado red squirrels cache in wet, saturated middens extending out onto creek bottoms, and also make "water caches," aggregations of cones on the bottoms of small pools of water and under roots and undercut stream banks. Sometimes cones may be more widely scattered in small groups between rocks on the bottom of a flowing stream.

Cones that rest on the bottom are all closed and must have been cut from the branches. The more scattered ones may have been cut and dropped directly from overhanging tree branches. At first I suspected that the cones in pools came to rest in aggregations by the actions of currents and eddies. However, I found many in small isolated pools with no water flow, and many stuffed in holes and crannies under water. The caches were often of such size (one to two bushels) as to make accidental accumulation under water almost inconceivable. Red squirrels have been reported by many authors to be good swimmers (Seton, 1929, 4:120), and Mr. Swift also reported to me that they swim under water both to cache cones and to retrieve them. He told me of finding a large midden filled with ponderosa cones under spruce trees on one side of a swift stream several yards across. The only ponderosa pines were on a dry slope on the opposite side of the stream, which could not be crossed except by swimming.

In November, 1963, I found a "water midden" on a small creek bottom near Wellington Lake, Park County, Colorado. A bed of cone debris had built up under the branches of a blue spruce much used as feeding posts. It formed a mound 14 inches deep like a small dam covering the mud creek bottom, through which only a trickle of water was flowing. The top three inches of fresh midden were dry, and the bottom portion was blackened and saturated by creek water, which percolated out of the midden at the base of an undercut bank. Many ponderosa cones were dug out of this midden in 1963, but in June of 1968 it contained only some blue spruce cones.

Another water midden, on a tributary of Redskin Creek, Park County, covered the bottom of a shallow creek three to seven feet wide that flowed without entrenched channel through a dense blue spruce grove between hillsides clothed in ponderosa pine. The midden was 38 feet long on one side of the creek and extended as an apron across the mud creek bottom and beyond. A prime reason for the large amount of cone litter on the creek bottom was a big spruce log that had fallen across the creek and was heavily used by squirrels as a feeding station and bridge. The water line on the midden was marked by a sharp change in color from light brown fresh cone litter above to black discolored litter under water. In September, 1965, this midden was a rich source of ponderosa cones buried in litter both above and below the water line. It contained mostly blue spruce cones in 1967.

A creek bed was used as a water cache without a midden on Cub Creek southwest of Evergreen, Colorado, in October, 1965. The creek passed through a group of eight large blue spruce trees 50 to 80 feet tall and 13 to 18 inches d.b.h. There was no midden on either bank deep enough to cache in. I gathered about two bushels of blue spruce cones and a bushel of Douglas-fir from along the stony creek bottom, many submerged on the bottom in water two to six inches deep, some floating in backwater pools, and many stuffed in holes or hollows under the steep banks. The creek, three to eight feet wide, was flowing rather swiftly, and many of the cones were on the bottom well out from the edge of the water.

On Beaver Creek, in 1963, I found a much more concentrated water cache associated with the large midden under a blue spruce stand described above (in the section entitled "Blue spruce in valley bottoms"). It was in a pool of water about four feet long and 10 inches deep on the shore of the main stream. The pool was in gently flowing water where the soil had washed away under and between roots of one of the big spruces. The bottom of the pool was covered with green closed ponderosa pine cones and many were lodged among the exposed roots under the bank. Some closed cones were floating but were kept from drifting downstream by a large root and a few fallen branches. This pool yielded more than a bushel of pine cones. About a mile farther upstream a similar pool against the bank of the main creek contained over a bushel of blue spruce cones.

Caching Behavior and Seed Consumption

In Colorado, red squirrels begin cutting new spruce and Douglas-fir cones in August while the seeds are still in the milk stage and not ripe enough to store. Such cones are eagerly stripped of scales and the seeds consumed as a welcome addition to the current food supply. Large numbers of green, unopened cones can be seen scattered on the ground where squirrels have dropped them from the branches above. The manner and vigor with which this cone-cutting and tossing is done was described by Bell in 1898 (Klugh, 1927:19), and numerous later observers. Shaw (1936:348) timed a squirrel cutting white spruce cones. In two one-minute intervals it cut and dropped 28 and 29 cones.

Although a few of the early-cut green cones may be stuffed into shallow pockets on the midden or ground surface, they are not cached in quantity until the seeds have reached the dough stage, beginning in late August or early September in Colorado. At this time feeding on the new cone crop continues, and immense numbers of ripe but still closed cones are cut from the trees, gathered from the ground, and cached in the midden for future use. Harvesting of cones is the major activity of red squirrels during daylight hours through the months of September and October. The numbers of cones that can be stored away in this period are truly prodigious. In October, 1963, I removed about a bushel of Engelmann spruce cones from a midden 5 mi. W Arapaho Basin, Summit County, Colorado. Two days later I visited the same midden again and found that the owner had already refilled most of the cache holes I had emptied. The slightly drier condition of the newly cached cones suggested that they had been gathered from the ground, not freshly cut.

Cones, particularly those of Douglas-fir, are sometimes cached after they have lain on the ground long enough for the scales to open partially. Such cones seem to have shed few, if any, seeds. Cones that have dried enough for the scales to open fully are not cached. But in June, when cones were scarce, I saw a squirrel pick up an open blue spruce cone lying on a midden and carry it up into a tree.

Most of the caching in Colorado is done in small holes dug into the midden material of loose cones, scales, and cores. After the caches have been exhausted, the surface of the midden remains riddled with these little pits. They are usually shallow, four to eight inches deep, but may extend as far as 20 inches under buried logs, roots or other solid objects. Such cache holes are sometimes dug into soft soil, but they usually stop when mineral soil is reached. The number of cones in a single pit may vary from only two or three pines cones to as many as 50 or more of the small cones of Engelmann spruce. In October, after a heavy cone crop has ripened, an active midden is usually crammed with cached cones. Many cache holes are stuffed full to the surface, with clusters of fresh cones projecting out of the midden. But most of the cache pits are invisible on the surface, having become covered with a seemingly undisturbed layer of cone debris.

During the winter and following spring the squirrel digs up the cached cones and carries them to logs, branches or other feeding stations, where it gnaws the scales off the cores to get at the seeds. The accumulation of cone scales and cores around preferred feeding stations and trees provides the source of new midden material, which subsequently becomes spread more widely over the area as the squirrel digs into and reworks the material year after year.

In areas of prolonged snow cover, squirrels dig tunnels into the snow, and under it on the surface of the midden to reach cached cones. A few such tunnels kept open provide essential access to the midden when it is covered with heavy, crusted snow.

Edibility and Viability of Stored Seed

Loss of the potential winter seed supply can result from spoilage as well as from opening of cones and shedding of seeds in the tree tops. Insofar as edibility is concerned, seeds of conifers store well when the cones are kept wet. I have dug cones of blue spruce and

Douglas-fir out of wet caches in June and found them to be black but firm and still retaining some pitch. These cones were probably nearly a year old, and still contained many sound seeds. However, cones removed from the same caches and kept wet at room temperature in June had most of the seeds spoiled after less than a month. Apparently seeds must be kept cool to be preserved in summer. Wet middens excavated in June were distinctly cool in Colorado, some at 10,000 feet elevation even retaining frost near the bottom. However, by the end of the summer, middens in most of this region probably reach temperatures too high for preservation of the seed as food.

Cones of Douglas-fir and blue spruce excavated from caches in October and November are easily separable into sound cones of the year and older rotting cones. The sound cones, although generally brown, retain a little straw or greenish color at the tips of the scales. Older cones are completely brown or black, have looser cone scales, and can easily be twisted in two with the hands. Much of the woody material has rotted and the seeds are black or completely decomposed.

Many of the current year's cones cached within the preceding four to six weeks may be enveloped in a mesh of fungal mycelia, which also penetrates the midden matrix. The fungus seems to have no effect on the edibility or viability of the seeds, at least during the first several months.

I doubt that the squirrels in Colorado can get many edible seeds out of cones cached longer than a year, but they are reported to dig them up and use them in Montana (Halvorson, unpublished) and Alaska (M. C. Smith, 1968). Perhaps in those areas summer temperatures do not cause as much spoilage of seed.

Red squirrels rarely cache cones that are too green to yield ripe seeds or that contain predominantly unfilled or insect-infested seeds. Nevertheless, a significant but highly variable percentage of seeds in all cones is empty or incompletely filled. In general, in years of poor cone crops the cones have lower percentages of sound seeds (Toumey and Korstian, 1942:105), which further reduces the available squirrel food. Viability for germination is highly variable, even for seeds solidly filled and apparently sound, but many filled seeds remain edible even when no longer capable of germination.

In spite of the high viability of seeds in caches for nearly a year, there is little opportunity for such seeds to germinate naturally and produce successfully established seedlings. Stored seeds, if not eaten usually decompose in the cone. In July I have found some germinated seedlings emerging from cones in wet middens, but all died in the midden without establishing roots in the soil below. If the midden dries enough for the cone scales to open, the seeds are apt to be released into an unsuitable sprouting medium, too far above the mineral soil and where the chance of reaching sunlight is slight. Seedlings of conifers are almost never found on squirrel middens, except occasionally in marginal situations of more open tree canopy and where cones are cached in damp soil. I think Bailey (1931:79) exaggerated the value of red squirrels as agents in natural forest regeneration.

Comparative Interpretations of Cone Cache Ecology

Cone-caching behavior of the species as a whole is highly diverse and seems to indicate merely a wide range of tolerance. However, when geographic and ecological variations of caches and middens are compared locally as well as regionally, some explanations of the pattern seem to make sense.

The range of local variation in cache sites is not so great as the regional variation because each local area offers only a limited set of forest conditions suitable for red squirrels. Kinds of trees used for midden sites and kinds of topographic situation occupied in different areas are related to differences in temperature and moisture at the ground level, hence to the microclimate as well as the regional climate.

Tamiasciurus is primarily a boreal genus. Its special adaptations for feeding on stored conifer seeds require cool moist sites where cones can be stored without opening and without spoilage for a year or more. Such conditions are easy to find almost anywhere in the boreal conifer forests. Hence red squirrels are continent-wide in distribution in the Canadian Taiga and occur southward throughout the Canadian Life-Zone in the higher mountains. In western Montana they occur as low as 3000 feet elevation, but in Colorado come down only to about 7000 feet in the Transition Life-Zone. From about 9500 feet up to timberline in Colorado the spruce-fir type, both on flats and steep slopes, provides plenty of cool moist cache sites.

The driest conditions are in lodgepole, limber, and bristlecone pine forests, mostly on south-facing slopes, where conditions for caching are marginal. At Geneva Basin, Colorado, for instance, large middens were occupied at 10,000 feet in the shadier parts of a fairly open limber pine—bristlecone forest, and the middens were still partly damp in June on southwestern slopes. Smaller middens in more open situations had already dried out. Some lodgepole stands as low as 9000 feet are occupied by red squirrels because of their perpetual supply of closed cones, but this habitat seems to be less than optimum.

At lower elevations the drier forests, mainly ponderosa pine, are more extensive. In this zone only the blue spruce stands occupying the wettest and deepest soils along the valley bottoms provide enough shelter to retain cool moist conditions through most of the year. Hence the red squirrels are restricted to within "commuting distance" of the blue spruce stands. Middens under such stands usually contain ponderosa cones if there is a good ponderosa seed crop on the adjacent sunny slope.

Tamiasciurus is absent from the Black Forest, a flat upland divide about 7000 feet in elevation between the South Platte and Arkansas drainages northeast of Colorado Springs. It is a solid stand of ponderosa pines on dry sandy soil and lacks blue spruce in the small tributary canyons leading from it.

Farther to the south, the altitudinal restriction of red squirrels in Arizona and New Mexico is more limiting. The Canadian Life-Zone is less extensive than in Colorado and the squirrels are scarcely found below about 8000 feet, except in shady ravines. In New Mexico, according to Bailey (1931:76): "They rarely come down into the edge of the yellow pine belt farther than the spruces extend on cold slopes."

On the Kaibab Plateau in Arizona, a marked difference in use of forest types is evident. The higher parts of the plateau, above about 8400 feet, are covered with a mixed conifer type composed of blue spruce, white fir, Douglas-fir, and some ponderosa pine. Below 8400 feet the pure ponderosa type extends down to about 7000 feet where it gives way to pinyon-juniper. The ponderosa pine forests of the Kaibab bear little resemblance to those of Colorado east of the Continental Divide. On the Kaibab the trees are much taller, larger, and faster-growing and cover the bottoms of the draws as well as the slopes and upland flats. Blue spruce does not extend down the valleys through the pine type, perhaps because of the limestone parent material and subsurface drainage.

Red squirrel middens on the Kaibab occur in great abundance throughout the mixed conifer type and in much less abundance in the upper part of the ponderosa pine. The middens under large mature pines and around logs and stumps in pine forests were unlike any seen in the eastern Transition Zone in Colorado. But on the Kaibab, in spite of the fairly open tree stand and lack of low branches, the ground has a good layer of forest litter that retains moisture a few inches below the surface. Middens under pines were wet in August, and the abundant down-timber provided plenty of good feeding stations, some of which served as the nuclei of middens even without any tree overhead. In general, ponderosa middens on the Kaibab resembled bristlecone middens more than any other kind in Colorado.

Middens higher up in the mixed conifer type were mostly under large white fir (Fig. 6), Douglas-fir, and blue spruce trees, as well as against logs and stumps. Some of the fir middens were on fairly open sites much like those in the ponderosa type, but middens were scarce under pines in the mixed forest, perhaps because the pines were often on the drier sites at the higher elevation. In general, in both forest types the squirrels preferred locations with more than average shade or shelter of some kind.

To provide moisture in the period of cone caching and until the arrival of winter snows, good rainfall in late summer and autumn is required. Total rainfall on the Kaibab Plateau is not particularly high but has a peak in late summer, as shown by the graph for central Arizona in figure 8-2 of Barrett (1962:348). The average precipitation for the four months of July through October for nine stations in Coconino County, Arizona, was 8.88 inches, whereas the average for nine stations in the eastern Transition Zone of Colorado was 7.45 inches (Greening, 1941:761; Gittings, 1941:798).

Although moisture conditions were adequate in August, 1968, for cone caching in the ponderosa forest on the Kaibab, I noted a different deficiency. The second of two successive pine seed failures had left the squirrels with their caches exhausted and no alternative kind of cones to harvest. In the mixed conifer forest, however, some white fir cones were available to eke out a generally poor cone year. The presence of a low density of middens in the pine forest and a high density in the mixed conifers is compatible with my interpretation that, on the Kaibab, midden sites are adequate though not abundant in the pine type, but the unreliability of the pine cone crop does not permit a good population to build up there.

Rasmussen (1941:262), in his study of the communities of the Kaibab Plateau, wrote of the red squirrel: "Its distribution is confined to areas where *Abies*, *Pseudotsuga*, or *Picea* occur. . . . But

Fig. 6. A simple *Tamiasciurus* midden around the base of a white fir on the Kaibab Plateau, Arizona. The midden is composed of cone scales and cores of white fir, Douglas-fir, and ponderosa pine.

at . . . lower elevations the squirrel middens show great preponderance of yellow pine [ponderosa] cones." He thought that some factor other than food prevented red squirrels from occupying the pure pine forest, but he seems not to have observed any years of pine seed failure on the Kaibab.

C. H. Halvorson has seen cone caches in middens under ponderosa pines about 40 mi. E Lewistown, Montana. It was in an area of low wooded hills and ridges bordering sagebrush plains, with wet meadows along the narrow creek bottoms. Middens and caches were seen only on the slopes under pines or against logs and stumps.

Red Squirrels and Silviculture

Caches as a Source of Seed for Silviculture

Since the early years of reforestation on the national forests, red squirrel cone caches have been utilized as a source of seed for planting. Cox (1911) gave a good account of early reforestation work and described some of the cone collecting and processing operations in the western states. He wrote (p. 17): "Squirrels' caches are often excellent places from which to get cones . . . it is not uncommon to find in a single one of their caches from 8 to 12 bushels of good cones, though the average quantity is about 2 bushels. These caches are located by old rotten logs, in springy places and muck, and in duff, sometimes at a considerable depth, as well as under bushes and felled tree tops, along streams, and beneath overhanging stream banks. . . . Among the species of cones which are often obtained from caches are Douglas-fir, Engelmann spruce, western yellow pine, lodgepole pine, and western white pine. Usually, however, the cones of but one species are found in a single cache. In collecting from squirrels' hoards it is well to have a pack horse along for immediate transportation, since if cones are dug out and left on the ground for any length of time they will be carried away and cached again by the industrious animals."

Korstian and Baker (1925:2) reported that in the intermountain region, lying between the Sierra Nevada and the Rocky Mountains, "seed collecting has been confined almost entirely to squirrel caches, because logging operations have never been large enough to make the usual method of collecting seed from felled trees economical." Cones were commonly bought by the Forest Service directly from individual cone collectors scattered over wide areas and were processed in central seed extraction plants. Seeds of nearly all the major timber species were collected by this method in quantities as high as 6000 pounds in a single operation.

Some of the long recognized advantages of collecting seed from squirrel caches are ease of collection, high quality of seed (ripeness, viability, and freedom from insect or disease damage), and the extended period during which closed cones can be gathered after cones on the trees have opened and shed their seeds. Seed collecting from caches also has some disadvantages, such as occasional scarcity of squirrels and caches in forests from which seed is desired, and inability to restrict harvesting to trees of selected seed-producing characteristics.

Some Forest Service silviculturists have expressed dissatisfaction with the poor quality of seed obtained from squirrel cached cones, but their problem is mainly one of finding reliable private cone collectors who know squirrel caching habits and will sack up only the sound, freshly cached cones. If large quantities of cones are bought from individuals who irresponsibly gather up old rotting cones as well as dry open cones from the surface of the ground, it is not realistic to blame the poor quality of the cones on the squirrels.

Private nurserymen and seed dealers also have made large-scale use of squirrel caches in the western states as a source of supply.

They collect cones themselves or purchase cones from many individual collectors. Two nurserymen known to me buy many thousand bushels of squirrel-cached cones each year at prices ranging from $1.50 to $3.00 per bushel. They buy only sound, closed cones of the current year's crop and obtain high per cent germination. Since the kinds and amounts of cones vary greatly from year to year, depending on the crops, cone buyers try to process and store an excess supply during good seed years, in order to carry them over the years of seed failure. Most of the commercial market seems to be for horticultural use, though seed is also sold for reforestation. Mr. Swift buys cones of most kinds of Colorado conifers, but relatively few of lodgepole pine and subalpine fir, because of their low horticultural value.

In recent years there has been increasing interest by the Forest Service and the timber industry in obtaining higher quality seed for reforestation. There also has been an increase in research in tree genetics and the development of tree seed farms, particularly in the South and Pacific Northwest. But tree seed farms and direct picking of cones in the West still provide only a small part of the seed needed for forest planting and seeding. More effort is being made in some areas to obtain seed from selected forest trees by direct picking from standing or felled trees. Efforts are also made to obtain seed from the same latitudinal and elevational tree seed zone where it is to be used, or even from within the same national forest.

Present methods of obtaining tree seed practiced by the Forest Service vary in different regions, depending on the local conditions and seed years. Some seed is collected by Forest Service personnel, but most is purchased from individual private collectors, or from commercial seed dealers. However it may be obtained by the user, the great bulk of conifer seed used in the Pacific Northwest and the Northern and Southern Rocky Mountain regions is initially harvested by *Tamiasciurus*. There seems to be no other source at present from which the required amounts can be obtained at reasonable cost. The continued existence of large and healthy populations of red squirrels is a major asset not widely appreciated.

Seed Biomass in Relation to Squirrel Energy Requirements

The amount of conifer seed cached by red squirrels and the amount actually consumed are of interest from several aspects. Is the available cone crop a limiting factor on the population or the productivity of red squirrels? Do the squirrels ever harvest enough cones to reduce natural forest regeneration? Does the amount of cones gathered from caches by people affect a squirrel's chance of survival? Clear cut answers to these questions cannot be given, but enough information is available to justify some discussion and tentative conclusions. Perhaps presenting them may stimulate the collection of needed facts.

Although a great deal of work has been done on the silviculture of the major timber trees used by squirrels, little has been published on the biomass of seed produced by most species. Seed productivity fluctuates widely from year to year and also from tree to tree even in a "bumper" seed year. Cone and seed production of a given tree is influenced by age, dominance in the stand, site quality, prevailing weather conditions, inheritance, and factors still unknown (Toumey and Korstian, 1947:272). Available data cannot be regarded as definitive or "average" for any part of the country, but for the sake of discussion I have used whatever information I could get, to see if calculations and reasoning based on these data would lead to plausible conclusions. The same may be said for data on the energy budget and behavior of red squirrels, but here we seem to be dealing with less wide-ranging variables.

Data I have been able to find on seed productivity of several species of Rocky Mountain conifers are compiled in Tables 1-5. Sources are indicated, many of which are for studies outside the geographic region covered in this report. It should be remembered that information obtained for Douglas-fir and ponderosa pine, and perhaps other species, in the Pacific Northwest will not be strictly applicable to the Rocky Mountains, because of considerable intraspecific differences between trees of these regions. For some species, such as the blue spruce, I have been able to find few data. Seed production data based on cone counts on trees may give estimates of production prior to, or after, cone cutting by squirrels; whereas data on seed fall per acre, based on use of seed traps, give only estimates of production *after* squirrels have taken their toll.

Red squirrel energy requirements.—C. C. Smith (1968) studied the food consumption of *Tamiasciurus hudsonicus streatori* in relation to behavior and territoriality in southern British Columbia. He arrived at the following values for ingested energy of a few individual squirrels: an adult male, 117 kg. calories per day; a female at the height of lactation, 322 kg. calories per day; and six juveniles (134 to 170 grams) 80.5 to 95.4 kg. calories per day. From extremely limited samples of seed he obtained the energy content (dry-weight basis) of several kinds of conifer seed: Douglas-fir, 7131 calories per gram; Engelmann

TABLE 1.—SEED PRODUCTION DATA REPORTED FOR DOUGLAS-FIR.

Amount		Area	Reference
Thousand seeds/pound	42	Central Rockies	Anonymous, 1948
	44	Pacific Northwest	Isaac, 1943
	24-49	Utah and Idaho	Korstian and Baker, 1925
Seeds/cone	44	British Columbia	Garman, 1951
	45	Utah	Hayward, 1940
Pounds seed/bushel	.76 (.36-1.33)		Korstian and Baker, 1925
	1.0		Tillotson, 1917
Cones/bushel	1584	Colorado	R. B. Finley
Cones/tree	1126	Pacific Northwest	Winjum and Johnson, 1964
	1300 (1000-4000)	British Columbia	Garman, 1955
Bushels cones/tree	1.5	Pacific Northwest	Isaac, 1943
	2.5		Anonymous, 1948
Pounds seed/tree	.1-1.0		Fowells, 1965
	1.	Pacific Northwest	Isaac, 1943
Thousand seeds/acre	34-123	Pacific Northwest	Isaac, 1943
	168-1500	British Columbia	Garman, 1951
	291	New Mexico	Krauch, 1945
Pounds seed/acre	.85-3.1	Pacific Northwest	Isaac, 1943
Seed trees/acre	10		Cox, 1911
Cal/g dw whole seed	5998		Long, 1934
Cal/g dw kernel	7131		C. C. Smith, 1968
Kernel corr factor	.686		R. B. Finley

spruce, 7107 calories per gram; lodgepole pine, 6827 calories per gram; and ponderosa pine, 7558 calories per gram. These values are for only those parts of the seed consumed by squirrels—the endosperm and embryo. Hence, an adult male would require 42,700 kg. calories per year which, if provided *entirely* by Douglas-fir seed, would amount to 5.99 kilograms (dry weight) of seed per year.

Douglas-fir.—Korstian and Baker (1925:3) give the pounds of clean seed per bushel for Douglas-fir as from 0.36 to 1.33 pounds (averaging 0.76). But these values are for seed with the seed coat, live, as used for planting. I dissected the edible parts out of the hulls of 100 seeds and weighed them in 10 lots of 10 seeds each. The endosperms and embryos combined weighed 71.2 per cent of the total seed weights. Since the moisture content of commercially stored seed is usually six to 10 per cent, I assumed eight per cent, converted the fresh weights to equivalent dry weights, and computed a corrected value for the edible parts of 68.6 per cent of total seed weight. Assuming the same moisture content in the seed weights per bushel, and applying the

68.6 per cent correction factor to convert to edible seed weight, one obtains 0.52 pound, or 236 grams of food (dry weight) per average bushel of Douglas-fir cones. Hence, Smith's adult male would require 25.4 bushels of Douglas-fir cones to meet his energy requirements for an entire year. I have not applied any correction for per cent of sound or filled seed in cones because this is highly variable and no data are available for cones cut by squirrels. This factor would tend to increase the required number of cones in poor seed years more than it would in good years, when high percentages of seed are sound.

According to Isaac (1943:16), "the average forest-grown tree, which has a narrow crown, yields about 1½ bushels during a good seed year. This amount of cones produces about one pound of cleaned seed." At this productivity the 25 bushels of cones required by one male squirrel would be provided by 17 "average" trees. But the number of cones produced per tree is notoriously variable. Winjum and Johnson (1964) studied variation in Douglas-fir cones and seeds in young, open-grown Douglas-fir trees in Oregon and Washington and found from 151 to 6000 (average 1126) cones per tree. (I counted 1584 cones in a bushel.) Because trees in closed stands produce far fewer cones, a squirrel would probably be able to harvest less than a bushel per average tree. However, in most situations cone cutting is concentrated on those few trees in a stand that are the best seed producers. Cox (1911:13) estimated 10 trees per acre bearing seeds in appreciable quantities.

A perhaps better way to judge the seed crop requirement of a squirrel is on the basis of seeds produced per acre of forest. Isaac (1943:17) reported the seed fall in a 100-year-old stand to vary from 34,000 to 123,000 seeds per acre. If we assume 126,000 seeds per acre and accept the value of 42,000 seeds per pound (Anon., 1948:291), this amounts to three pounds of whole seed per acre. Applying the 68.6 per cent correction factor for edible dry weight, we get 2.06 pounds (934 grams) of dry squirrel food per acre. Hence, to obtain 5.99 kilograms of seed in a year, our male squirrel would require 6.4 acres of Douglas-fir forest producing 126,000 seeds per acre. Unfortunately, in the Rocky Mountain region the Douglas-fir would probably produce this good a crop only two or three years out of 10.

I have not found more than two bushels of Douglas-fir cones in a cache, and they have always been mixed with blue spruce, or sometimes ponderosa pine cones. H. M. Swift has found six to eight bushels of Douglas-fir cones in a single mixed cache—still considerably below the theoretical maximum requirement of 25.4 bushels a year. The seeming discrepancy between the requirement and the magnitude of caches usually found is, no doubt, explained by the fact that squirrels do not subsist entirely on Douglas-fir cones, or even on cones of all species available. Conifer seeds are the mainstay in winter months, but in summer large amounts of other kinds of plant food are eaten, particularly fungi (Buller, 1920; Hatt, 1929; and C. C. Smith, 1968). A more realistic estimate of conifer seed required by a red squirrel would be 40 or 50 per cent of the theoretical yearly requiremnt; and in most localities and years only part of the conifer seed would be provided by Douglas-fir. Fifty per cent of the yearly requirement would be provided by 12.7 bushels of cones, which might be produced by about nine mature trees, or, by the alternative estimate, by 3.2 acres of forest.

Engelmann spruce.—Seed productivity for the Engelmann spruce is less well known than for the more commercially valuable Douglas-fir. However,

TABLE 2.—SEED PRODUCTION DATA REPORTED FOR ENGELMANN SPRUCE.

	Amount	Area	Reference
Thousand seeds/pound	135 (69-200)		Anonymous, 1948
	175	Northern Rockies	McKeever, 1942
	69-135	Utah and Idaho	Korstian and Baker, 1925
Pounds seed/bushel	.50 (.40-1.)		Korstian and Baker, 1925
	.8-1.2	Montana	Lowdermilk, 1925
Cones/bushel	2800	Colorado	R. B. Finley
Bushels cones/tree	1.25		Cox, 1911
Thousand seeds/acre	570-760	Montana	Lowdermilk, 1925
	200-2000		Roe, 1967
Pounds seed/acre	12		Cox, 1911
Seed trees/acre	12		Cox, 1911
Cal/g dw kernel	7107		C. C. Smith, 1968
Kernel corr factor	.770		R. B. Finley

the Engelmann is the most important tree in this region for the red squirrel and commonly provides practically its entire winter cone supply. To supplement the data on Engelmann spruce in Table 2, I dissected and weighed three lots of 10 seeds as was done for Douglas-fir. The weight of live endosperms and embryos averaged 78.9 per cent of the whole seed weight and the corrected value for dry weight was 77.0 per cent. Applying this conversion factor to the 0.50 pound of seed per bushel in Table 2 gives 0.385 pound of dry food per bushel, or 175 grams. An adult male requiring 42,700 kg. calories per year would thus need 6.01 kilograms of Engelmann seed, or 34.3 bushels of cones. If 50 per cent of the squirrel's diet were provided by other foods, this would still leave 17 bushels of cones needed. The only figure available for cones per tree is 1.25 bushels, by Cox, for a "good crop." Assuming such a cone production, 14 good seed trees would provide 50 per cent of the squirrel's annual energy requirement.

For an estimate per acre of forest we can use 135,000 seeds per pound and 600,000 seeds per acre (Table 2) and compute, as before, 3.42 pounds (1.55 kilograms) of dry food per acre, or 3.9 acres to meet the full energy needs for one year. Only 2.0 acres would be needed to provide the 17 bushels of cones for half the diet. Mr. Swift has collected as much as 15 bushels from a single midden, and many bushels may have been left because of the small size of Engelmann cones and the tediousness of digging them. However, most middens yield much less.

Blue spruce.—The blue spruce is the most dependable seed producer for red squirrels in the Transition Zone of the Colorado East Slope. Unfortunately, little information has been published on its cone and seed production. If we assume the same values as used for Engelmann spruce, for the energy content

TABLE 3.—SEED PRODUCTION DATA REPORTED FOR BLUE SPRUCE.

	Amount	Area	Reference
Thousand seeds/pound	106 (80-163)		Anonymous, 1948
	80-85	Utah and Idaho	Korstian and Baker, 1925
Pounds seed/bushel	1.0 (.75-1.25)		Korstian and Baker, 1925
Cones/bushel	989	Colorado	R. B. Finley
Cones/tree	500 (200-2000)	Colorado	R. B. Finley

of seed and the correction factor for edible dry weight, the error should not exceed 10 per cent. I counted 989 cones in one bushel. In the vicinity of Evergreen, Colorado, I made some rough visual estimates of cones on trees, and concluded that they averaged about 500 per tree for a good seed year. With these figures and the few data in Table 3, we can come up with the following for blue spruce: 0.77 pound, or 350 grams, of dry food per bushel; 6.01 kilograms of dry seed, or 17.2 bushels of cones to fill the total annual need; 0.506 bushel of cones per tree; and 34 trees to fill the annual need. The more likely consumption, for 50 per cent of the diet, would be 8.6 bushels from 17 trees.

I have no figures for seed fall per acre, but we may reasonably assume 10 good seed trees per acre, in which case 1.7 acres would provide enough blue spruce seed for 50 per cent of the annual diet. Mr. Swift reports that he has obtained as many as 13 bushels of blue spruce cones from a single midden, considerably more than the 8.6 needed for half the diet.

Ponderosa pine.—Although the ponderosa pine is a less important food source for red squirrels than the preceding tree species, its seed productivity is one of the better known (see Table 4). I dissected and weighed six lots of five seeds each and found that the live kernels weighed 57.6 per cent of the whole seed, and the corrected dry weight was 53.9 per cent of the whole seed weight. Accepting 1.32 pounds of seed per bushel and 1.5 bushels of cones per tree from the table, we obtain 0.71 pound, or 323 grams, of dry food per bushel; 5.65 kilograms of dry seed, or 17.5 bushels of cones for a year's supply; and 12 "good seed trees" to yield this many cones. The seed study by Fowells and Schubert (1956) is one of the most detailed yet published. It analyzes seed data obtained over a 28-year period from several species in mixed stands in the pine region of California. From their data on ponderosa pine we obtain 71 seeds per cone (p. 10) and 150 cones per tree (p. 21), which, using 9700 seeds per pound, we can convert to 0.593 pound or 269 grams (dry weight) per tree, and 21 "dominant trees" to produce a one year supply.

Of the several reported measurements of ponderosa pine seed fall, we can take 205,000 seeds per acre from Roeser (the average of two good seed years out of nine in Colorado) and his 14,700 seeds per pound to compute 7.49 pounds or 3.40 kilograms (dry) per acre, and 1.66 acres to meet the needs of a full year, or 0.83 acre for half that need. Because ponderosa pine produces notoriously erratic seed crops in Colorado, in most years an acre of timber would produce considerably less seed than required to provide half the energy needs of a squirrel.

TABLE 4.—SEED PRODUCTION DATA REPORTED FOR PONDEROSA PINE.

	Amount	Area	Reference
Thousand seeds/pound	14.7	Colorado	Roeser, 1941
	16 (13-19)	Utah	Korstian and Baker, 1925
	9.7 (8.3-12)	Idaho	Korstian and Baker, 1925
Seeds/cone	64-92		Anonymous, 1948
	69-73	California	Fowells and Schubert, 1956
Pounds seed/bushel	1.32 (.75-2.)		Korstian and Baker, 1925
	1.5		Cox, 1911
Cones/bushel	200-300		Anonymous, 1948
	218	Idaho	Miller and Lemmon, 1943
Cones/tree	200		Fowells, 1965
	50-2250	California	Fowells and Schubert, 1956
Bushels cones/tree	1-1.5		Rudolf, 1961
	4		Cox, 1911
Pounds seed/tree	2	Southwest	Pearson, 1950
Thousand seeds/acre	205	Colorado	Roeser, 1941
	164	California	Fowells and Schubert, 1956
	123-345	Idaho	Curtis and Foiles, 1961
Pounds seed/acre	30		Cox, 1911
Seed trees/acre	5		Cox, 1911
Cal/g dw whole seed	5626		Long, 1934
Cal/g dw kernel	7558		C. C. Smith, 1968
Kernel corr. factor	.539		R. B. Finley

Lodgepole pine.—Lodgepole pine seed is not a preferred food of the red squirrel but its widespread and almost continuous availability make it an important reserve or emergency food. Using the data in Table 5, and assuming the same correction factor for edible dry weight as with ponderosa pine (which may be considerably in error because of the great differences in seed size), we can compute the following estimates for lodgepole pine: 0.291 pound or 132 grams of dry food per bushel, and 6.26 kilograms of dry seed, or 47.4 bushels of cones, to fill the annual requirement, which might be produced by 95 trees. From this we see that almost three times as many bushels of cones are required as for ponderosa. This is a consequence of the small number of lodgepole seeds per cone and their very small size.

If we use an estimated annual yield in Colorado of 320,000 lodgepole seeds per acre, this amounts to 1.69 pounds or 0.77 kilograms (dry) per acre. The 6.26 kilogram annual requirement would be produced by 8.2 acres of lodgepole forest. Lotan's estimate of 3,228,000 seeds in Montana was based on counts of total serotinous cones on branches and is not annual production. It is a measure

TABLE 5.—SEED PRODUCTION DATA REPORTED FOR LODGEPOLE PINE.

	Amount	Area	Reference
Thousand seeds/pound	102		Anonymous, 1948
	120		Cox, 1911
	85-160		Bates, 1930
Seeds/cone	21.1	Montana	Lotan, 1967
	1-50		Fowells, 1965
Pounds seed/bushel	.54 (.34-1.)		Korstian and Baker, 1925
	.40		Tillotson, 1917
Cones/bushel	1778	Colorado	R. B. Finley
	1500-2000		Bates, 1930
Bushels cones/tree	.5		Cox, 1911
Thousand seeds/acre	320 (30-700)	Colorado	Bates, 1930
	3228	Montana	Lotan, 1967
Pounds seed/acre	3 (.3-7.5)		Bates, 1930
Seed trees/acre	40		Cox, 1911
Cal/g dw whole seed	5989		Long, 1934
Cal/g dw kernel	6827		C. C. Smith, 1968

of total stored seed per acre available in cones of the crops of many years. A squirrel obliged to subsist for a year entirely on such a diet could get by on only 0.8 acre, but could do it for only one year. Lodgepole stands differ widely in proportion of serotinous cones. Bates (1930:11) reported about three times as much seed retained in older persistent cones as was produced in the current cone crop.

Cox (1911:18) reported as much as seven bushels of lodgepole cones collected from a single cache in Wyoming. Although this is far below the 24 bushels providing half the annual requirement, the squirrels are not dependent on cached lodgepole cones. Indeed, such industrious activity seems to serve little more than convenience and an urge for "busy work."

Estimated seed requirements.—To summarize and compare the estimated seed requirements of a squirrel for half a year, the amounts calculated from Tables 1-5 as described above are presented in Table 6. Requirements have also been expressed in numbers of fresh whole seeds by using the correction factors for edible dry weight, and the numbers of seeds per pound.

It must be emphasized that a wide degree of variation enters into most of the parameters of Table 6, particularly those expressed in trees or acres. Nevertheless, rough though these estimates are, they provide a quantitative basis for consideration of several questions of red squirrel ecology.

Rate of midden accumulation.—How many squirrel-years of cone-stripping were required to produce a midden of the magnitude of those described? The blue spruce midden by Beaver Creek was sufficiently well demarcated to permit easy measurement. From its surface area and 30 depth measurements, I estimated its total volume to be 602 cubic feet, or 484 bushels. Three samples of mixed midden material totaling one bushel were taken from three parts of the midden and examined for content. The bushel contained the cores of 239 blue spruce, 52 ponderosa, and 57 Douglas-fir cones, which were equivalent to uneaten closed cones amounting to 0.24 bushel blue spruce, 0.17 bushel ponderosa, and 0.036 bushel Douglas-fir. These total 0.45 bushel of mixed cones from which the bushel of midden was derived. This ratio indicates that the 484 bushels of midden were derived from 218 bushels of fresh cones. If the fractions of each kind of cone in the sample bushel are the same as for the entire midden, they represent 117 bushels of blue spruce, 83 bushels of ponderosa, and 17½ bushels of Douglas-fir cones.

This amount of cones could have been consumed by one adult male squirrel in a 25-year period (13.6 plus 9.6 plus 1.3 years, respectively), based on the estimates in Table 6. Five squirrels could have stripped that amount of cones in only five years. If the squirrel lived on cones for substantially more than 50 per cent of his diet, that amount might have been consumed by one squirrel in only 15 or 20 years. I have no information on the rate of weathering and decomposition of squirrel middens, but have seen noticeable deterioration of a few middens in a five-year period when these were little used. Still, since that stand of blue spruces was undoubtedly occupied by squirrels for many decades, five years seems to me an unbelievably short period in which all preceding debris should have disappeared. These considerations are compatible with the view that such a midden is utilized by no more than a single family group of squirrels at one time, and probably for most of the time by only a single territorial individual, as believed by numerous previous workers.

Effects of Cache Raiding by Man on Red Squirrels

Does the practice of raiding cone caches for nursery seed reduce the squirrels' chances of survival or affect their reproduction? The amount cached in a single midden varies greatly. As much as 15 bushels has been reported from a single cache (Toumey and Korstian, 1942:116), but the average amount is probably between two and five bushels. This almost never makes up the total seed supply in the midden, because most cones are well concealed and the average person digging them out moves on to another midden when the work becomes less productive. I have no basis for judging what percentage of cached cones is found by the average "cone-digger."

When amounts usually gathered from single middens are compared with estimated squirrel requirements (Table 6), the amounts lost by a squirrel seem to be a substantial fraction of its total winter needs. If its needs are as great as indicated in Table 6, it seems evident that they would not always be satisfied by a single cache. The common occurrence of small to medium-size middens and caches, often close together, leads me to believe that individual squirrels often control or utilize more than one midden, especially

TABLE 6.—ESTIMATED AMOUNTS* OF SEED NEEDED TO PROVIDE 21,350 KG. CAL, HALF OF THE ANNUAL ENERGY REQUIREMENT OF AN ADULT *Tamiasciurus*.

	Douglas-fir	Engelmann spruce	Blue spruce	Ponderosa pine	Lodgepole pine
Thousands fresh whole seeds	400	1200	910	170	1300
Kg of fresh whole seeds	4.4	3.9	3.9	5.2	5.8
Kg of dry seed kernels	3.0	3.0	3.0	2.8	3.1
Number of cones	9200	......	......	2400	62,000
Bushels of cones	13	17	8.6	8.7	24
Number of good seed trees	8.5	14	17	6	47
Acres of forest	3.2	2.0	1.7	.8	4.1

* The values in this table are internally inconsistent because they are derived from several independent sources.

when populations are low. If so, the squirrel is less likely to lose most of his winter supply to cone collectors.

The seriousness of the cone loss varies with the site and cone crop. Loss of a cache of ponderosa or Douglas-fir cones from a blue spruce midden in the Colorado Transition Zone would be of little consequence because the squirrels are limited by cache sites, not cones, plenty more of which can be gathered farther up the hillside. On the other hand, in a year of seed failure in these species and when blue spruce cones are being cached, loss of the latter could be critical, because blue spruce stands and cache sites are restricted to narrow dendritic distribution patterns easily accessible and sought out by cone collectors. At higher elevations, in Engelmann spruce forests, distribution of squirrels and caches is more widespread and unrestricted by suitable midden sites. In such forests a squirrel that loses most of its winter supply may be unable to obtain replacement cones from trees closer to the middens of its neighbors and may be obliged to fall back on lodgepole cones or other second-choice foods. Hence, the seriousness of cache loss in the spruce-fir forest may depend on the population density and territorial pattern of the squirrels in the local area.

Foresters and silviculturists have expressed the view that red squirrels are not adversely affected by cone gathering (Cox, 1911: 17; Baldwin, 1942:48). This belief is supported by the general observation that in good seed years squirrels cache far more cones than they need, and that excess cones a year or more old are commonly found in later years by cone collectors. They also note that squirrels survive bad cone years in substantial numbers and are on hand to exploit the next good crop that appears (Garman, 1955:9). I, too, have sometimes found excess cones cached in large numbers from previous years, but I have also found in other years and localities almost total exhaustion of cones from caches, even those a year or more old. The ability of red squirrels to survive cone crop failures is aided by their remarkable ability to locate and utilize such old "excess" cones (M. C. Smith, 1968:308) as well as their ability to subsist on dried fungi, cambium, buds, and other plant parts.

Halvorson (unpublished data) found evidence, however, that squirrels surviving a winter of cone crop failure have lower reproductive success than in years when a good crop of conifer seed is available. C. C. Smith (1968:53) stated that during the height of lactation a female would have been unable to extract and consume enough lodgepole pine seed to equal the amount of energy she obtained from Douglas-fir seed. Any inadequacy of lodgepole seed is caused by the time and energy required to strip the cones, not the total amount of seed available. It is perhaps possible that dependence on lodgepole seed would reduce the survival of young if other good food sources were not available, but squirrel populations seem able to maintain themselves in pure lodgepole forests in Colorado. Gathering of lodgepole cones from such caches would have, in any case, no noticeable effect on either survival or reproduction of squirrels in the Central Rockies, because in this region a high percentage of the available seed always remains in the serotinous cones on the branches. The circumstance most likely to affect squirrel reproduction would be loss of a large spruce cache after the remaining cones on the trees have opened, and in a year preceded by a year of cone crop failure.

Effects of Red Squirrels on Natural Forest Regeneration

The value of red squirrels as harvesters of conifer seed for tree planting must be weighed against the harm they do in cutting down cones that would otherwise shed their seeds and contribute to the replacement of the forest stand. The actual harm done is not easy to assess because only a tiny fraction of any year's seed crop, or often none at all, survives to produce mature trees. A large proportion of the seed crop is normally consumed by birds and mammals, without preventing, under natural conditions, the successful replacement of old forests with new. But under the impact of logging and the demand for rapid regeneration of the forest, the problem of seed loss becomes more acute.

A few intensive studies in the Pacific Northwest have clearly defined and quantified the large number of environmental factors that cut down the survival of Douglas-fir seeds and seedlings (Isaac, 1943; Garman, 1955; Gashwiler, 1967). Other studies on regeneration of ponderosa pine (Roe and Squillace, 1950; Foiles and Curtis, 1965) have described the infrequent and improbable circumstances required for the replacement of ponderosa. From Munger's (1930) vivid review essay on forest regeneration, it is clear that densities of seed fall in the tens or even hundreds of thousands of seeds per acre are required even in favorable years if nature is to have a good chance to achieve a satisfactory stocking of young trees within a few years. In view of the high seed fall required, it is important to know whether *Tamiasciurus* is capable of cutting such a high proportion of a good cone crop that enough seeds are not left to overcome the extremely high odds against survival.

In Table 6 the figures given for acres of forest of the various timber types are estimates of area required to provide half of the squirrel's needs, assuming that the seed fall is of the density specified under that tree species in the section on seed biomass. One may estimate the area of forest required under different conditions of seed fall by assuming any seed fall figures from Table 6, or any desired density of seed fall, and dividing it into the number of fresh whole seeds required, as given in Table 6. For example, the 1,500,000 Douglas-fir seeds reported for a virgin stand in British Columbia, divided into 400,000 seeds required, give 0.27 of an acre per squirrel. It is extremely unlikely that a population density as high as this could occur and consume all of such a bumper seed crop.

Squirrel densities as high as the figures in Tables 1-5 (from 0.8 to four acres per squirrel) are remarkably similar to squirrel population estimates reported by several workers (Grinnell and Storer, 1924:207; Seton, 1929, 4:119; Hatt, 1929:50; C. C. Smith, 1968:55). Indeed, they are probably no more than coincidence, for it is obvious that red squirrels do not consume all of the conifer seed produced. Forests with squirrel populations do regenerate successfully, and an abundance of cones is often left in the trees to open and shed seed, even in areas where many squirrels are actively harvesting cones. Nevertheless, these calculations and comparisons indicate that a high population of red squirrels may be capable of harvesting practically an entire crop of cones even in a good seed year. The fact that a fairly good seed fall does ocur now and then can be explained by two variables; on the one hand, bumper seed crops sometimes produce far more seed than shown in Tables 1-5, and on the other hand, squirrel population densities are often much lower than the estimates given above.

A great many shaky assumptions and narrowly based estimates entered into the calculations of seed production and food requirements presented in Tables 1-6. The variables range so widely that some of the averages could be in error by two or three times. Much better biomass and consumption data are needed, in particular, for years and forests of interest.

The theoretical deduction reached above, that red squirrels may be capable of harvesting an entire cone crop, is supported by a number of reports on the magnitude of depletion of cone crops in particular situations. In California, during a year when sugar pines were the only trees bearing cones, *Tamiasciurus douglasii* cut down 896 (54 per cent) of an original crop of 1656 sugar pine cones on 20 marked trees (Tevis, 1953:130). On the Stanislaus Experimental Forest in 1952 many ponderosa pines had more than 50 per cent of their cones cut; one tree that started with 926 cones lost 93 per cent (Schubert, 1953). In a study of cone losses on ponderosa pines on the Kootenai National Forest, Montana, Squillace (1953:2) found that 60 to 89 per cent of the cones produced in poor and fair seed years were cut by squirrels.

Garman (1955:9) reported that in 1948 at the Cowichan Lake Experiment Station, British Columbia, *Tamiasciurus* was very active in 24-inch Douglas-firs after two years of poor cone crops. Four trees that had an average crop of 3000 cones in July were remeasured in September; by that time the squirrels had taken 70 per cent of the cones. According to Garman: "A good crop may coincide with a low level of squirrel activity and its abundance be far more effective than another crop with similar potential but subject to intensive depredation."

In summary, I do not agree with the view of Grinnell and Storer (1924:207), also accepted by Hatt (1929:132), when they wrote: "It would appear that the squirrels merely harvest a surplus." The evidence that I can bring together on the subject seems to fit better the view of Isaac (1943:23): "The rodents and birds together practically clean up the seed in years of light or medium crops; apparently a surplus is left for germination only when there is a heavy crop." It may well be that the habit of producing a "bumper" seed crop only once in many years is an adaptive response to populations of squirrels and other seed eaters. This view was expressed more than 50 years ago by a forester (Cox, 1911:16), who wrote: "It is only by the production of occasional or periodic crops of seed that conditions are made favorable for the natural reproduction of the tree species."

This situation poses no threat to the regeneration of forests uncut by man, because delays of 10, 20, or even 40 years in the establishment of a stand of young trees in a forest opening or burn are normal features of plant succession and provide a beneficial degree of ecological diversity. When it is desirable to speed up the replacement of mature trees on logged or burned areas, the potential effects of red squirrels on natural seed dissemination should be taken into consideration.

SUMMARY

Red squirrels in the Rocky Mountain region are well adapted to the montane coniferous forests by their habit of storing cones in damp places for winter use. They are able to subsist on seed of any species of spruce, fir, or pine available. Cones of the Engelmann spruce and lodgepole pine are most important because of the wide distribution of these trees in the Rockies and the relative dependability of their seed crops.

In this semiarid region, cones are cached mainly in the large middens of cone litter that accumulate under trees where squirrels feed. Such shady sites provide the moisture required to preserve cones in the closed condition. A large midden commonly covers an area of forest floor 20 to 30 feet across and may contain as many as five to 10 bushels of cached cones. Amounts up to a bushel are often cached under water in shallow pools, bogs, or mountain streams.

Not all conifers provide adequate shade for cone storage. The Engelmann and blue spruces are ideal because of their dense lower branches, which often extend to the ground. The ponderosa pine, having fewer lower branches and a more open crown, rarely provides suitable cone-caching sites. Lodgepole pines, although providing poor cache sites, retain a seed supply in persistent unopened cones. Lodgepole cones are most heavily harvested when other conifers have suffered poor cone crops.

The kinds of middens and caching sites used vary with latitude and elevation. Middens are widely distributed on almost any kind of terrain in the spruce-fir forests of the Canadian Life-Zone. At lower elevations and latitudes middens and caches are restricted to the wettest, coolest sites, mainly under spruce stands along stream bottoms.

Cone caches of *Tamiasciurus* have been used by foresters and nurserymen as the main source of conifer seed in the western states since the beginning of large-scale reforestation. Many thousands of bushels of cones are harvested each year by raiding squirrel caches. Successful exploitation of this source of supply requires a good knowledge of the caching behavior of squirrels as well as the site requirements and cone-bearing characteristics of the various tree species in the area.

Published information on the seed productivity of five conifer species and the energy requirements of *Tamiasciurus* served as the basis for computing the seed requirements of the squirrel and its impact on the seed crop of the forest. These theoretical calculations indicate that a single male may require from eight to 24 bushels of cones to meet energy requirements for half a year. Depending on the tree species, such quantities of cones might be produced by eight-tenths of an acre to four acres of forest in a good seed year. Measurement and sampling of the cone litter in one midden of 602 cubic feet indicated that this midden could have been accumulated from the feeding activity of one squirrel in a period of 25 years.

Comparisons of reported seed productivity of various conifers with the seed requirements of *Tamiasciurus* suggest that these rodents may be capable of harvesting an entire cone crop, at least in poor or moderate seed years. Although red squirrels pose no threat in the long term to natural forest regeneration, they may harvest enough cones to delay for several years an adequate natural reseeding of burned or cutover forest land. Nevertheless, a good population of *Tamiasciurus* is an invaluable asset wherever man must collect seed for artificial seeding or planting of conifers.

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LATE CENOZOIC BATS (SUBFAMILY NYCTOPHYLINAE) FROM THE ANZA-BORREGO DESERT OF CALIFORNIA

BY

JOHN A. WHITE

In the summer of 1967 almost six tons of matrix were washed using modifications of the techniques originated by Hibbard (1949) and McKenna (1962). The matrix was obtained from 15 sites in that part of the Palm Spring Formation (Dibblee, 1954; Woodring, 1931; and Woodard, 1963) in the Fish Creek-Vallecito Creek areas in the Anza-Borrego Desert State Park, San Diego County, California. Washing was done under the auspices of the Los Angeles County Museum of Natural History and supervised by Theodore Downs and George J. Miller. Locality LACM 6583 proved to be especially rich in small vertebrate bones, and except for one specimen from locality LACM 6552, it is from this site that all specimens discussed herein were recovered.

I thank Theodore Downs for his continued support, advice, and encouragement. David E. Fortsch and George J. Miller critically read the manuscript. I am indebted to J. Knox Jones, Jr., and Richard G. Van Gelder for valuable suggestions, including the providing of clues to the literature on Recent *Antrozous*, and to Lisa A. Hansen, who made the illustrations. The cooperation of the personnel and management of the Anza-Borrego Desert State Park is gratefully acknowledged. This research was supported by the National Science Foundation under grant GB-5116. For permission to use comparative specimens I thank J. Knox Jones, Jr., Museum of Natural History, University of Kansas (KU), Richard G. Van Gelder, American Museum of Natural History (AMNH), and Edson Fichter, Idaho State University Museum (ISUM). Theodore Downs and J. R. Macdonald, Los Angeles County Museum of Natural History (LACM) made the fossil bat material available for study. Measurements of specimens were made with a Gaertner measuring microscope to the nearest micron. Symbols used here to identify individual teeth are as follows: in the upper half of the dentition individual teeth are identified with capital letters and numbers, thus I2 refers to the upper second incisor; teeth in the lower half of the dentition are identified with lower case letters and numbers, thus i3 refers to the third lower incisor; L or R indicates left or right side of the jaw.

The genus *Antrozous* is currently subdivided into two subgenera —*Antrozous* and *Bauerus* (Van Gelder, 1959). There are two species in the former (*A. pallidus* and *A. koopmani*), which are closely related (Orr and Silva Taboada, 1960), and only one species in *Bauerus (A. dubiaquercus).*

The nyctophiline bats from the early Pleistocene of the Anza-Borrego Desert are morphologically distinct from the two currently recognized subgenera in North America to the same extent that these two differ from one another. It is for this reason and on data presented subsequently in this paper, that a new genus is here established, and *Bauerus* is regarded as a genus distinct from *Antrozous.*

Anzanycteris, new genus

figures 1-5

Type species.—*Anzanycteris anzensis* (new species).

Diagnosis.—Mandible with i1 and i2 crowded together, i2 markedly reduced, with simple crown, and appressed into indentation near base of lower canine; angular process slender and projecting almost horizontally and posteriad; weakly developed cingulum on lingual edge of C-M3.

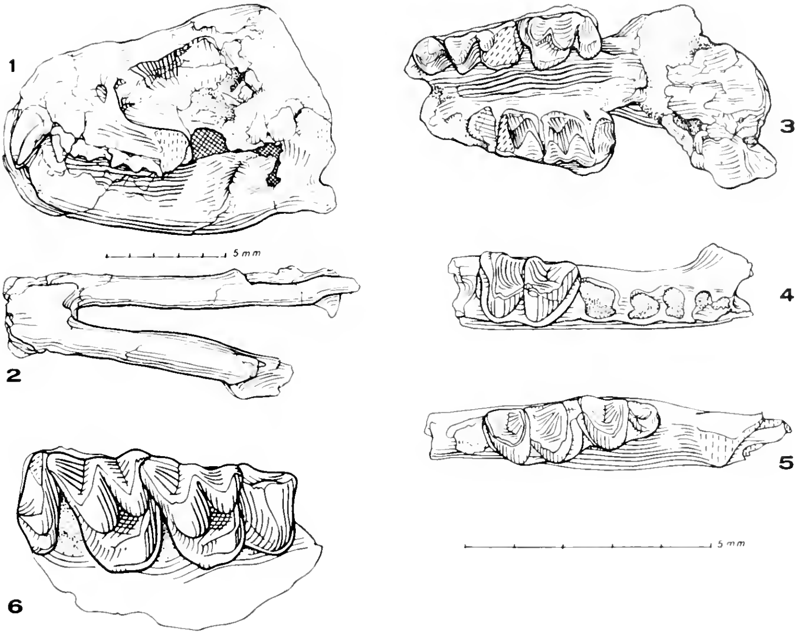
Anzanycteris anzensis, new species

Holotype.—LACM 19300, skull with jaws in articulation, with posterior part of cranium missing from the postglenoid process posteriad; skull crushed laterally; a left-lateral and two medial incisors missing from mandible; alveoli for missing incisors visible.

Diagnosis.—Same as for the genus.

Type locality and stratigraphy.—Locality LACM 6583, Upper Tapiado Wash, Badlands in Anza-Borrego Desert State Park, San Diego County, California; approximately 4850 feet (1478 meters), stratigraphically below top of Palm Spring Formation in the Diablo member of the formation; late Blancan (early Pleistocene) in age, Arroyo Seco Fauna.

Referred specimens.—Topotypes: LACM 19301, fragmentary cranium with incisors and right canine missing, RP4 and LM1 broken, posterior end of cranium missing, fragmentary right petrous portion of inner ear imbedded in the matrix near forward end of braincase; LACM 19303, maxillary fragment with RM2 and broken RM1; LACM 19304, fragmentary left dentary with m2 and broken m1 and m3; LACM 19305, fragmentary right dentary with m2, alveoli for c, p3, p4, and m1, and mental foramen; LACM 19306, fragmentary right dentary with m3, ventral part of masseteric fossa, and dentary foramen; LACM 19307, fragmentary left dentary with m2, m3, and ventral part of masseteric fossa; LACM 19309 fragmentary left dentary with m2 and m3; LACM 19515, Lm1 or Lm2; LACM 19516, fragmentary left dentary with m1 and broken p4 and m2. Locality LACM 6552: LACM 19308, fragmentary left dentary with m2 and m3.



Figs. 1-6. *Anzanycteris anzensis* new genus and species. 1, left lateral view of skull (holotype); 2, ventral view of mandibles (holotype); 3, ventral view of cranium (LACM 19301); 4, dorsal view of right mandibular fragment with m2 (LACM 19305); 5, dorsal view of left mandibular fragment with m2-m3 (LACM 19307); 6, cf. *Anzanycteris* sp., ventral view of right maxillary fragment with P4-M3 (LACM 19302). The short scale refers to Figs. 1-3, the long scale to Figs. 4-6.

Specimens used in comparisons.—Antrozous pallidus. California: San Bernardino County, KU 63546; Contra Costa County, KU 11373, 11374. Idaho: Idaho County, ISUM 7370; Bannock County, ISUM 7304, 7305. Kansas: Barber County, KU 11179, 76874. Nevada: Churchill County, KU 75891. *Bauerus dubiaquercus.* Nayarit: Tres Marias Islands, AMNH 180841.

Description.—Two incisors (i1 and i2) present, i2 markedly reduced, having a single crown and appressed into an indentation on the medial side near base of the lower canine; this indentation is bounded by the cingulum dorsally and antero-posteriorly. The lower cheekteeth are essentially as in *Antrozous* and *Bauerus.* The coronoid process is oriented almost vertically as in *Antrozous.* The angular process is slender and projects nearly horizontally and posteriorly and approximately parallel to its mate. The masseteric fossa is moderately deepened, the deepest portion antero-ventral. The shafts of the upper incisors are more than half as long as those of the canines, and the roots of the canines and incisors are pressed close together. The spaces between the upper molars are V-shaped, the apices of the V's projecting laterad. The contact between P4 and M1 is almost parallel, thus leaving no space between them, and the

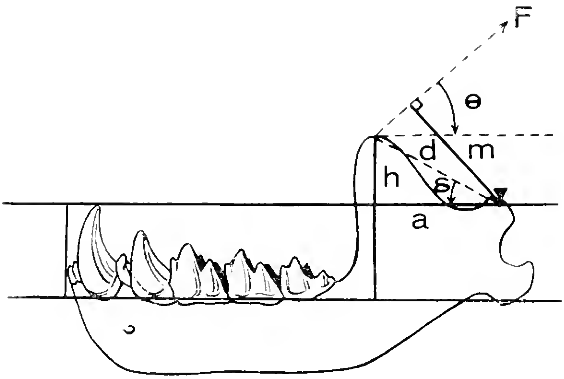


Fig. 7. Left lateral view of the mandible of *Bauerus dubiaquercus* (AMNH 180565), modified from Van Gelder, 1959: fig. 1A. See text for explanation of symbols pertaining to the jaw as a mandibular lever.

canine is closely appressed to the P4. There is no hypocone on M1 and M2, but a loph extends posteriad to the level of the metacone and almost parallel to the longitudinal axis of the palate. The M3 is essentially as in *Antrozous*, as is the infraorbital canal. The upper dentition is probably only slightly upturned as in *Antrozous*. The cingula on the upper cheekteeth are weakly developed when compared to those in *Antrozous* and *Bauerus*.

Comparisons.—In *Anzanycteris* the number of teeth is the same as in *Antrozous* and two less than in *Bauerus* (Van Gelder, 1959). In the latter genus, i3 is a tiny, button-like tooth crowded between i2 and the canine; it is appressed into an indentation on the medial side of the canine. In *Anzanycteris*, i2 is markedly smaller than i1 and is appressed into an indentation on

Table 1.—Comparisons of the structures in the four genera of the subfamily Nyctophilinae, using characters noted in Miller (1907:235).

Character	*Nyctophilus*	*Bauerus*	*Antrozous*	*Anzanycteris*
Number and character of lower incisors	3, unreduced	3, i3 markedly reduced	2, unreduced	2, i2 markedly reduced
Character of lower canine	Probably "normal"	With excavation	"Normal"	With excavation
Hypocone	Absent	Present	Absent	Absent
M3	More than half crown area of M1 M2	Less than half crown area of M1 M2	Less than half crown area of M1 M2	Less than half crown area of M1 M2
m3	Talonid unreduced	Talonid reduced	Talonid reduced	Talonid reduced
Rostrum	Slightly upturned	Slightly upturned	Slightly downturned	Probably slightly downturned

TABLE 2.—CRANIAL MEASUREMENTS (IN MILLIMETERS) OF *Anzanycteris anzensis* NEW GENUS AND SPECIES AND CF. *Anzanycteris* SP. ALL NUMBERS RELATE TO SPECIMENS IN THE LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY.

Measurement	No. 19300	No. 19301	No. 19304	No. 19306	No. 19302
Length of maxillary toothrow	5.480	5.882	--------	--------	5.315
Length of infraorbital canal	.349	--------	--------	--------	--------
Depth of mandible at m2	1.948	--------	--------	--------	--------
From posterior end of m3 to posterior end of angular process	5.707	--------	--------	--------	--------
APL at cingulum of C	1.585	1.629	--------	--------	--------
Width at cingulum of C	--------	1.436	--------	--------	--------
APL P4	1.065	1.369	--------	--------	.985
Width P4	--------	1.633	--------	--------	1.824
APL M1	1.847	1.882	--------	--------	1.907
Width M1	--------	1.987	--------	--------	2.294
APL M2	2.108	1.973	--------	--------	1.948
Width M2	--------	2.097	--------	--------	2.539
APL M3	.543	.664	--------	--------	.818
Width M3	--------	1.874	--------	--------	2.043
Width talonid of m1	--------	--------	1.023	--------	--------
APL m2	--------	--------	1.694	--------	--------
Width trigonid of m2	--------	--------	1.164	--------	--------
Width talonid of m2	--------	--------	1.288	--------	--------
APL m3	--------	--------	--------	1.571	--------
Width trigonid of m3	--------	--------	--------	1.032	--------
Width talonid of m3	--------	--------	.448	.447	--------

the medial side near the base of the canine, whereas in *Antrozous* i1 and i2 are subequal in size and the canine has no indentation.

The upper toothrow in *Anzanycteris*, as in *Antrozous*, slopes slightly anterodorsad, whereas in *Bauerus* this upturning of the tooth row is more pronounced or more bulldog-like, and the sagittal crest is far more pronounced.

Because the holotype of *Anzanycteris* has undergone some distortion, presumably during preservation, the degree of upturning of the upper toothrow was determined by assuming the mandibles to move in articulation in a simple, hinge-like, up-and-down motion. The condyloid process has a configuration not unlike that of a canid and the postglenoid process is well developed. Assuming that the latter characteristics of the mandible would restrict it to a minimal amount of lateral motion, it follows that the temporal muscles would exert the principal force in adducting the mandible while the masseter and pterygoid musculature would function primarily in positioning the mandible with respect to the glenoid fossa.

Using a modification of a technique devised by Ostrom (1966), the center of the glenoid fossa was established as a fulcrum and the coronoid process above the level of the fulcrum as a lever. The mandible was then occluded and the center of origin of the temporal muscles was estimated. A line was then drawn from the tip of the coronoid process to the center of origin of the temporal muscles. Using these data the moment arm of the applied force

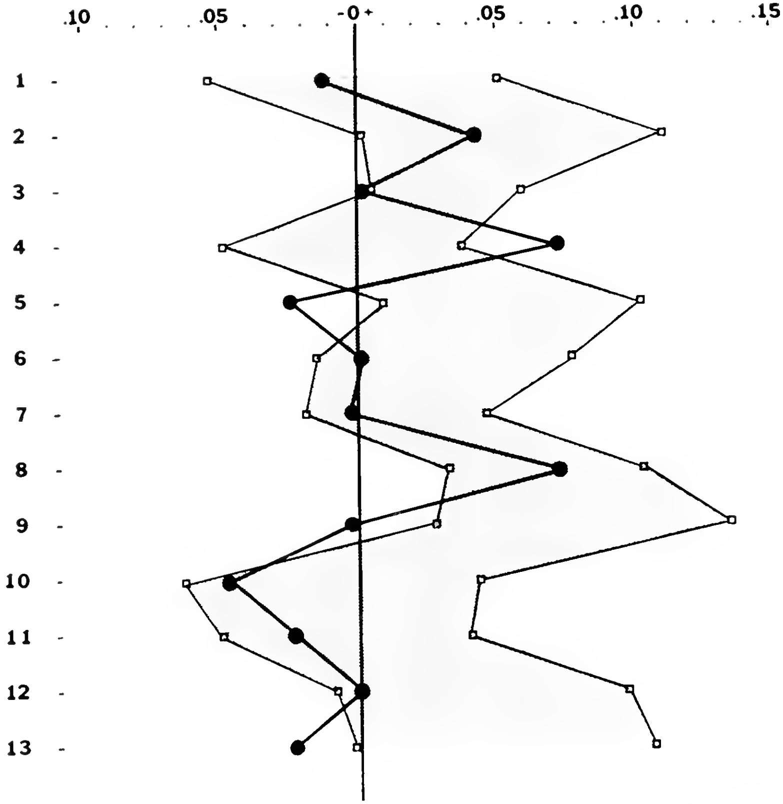


FIG. 8. Ratio diagrams modified from Simpson *et al.* (1960), comparing several cranial dimensions of the largest and smallest specimens of *Antrozous* (open squares) and *Bauerus* (solid circles) with *Anzanycteris* (the line at zero). The logs of the measurements of *Anzanycteris* are assumed to be zero, while the differences between the log of the measurements in the latter genus (standard) and genera being compared are plotted on the positive (+) or negative (—) sides of the zero line. The dimensions are as follows: 1 length of maxillary tooth row; 2 posterior end of m3 to posterior end of angular process; 3 APL C at cingulum; 4 W C at cingulum; 5 APL P4; 6 APL M1; 7 APL M2; 8 W talonid m1; 9 APL m2; 10 W trigonid m2; 11 W talonid m2; 12 APL m3; 13 W trigonid m3.

(by the temporal muscles) was calculated for the holotype and for all comparative specimens, and expressed as percentages of jaw lengths to eliminate size as a factor in comparisons. To quote from Ostrom (1966: 302-303): "It is not possible to measure this moment arm directly with any precision when the jaw is in articulation and fully adducted (the critical position), it must be calculated from other parameters taken from the skull and jaws." See Figure 7.

Ostrom continued: "For example: the moment arm of the applied force is a function of 1) the height (h) of the articulation, 2) the lever distance (a) between the center of the articulation and the base of the coronoid process [determined by the level of the center of articulation, above or below the level of the toothrow] and 3) the attitude (angle θ) of the line of action of the applied force (F) relative to the fulcrum. . . . the moment arm of the applied force is calculated by $m = (\theta + \delta)$ d where m equals the length of the moment arm of the applied force, θ the angle between the applied force and the lever axis, δ the angle between the diagonal distance (d) from the coronoid apex to the center of the glenoid fossa and the lever axis." The length of the moment arm of the applied force is in direct proportion to the force applied to the mandible, and as such is a measure of the force itself.

The moment arm of the applied force (m) and the angle θ are greater in *Bauerus* than in *Antrozous* and *Anzanycteris*. This is thought to be related to the greater degree of the "bulldog" effect in *Bauerus* than in the other two genera.

Only the base of the coronoid process is known for *Anzanycteris*, but the slope of the anterior and posterior margins of the process are visible and match favorably the condition in *Antrozous*, but not *Bauerus*. The measurements of the moment arms expressed in percentages of mandible lengths are as follows: *Antrozous*—KU 11374, 29; KU 11373, 27; KU 63546, 28; KU 94363, 28; KU 94362, 26; KU 75891, 27; KU 76874, 25; KU 11179, 24; ISUM 7305, 26; AMNH 2159, 28 (calculated from Van Gelder, 1959: fig. 1B); *Bauerus*—AMNH 180841, 32; AMNH 180565, 31 (calculated from Van Gelder, *loc. cit.*: fig. 1A); *Anzanycteris*—LACM 19300: 22 (if θ is assumed to be 20 degrees) or 26 (if θ is assumed to be 50 degrees).

It can be inferred from Table 1 that *Nyctophilus* and *Bauerus* represent an adaptive type with a bulldog-like upturned rostrum as opposed to the condition in *Anzanycteris* and *Antrozous*. The length of the upper incisor relative to the length of the upper canine seems to vary inversely with the degree of upturning of the rostrum.

The bulldog-like upturning of the cheekteeth in *Bauerus* versus the downturning in *Antrozous* and *Anzanycteris* may be related to feeding habits. *Antrozous* is known to feed at times almost exclusively on flightless insects (Orr 1954). Although the feeding habits in *Bauerus* are unknown, it is possible that food is obtained exclusively in flight, the "bulldog" effect enabling a stronger hold on larger insects than *Antrozous* and presumably *Anzanycteris*.

The three genera are almost equally morphologically distinct from one another (Fig. 8). Study of the reproductive systems in the living forms of the subfamily Nyctophilinae probably would shed further light on their relationships.

The number and character of the lower incisors and the related character of the lower canine seem to provide clues to the diversification within the Nyctophilinae. *Nyctophilus* seems to be the most primitive genus in that it has three fully developed lower incisors, probably no indentation on the lower canine, relatively large M3, and an unreduced talonid on m3. From this primitive condition a morphological series develops, proceeding from *Nyctophilus* to *Bauerus* to *Antrozous* to *Anzanycteris*. Since *Anzanycteris* is known to occur only in the early Pleistocene, it is probable this diversification occurred sometime in the early or middle Tertiary.

Iguana, Hypolagus regalis, Perognathus, Geomys, Neotoma, and a small *Sigmodon* were found at approximately the same level and associated with *Anzanycteris*. A tropical or subtropical savannah is suggested by this faunal assemblage.

cf. **Anzanycteris** sp.

figure 6

LACM 19302 is a right maxillary fragment with P4-M3, and is not readily referable to any known genus. Here it is tentatively referred to *Anzanycteris* for the following reasons: (1) anterior to P4, the posterior and medial portion of the alveolus of the canine is visible and there is no evidence for the presence of a small premolar; (2) in all cheekteeth except P4, the dimensions are essentially as in *Anzanycteris*, P4 being markedly shorter antero-posteriorly (Table 2). Also the cingulum in M1 and M2 forms a prominence seen from an occlusal view, which projects from the center of each tooth, mediad.

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A REVIEW OF THE AFRICAN MICE OF THE GENUS DESMODILLISCUS WETTSTEIN, 1916

BY

HENRY W. SETZER

Wettstein proposed the generic name *Desmodilliscus* in 1916, with the type species, *D. braueri*, based on a specimen from the road between Um Ramad and Nubbaka, south of El Obeid, in the Sudan. In 1920, Thomas and Hinton described a second species, *D. buchanani*, from near Kano, Nigeria. Ellerman (1941) regarded *braueri* and *buchanani* as synonymous at the specific level, but retained *buchanani* as a distinct subspecies. Few specimens have been recorded since the original descriptions of *braueri* and *buchanani*, although Dekeyser (1955:220) reported material from Niger, Mali, and western Chad; these specimens have not been seen by me. Also, a recent paper by Heim de Balsac (1967) recorded some additional interesting localities based on specimens now housed at the Museum National de Histoire Naturelle in Paris.

The majority of the specimens mentioned above are from owl pellets. It should be noted further that not a single individual here reported was taken in a trap; all were obtained at night by hand or in an insect sweeping net. The fact that no specimens were trapped is rather significant in that animals of even smaller size *(Mus minutoides)* were taken in Museum Special traps in the same areas where *Desmodilliscus* was caught by hand.

Other than the above-mentioned new cranial material, which I have not seen, the specimens of *Desmodilliscus braueri* available for study were pitifully few until 1966, when field teams of the Smithsonian Institution African Mammal Project obtained material from Senegal and Nigeria. Additional specimens were obtained in 1967 from Mauritania and Nigeria. As a result of the acquisition of this new material, it is felt that enough specimens now exist to warrant an attempt to define sexual as well as geographic variation in this genus. All measurements are in millimeters and color terms are from Ridgway (1912).

Tooth wear seems to be rather consistent in the populations studied, and it has been possible to sort out five age classes based on this criterion. Age class I consists of animals with unworn or relatively unworn teeth, but with M3 in place; individuals younger than this were not considered. The remaining four age classes were arbitrarily selected based on the degree of closure of various enamel lakes with each other. Age classes II and III are relatively close, the last loph in M1 being contiguous in class III, but separate in class II. Class IV was determined by the closure of the enamel lakes in M2, whereas age class V was characterized by the absence of cusps but with all enamel lakes complete. No individuals showing extreme old age have been seen. The degree of wear for the various age classes is illustrated in Figure 1.

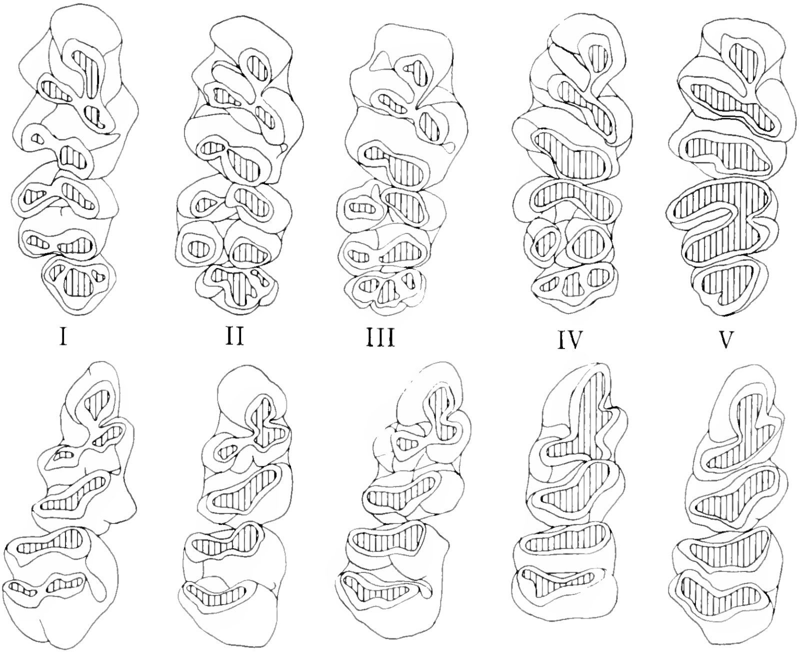

FIG. 1. Crown patterns of upper and lower molar teeth of five age classes of *Desmodilliscus braueri*. Top figures are right upper molars; lower figures are right lower molars.

A small sample of comparably aged males and females from the vicinity of Aleg, Mauritania, was tested for sexual variation. In only two characters, greatest breadth of rostrum and greatest breadth across zygomatic arches, of the 16 tested was any significance noted. Thus, in future studies it may be possible to pool males and females of comparable ages to enlarge samples for statistical purposes.

Further statistical testing between populations was attempted but sample sizes were so small that realistic interpretation of the results was not reasonable. However, certain morphological features of the Senegalese and Mauritanian specimens indicate the presence of an undescribed subspecies of this small gerbil, which is named beyond, followed by a synopsis of the other two subspecies of *D. braueri*.

Desmodilliscus braueri fuscus, new subspecies

Holotype.—Adult male, skin and skull, U.S. National Museum no. 378291, from Richard Toll, River Region, Senegal; obtained on March 18, 1966, by Richard M. Davis, original no. 2752.

Diagnosis.—Upper parts Olive-Brown in general appearance but most hairs tipped with Tawny-Olive; pure color (Tawny-Olive) edging dorsal Olive-Brown pattern; dorsal pattern generally strip-shaped, but extending from between the eyes over head and neck, dropping over shoulders then over back, tapering to a point at the base of the tail (if the skin were to be laid flat a cross-shaped pattern would be visible); underparts, dorsal surfaces of front and hind feet, minute supraorbital and postauricular spots pure white; tail sparsely covered with short, white hairs; skull small and delicate; auditory bullae extremely inflated; braincase broad and somewhat inflated; rostrum relatively short; and anterior palatine foramina long and wide open.

Comparisons.—When compared with a specimen of *Desmodilliscus braueri buchanani* of comparable age from Panisau (=Farniso), Northern Region, Nigeria, individuals of *D. b. fuscus* are generally darker and slightly smaller in external measurements. The rostrum is generally broader, the breadth of the braincase is less, the zygomatic arches are more nearly parallel sided, the anterior palatine foramina are longer, and the auditory bullae are slightly less inflated.

Specimens of *Desmodilliscus braueri braueri* have been studied at the British Museum (Natural History) but unfortunately these have not been compared directly with specimens of *D. b. fuscus*. However, because the range of *D. b. buchanani* lies between the ranges of *D. b. braueri* and *D. b. fuscus* it may be assumed that these latter two kinds differ from each other.

Measurements.—External and cranial measurements of the holotype are as follows: total length, 97; length of tail, 43; length of hind foot, 15; length of ear, 8; greatest length of skull, 21.2; least interorbital breadth, 3.8; condyloincisive length, 18.8; breadth across zygomatic arches, 12.2; greatest breadth of braincase, 10.5; greatest length of nasals, 6.0; greatest breadth of rostrum, 2.5; greatest length of audital portion of auditory bulla, 9.4; greatest breadth across auditory bullae, 12.6; length of anterior palatine foramina, 3.5; length of posterior palatine foramina, 2.5; crown length of maxillary toothrow, 2.9.

Average and extreme measurements for six males from Richard Toll, River Region, Senegal, and six females from Ranerou, River Region, Senegal, are, respectively: total length, 99.5 (95-111), 102.8 (96-111); length of tail, 41.3 (39-43), 40.0 (38-45); length of hind foot, 15.0 (15), 14.6 (14-15); length of ear from notch, 8.7 (8-9), 8.3 (8-9); greatest length of skull, 21.5 (21.2-21.9), 20.9 (20.0-22.3); least interorbital breadth, 3.8 (3.5-4.0), 3.7 (3.5-3.9); condyloincisive length, 18.9 (18.5-19.3), 18.4 (17.6-19.1); greatest breadth across zygomatic arches, 12.5 (12.0-13.7), 12.3 (11.6-13.0); greatest breadth of braincase, 10.5

(10.1-10.7), 10.4 (9.9-10.7); greatest length of nasals, 6.9 (6.0-7.6), 7.0 (6.5-8.1); greatest breadth of rostrum, 2.6 (2.3-3.0), 2.4 (2.2-2.6); greatest length of audital portion of auditory bulla, 9.2 (8.7-9.5), 8.9 (8.4-9.6); greatest breadth across auditory bullae, 12.5 (12.1-12.8), 12.3 (11.7-12.8); length of anterior palatine foramina, 3.6 (3.2-3.8), 3.4 (3.0-3.7); length of posterior palatine foramina, 2.4 (2.3-2.5), 2.4 (2.2-2.6); crown length of maxillary toothrow, 3.0 (2.9-3.3), 2.9 (2.7-3.0).

Remarks.—The influence of the Senegal and the Niger rivers on the distribution of these small rodents is not at all clear. It appears that the Mauritanian and Senegalese populations of *Desmodilliscus* have not been long separated by the Senegal River. Assuming a center of dispersal in northern Nigeria, it is possible that the westward dispersion was north of the Niger and then southwestward and westward around the headwaters of the Senegal River. If this assumption is accepted, then we would expect to find markedly closer relationship between populations on either side of the Senegal River than would be expected between these populations and a population nearer the center of dispersal. This is actually what has been observed.

Heim de Balsac (1967:162) cited *Desmodilliscus* from Dori, Upper Volta, which lies south of the great bend of the Niger River. If this is a valid locality record, it is of extreme interest inasmuch as all other distributional records for this genus lie to the east, north, and west of the Niger. The zoogeographic implications of this distribution are difficult to explain. It can only be hoped that additional material can be obtained from the region of the great bend of the Niger to enable us to furnish some explanation of this rather odd pattern.

The habitat of *Desmodilliscus* appears to be rather level hard clay with small bushes and trees scattered throughout on small tussocks. Burrows, without any appreciable amount of dirt around or in front of them, were found under the scattered bushes (Fig. 2).

Other small mammals taken in this same habitat were *Jaculus, Taterillus,* and *Gerbillus* (subgenus *Dipodillus*).

Specimens examined, 72.—SENEGAL: Ranerou, River Region, 15° 18′ N, 13° 58′ W, 13; 5 km. S Bakel, River Region, 14° 51′ N, 12° 28′ W, 1; Linguere, Diourbel Region, 15° 24′ N, 15° 07′ W, 5; Ogo, 13 km. SW Matam, River Region, 15° 33′ N, 13° 17′ W, 5; Podor, River Region, 16° 40′ N, 14° 57′ W, 1; Richard Toll, River Region, 16° 28′ N, 15° 41′ W, 12. MAURITANIA: 3 km. S Aleg, 17° 02′ N, 13° 55′ W, 32; 5 km. S Aleg, 17° 02′ N, 13° 55′ W, 1; 6.2 km. S Aleg, 17° 02′ N, 13° 55′ W, 1; 26.7 km. S Aleg, 16° 48′ N, 13° 53′ W, 1.

Desmodilliscus braueri braueri Wettstein, 1916

Desmodilliscus braueri Wettstein, Anz. k. Akad. Wiss., Wien, 53 (14): 153, 1916; type locality, on the road between Um Ramad and Nubbaka, S of El Obeid, Sudan.

Measurements.—An adult male from 75 mi. W El Obeid measures as follows: total length, 102; length of tail, 45; length of hind foot, 15; greatest length of skull, 21.8; least interorbital breadth, 4.0; condyloincisive length, 18.5; greatest length of nasals, 7.7; greatest breadth of rostrum, 2.6; greatest length of audital portion of auditory bulla, 9.3; crown length of maxillary toothrow, 2.9.

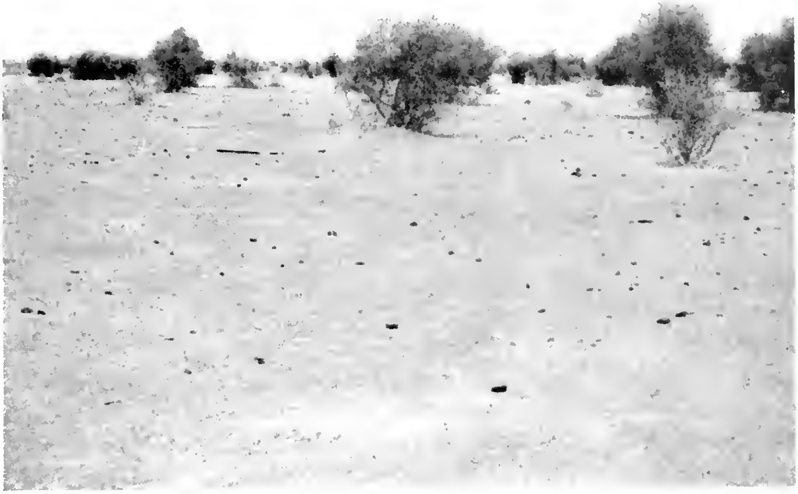

FIG. 2. Typical habitat of *Desmodilliscus braueri* at a site 3 km. S Aleg, Mauritania.

Remarks.—It must be assumed that the two specimens examined represent the nominate subspecies inasmuch as they come from relatively near the type locality. The type specimen of *D. braueri* has not been examined.

Specimens examined, 2, both in British Museum (Natural History).—SUDAN: 75 mi. W El Obeid, 1; 140 mi. E El Fasher, 1.

Desmodilliscus braueri buchanani Thomas and Hinton, 1920

Desmodilliscus buchanani Thomas and Hinton, Novitates Zool., 27:317, 15 June 1920; type locality, Farniso (=Panisau), near Kano, Nigeria.

Measurements.—Averages and extremes for seven males from Karaduwa, Northern Region, Nigeria, and measurements for a single female from 12 mi. N Sokoto, Northern Region, Nigeria, are, respectively: total length, 97.4 (95-101), 100; length of tail, 37.4 (36-39), 40; length of hind foot, 15.6 (15-16), 15; length of ear, 9.3 (9-10), 8; greatest length of skull, 21.1 (20.6-21.9), 21.0; least interorbital breadth, 3.7 (3.6-3.8), 3.4; condyloincisive length, 18.5 (18.1-19.0), 18.4; greatest breadth across zygomatic arches, 12.1 (12.0-12.2), 11.8; greatest breadth of braincase, 10.3 (10.1-10.5), 10.4; greatest length of nasals, 6.4 (6.0-6.9), 7.1; greatest breadth of rostrum, 2.4 (2.2-2.5), 2.5; greatest length of audital portion of auditory bulla, 9.2 (8.9-9.6), 9.1; greatest breadth across auditory bullae, 12.3 (12.0-12.7), 12.1; length of anterior palatine foramina, 3.2 (3.1-3.5), 3.0; length of posterior palatine foramina, 2.5 (2.2-2.7), 2.5; crown length of maxillary toothrow, 3.1 (3.0-3.2), 2.9.

Remarks.—Specimens from Sokoto and Panisau have been compared with the type specimen of *D. b. buchanani* in the British Museum (Natural History) and found to agree in detail both in color and cranial features. It is apparent, from the few specimens available, that *D. b. buchanani* is darker in coloration and somewhat larger in most cranial measurements than other subspecies.

Specimens examined, 23.—NIGERIA: Panisau, Northern Region, 12° 05′ N, 8° 32′ E, 3 (1 British Museum); Karaduwa, Northern Region, 12° 19′ N, 7° 41′ E, 11; Tangaza, Northern Region, 13° 08′ N, 5° 09′ E, 5. NIGER: Tegguida, N'tisem, W of Air, 1.

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AN ANALYSIS OF PATTERNS OF VARIATION IN SOME REPRESENTATIVE MAMMALIA. PART II. STUDIES ON THE NATURE AND CORRELATION OF MEASURES OF VARIATION

BY

CHARLES A. LONG

The coefficient of variation (CV) has been calculated for many mammalian measurements, and is usually used as a measure of individual variability. Understanding of variability is of importance in understanding evolution and in establishing classifications. Terms such as "conservatism," "genetic load," "evolutionary plasticity," and others have limited value until the complex and subtle contributions to variability are better understood. Therefore, a sample of 96 fairly representative species of mammals was obtained and analyzed to determine any apparent patterns of variability. Coefficients of variability were obtained for the available measurements of total length, length of cranium, length of maxillary toothrow, and cranial, zygomatic, and interorbital breadths. The raw CV's, mean dimensions, and standard deviations of the mean were tabulated in a preliminary paper (Long, 1968). The selection of data was discussed in that paper, and it is here sufficient to note that CV's were not taken in any order, but generally include values available from my own work, easily derived from published raw data or statistics, and known to me in the literature. A few values were obtained deliberately to make the sample as truly representative of mammalian orders as possible (e.g., whales and duck-billed platypus). I doubt that such choosing effected significant bias. The measurements likewise were chosen generally on the basis of availability, and it is noted that important measurements on teeth and other structures related to fitness and niche exploitation are not so abundant as the measurements used standardly by taxonomists, and utilized herein.

Methods and acknowledgments are listed in Long (1968). Some computations were performed by the University of Illinois SSUPAC computer. Some of the patterns of variation observed are statistically significant, in spite of numerous problems involved in sampling, whereas other results are inconclusive. The latter, however, have value as hypotheses that warrant further testing.

The problems discussed here generally are correlations of taxonomic position and amount of variation, the effect of size on variation, the intercorrelation of the variations of several measurements, the apparent influence of ecological niche, or function, on some variations, the degree of preponderance of high variation in either sex or in wild or domestic species, and the nature of frequency distributions of CV values for taxonomic categories. It is emphasized that the data utilized are *measurements of variation* that *estimate* amounts of variability, and are not morphometric values.

RESULTS AND CONCLUSIONS

Taxonomy, Variation, and Their Correlation

The class Mammalia has a good fossil record. Some orders studied, however, have problematical affinities. Nevertheless, arrangement of numerous rodents and carnivores juxtaposed between primitive monotremes, marsupials, insectivores, and bats on the one hand and advanced ungulates on the other, provides a meaningful analysis of "phylogenetic" variation in contemporaneous (Recent) taxa. The horizontal arrangement of Recent taxa (see Long, 1968) permits general comparison of taxa of different times of origin. For example, the rodents, having more recently radiated into various ecological niches than have the insectivores, may show different characters of variability from those of the insectivores. Biological factors, such as adaptation to flight in bats, may influence some examples of variation reported herein, but these may be indirectly related to phylogeny. Other causes of variation may cloud the comparisons, but significant correlations between taxonomic position and amount of variation were obtained (see below). They may result mainly from size or jointly from size and taxonomic position.

In animals of increased size, the CV measure of variability would be lowered unless the standard deviation had increased in step with the mean (Long and Frank, 1968, and others). A general rule of higher variation in larger mammals, discussed beyond, is opposite that which would be predicted. Large size tends to appear in more modern and more variable groups. It is well known that mammals generally have increased in size throughout their history, although small species are numerous.

Where several samples (e.g., sexes, subspecies) in a wild (nondomestic) species were available, mean CV's were determined; the available CV's of the six measurements were then correlated with taxonomic position scaled from one (the platypus) to 60 *(Rangifer)*, and from four to 60 for wild placentals (see Long, 1968).

Rather high CV's were obtained in the primitive Monotremata and Marsupialia, although more data are necessary for firm conclusions. Even so, in all wild species some positive correlations between taxonomic position and the amount of the CV were obtained, represented with significance levels showing the r's different from zero: position and skull length, 0.245, 0.1 level; maxillary toothrow, 0.394, 0.01; total length, 0.532, 0.01; cranial breadth, 0.186; zygomatic breadth, 0.041; interorbital breadth, 0.239.

When only wild placentals are considered, there are stronger correlations: position and skull length, 0.430, 0.001 level; maxillary toothrow, 0.396, 0.02; total length, 0.371, 0.05; cranial breadth, 0.186; zygomatic breadth, 0.107; interorbital breadth, 0.290, 0.01.

The significant correlations certainly reveal that variation is generally increased in some measurements in advanced placentals. A similar phenomenon was observed in variation of eggs in passerine and non-passerine birds by Fisher (1937). However, in the few primitive non-placentals sampled, variation appears higher than average placental variation. Also exceptional is the low variation seen in some of the higher placentals (e.g., *Peromyscus truei*, *Enhydra*, *Ovibos*).

One correlation that was surprisingly low is between taxonomic position and variation of zygomatic breadth of placentals or of all wild species. In this case phylogenetic effect seems unlikely. There is increased complexity of the masticatory apparatus in many advanced mammals (e.g., microtines, badger, horse), and the zygomatic arches are used more or less for muscle attachment. It is pertinent that in some primitive mammals the zygomata are incomplete (e.g., *Sorex*), and in fact appear in mammals as a consequence of related enlargement of ancestral reptilian fenestrae of the skull (see Romer, 1962).

In a different analysis of the data where *Eumetopias* and the wild horses were not included, and the whales were placed between Pinnipedia and Proboscidia, the r of cranial breadth CV's and taxonomic position was also significant, at the 0.1 level only. In yet another analysis where *Eumetopias* and all horses (even the domestic horse and ass) were included and the whales were placed between rodents and carnivores, the r's for taxonomic position and maxillary breadth (0.459) or cranial breadth (0.369) were increased.

Four analyses were made to determine the relative importance of phylogeny or size. In the first, the sexually dimorphic kinds are analyzed. The sexes have endured the same environments for the

TABLE 1.—COMPARISONS OF SIGNIFICANT SEXUAL VARIATIONS IN RELATION TO MEAN SIZE IN SOME WILD AND DOMESTICATED MAMMALS. VALUES REPRESENT THE FREQUENCIES OF MAMMALS FOR WHICH THE SEXES DIFFER SIGNIFICANTLY IN CV VALUE.

	Wild mammals		Domestic mammals	
Measurement	Males equal or larger	Females larger	Males equal or larger	Females larger
Skull length	Males more variable 5	Males more variable 0	Males more variable 4	Males more variable 1
	Females more variable 2	Females more variable 1	Females more variable 0	Females more variable 0
Maxillary toothrow	Males more variable 2	Males more variable 1	Males more variable 0	Males more variable 0
	Females more variable 1	Females more variable 1	Females more variable 0	Females more variable 0
Total length	Males more variable 0	Males more variable 0	Males more variable 1	Males more variable 1
	Females more variable 1	Females more variable 1	Females more variable 0	Females more variable 0
Cranial breadth	Males more variable 1	Males more variable 1	Males more variable 2	Males more variable 0
	Females more variable 0	Females more variable 0	Females more variable 0	Females more variable 0
Zygomatic breadth	Males more variable 0	Males more variable 0	Males more variable 1	Males more variable 0
	Females more variable 0	Females more variable 1	Females more variable 0	Females more variable 0
Interorbital breadth	Males more variable 1	Males more variable 1	Males more variable 0	Males more variable 0
	Females more variable 1	Females more variable 0	Females more variable 0	Females more variable 0

same time. Probably the genomes of the sexes do not differ greatly, such as those, say, between families. No evidence was found in this analysis that mean size is an important factor in effecting the general magnitude of CV values (see Table 1).

In the second analysis, comparisons of close relatives were made. Of *Sorex*, *Myotis*, *Peromyscus truei*, *Phyllotis*, *Clethrionomys*, *Martes*, and *Rangifer* (all of which had comparable intergeneric homogeneous samples), only *Rangifer* and *Peromyscus truei* showed any indication of trends in size. *Rangifer* tended to vary more when larger, and *P. truei* tended to the opposite (small samples, less than 16 specimens, were not used).

The third analysis involved matching some similarly sized mammals of different taxonomic advancement to see if the CV's varied independent of mean size. *Sorex* and *Myotis* hardly differed; *P. truei, Clethrionomys*, and *Blarina brevicauda* were about the same in CV amounts; *Mephitis* and *Lynx* were similar, but they exceeded *Taxidea*. Both whales had high variation. *Lepus flavigularis* showed less variation than *Ateles*, which is probably more advanced.

The final analysis involved the most mammals. By classifying them as minute, small, medium, medium-large, and large, it is apparent that mean variabilities increase with size. In Table 2, the minute mammals all show low variation. None of their orders, however, is far advanced. In the small category, some variations were significantly higher. Medium-sized and larger mammals show increasingly higher mean variations, and reveal some extremely high values in the largest wild mammals. Apparently the mean increase of variation with increased size is paralleled by a slight increase of variance of the CV's in each size group. Some of these means differed significantly (0.05 level) from one another, especially where the size discrepancies were greatest. The variances were seldom significantly different (using a one-sided *F*-test to show that the variance was larger in large mammals). (The ratio of variances of medium to minute was significant; the ratio of variances of small to minute was perhaps significant, at 0.1 level only, as was large to small.)

Scrutiny of Table 2 reveals three problems in determining the effect of phylogeny on variability. First, the samples are small for several size classes. Second, the primitive, small species are of only three genera, in two closely related orders, and the advanced, larger species are likewise closely related. Third, phylogeny is expressed at least as well from left to right as vertically. These facts defeat the purpose of a two-factor analysis of variance.

In Table 3, the species in Table 2 are arbitrarily lumped where necessary to form a table of five by five values (mean CV's) for a one factor analysis of variance, to determine any effect of size. None of the column variances is significantly different from another (but, of course, the degrees of freedom are only four). The mean CV for each column can be seen to vary directly with size. The ratio of mean square among size-classes to residual mean square is 3.53 with four and 20 degrees of freedom. The ratio is significant at the 0.05

TABLE 2.—List of CV values for cranial length of adequate samples of wild species selected from Long's (1968) compilation. These are categorized according to size as follows: minute (< 20 mm), small (< 30 mm), medium (< 100 mm), medium-large (< 200 mm), large (> 200 mm, except whales), and huge (*Physeter* and *Balaenoptera*). In the vertical columns, primitive taxa are arranged above advanced taxa.

Minute	Small	Medium	Medium-large	Large	Huge
Sorex	*Sorex*	*Tupaia*	*Canis*	*Ursus*	*Physeter*
1.98	2.48	2.24	5.80	4.39	18.97
1.35	*Blarina*	*Alouatta*	*Taxidea*	*Hydrurga*	*Balaenoptera*
2.64	2.30	2.68	2.49	2.88	7.99
Tadarida	*Macrotus*	*Ateles*	*Lutra*	*Odocoileus*	$\bar{X}$= 13.48
					N= 2
1.70	1.72	3.50	4.83	4.55	
Myotis	*Dipodomys*	*Ochotona*	*Enhydra*	*Rangifer*	
1.68	1.59	4.12	2.45	4.38	
2.30	1.76	*Sylvilagus*	*Lynx*	*Ovibos*	
$\bar{X}$= 1.94	*Peromyscus*	3.24	3.45	2.80	
N= 6	2.05	*Lepus*	$\bar{X}$= 3.80	$\bar{X}$= 3.80	
S^2= 0.22	*Phyllotis*	2.21	N= 5	N= 5	
	4.05	*Spermophilus*	S^2= 2.18	S^2= 0.77	
	3.22	3.01			
	4.02	*Thomomys*			
	3.43	4.17			
	Microtus	*Ondatra*			
	4.82	3.92			
	2.58	*Rattus*			
	Clethrionomys	5.91			
	2.50	*Martes*			
	2.95	2.76			
	Zapus	*Mephitis*			
	2.66	3.66			
	$\bar{X}$= 2.81	$\bar{X}$= 3.45			
	N=15	N=12			
	S^2= 0.89	S^2= 1.05			

level, showing a definite effect of size. But an effect of phylogeny is not precluded. In Table 3, as in Table 2, the rows express phylogeny at least as well as the columns. For example, in the first column, compare three species of *Sorex* and two bats with a bat, rodents, carnivores, and the musk ox in the lowest row.

Intercorrelation

Intercorrelation of the *measures* of variation of the morphometric values yielded some positive correlations. Including the non-placentals with the placentals, the levels of significance for the *r*'s that significantly differ from zero are as follows: skull length and total length, 0.01 level, and interorbital breadth, 0.01; maxillary toothrow and zygomatic breadth, 0.1; total length and interorbital breadth, 0.01; cranial breadth and maxillary toothrow, 0.01, and zygomatic breadth, 0.02; zygomatic breadth and interorbital breadth, 0.05.

Considering only the placentals, the significant correlations are as follows: skull length and total length, 0.01 level, and interorbital breadth, 0.001; maxillary toothrow and cranial breadth, 0.01, and zygomatic breadth, 0.05; total length and interorbital breadth, 0.02; cranial breadth and zygomatic breadth, 0.02; zygomatic breadth and interorbital breadth, 0.05. Placentals in general show a high amount of correlation of measures of amounts of variation.

Adaptive Variability

Sympatric differentiation of phenotypes in a population theoretically permits superior exploitation of the ecological niches and is considered adaptive (Ludwig, 1950; Dobzhansky *et al.*, 1950; Dobzhansky, 1951; da Cunha and Dobzhansky, 1954; Dobzhansky and Pavlosky, 1961; Van Valen, 1965; and others). Probably related is increased abundance of individuals in variable species (Darwin, 1859; Fisher and Ford, 1928; Dobzhansky *et al.*, 1950; and others). Cain and Sheppard (1954) questioned whether adaptiveness resulted from polymorphism and several authors (Simpson, 1953; Bader and Hall, 1960; and others) have pointed out that vestigial (functionless) structures are highly variable. Considering samples from nature, not only are the causes of high and low variation numerous and complex, but even the contributions of adaptive and inadaptive variability are greatly complicated (see Mayr, 1963). Van Valen (1965) used bill width (often considered closely associated with the mechanics of food utilization and "observational" niche size) to compare variations of several birds having wide niches with those of several others having narrow niches. His results were consistent with the hypothesis that high variation is adaptive.

Efficient support of weight requires some expenditure of energy and is, therefore, more or less adaptive. Coefficients of variation in three groups of taxa with different problems of weight are compared: bats, which fly, have a tangible weight problem; rabbits, rodents, and carnivores apparently have a lesser problem; some aquatic mammals probably have the least weight problem, owing perhaps to buoyancy (data in Long, 1968). Bats show the lowest overall variation of the mammals studied (Long, 1968). The Insectivora, including or not including the subprimate *Tupaia*, are also low in variation but usually exceed the variation found in bats. Rodents, carnivores, and lagomorphs show a wide range in variation, low to moderately high.

The aquatic mammals sampled are diverse in phylogeny, morphology, size, diet, and even in their aquatic adaptations. Hence, buoyancy is hardly a sole factor involved with variation. The animals included are the platypus *(Ornithorhynchus)*, water shrew *(Sorex palustris)*, muskrat *(Ondatra)*, river otter *(Lutra)*, sea otter *(Enhydra)*, leopard seal *(Hydrurga)*, sea lion *(Eumetopias)*, walrus *(Odobenus)*, and two cetaceans *(Physeter, Balaenoptera)*. Variability in some of these mammals is high—*Ornithorhynchus* (unfortunately a small sample), *Lutra* (as compared to other mustelids), and *Odobenus*, *Physeter*, and *Balaenoptera* (which by virtue of huge body size rely primarily on buoyancy). These sketchy observations are consistent with the hypothesis that variability generally varies inversely with these weight limitations, perhaps directly with niche size.

TABLE 3.—A FIVE-BY-FIVE MATRIX OF EXACT OR MEAN CV VALUES THAT ARE DERIVED FROM TABLE 2. THE COLUMNS ARE SIZE CATEGORIES. THE MEANS IN THE TABLE ARE ACCOMPANIED BY LETTERS, WHICH DENOTE THE GENERA THAT THE MEANS REPRESENT (SEE TABLE 2). THE ANALYSIS IS EXPLAINED IN THE TEXT. THE GRAND MEAN AND TOTAL VARIANCE ARE IN THE LOWER RIGHT BLOCKS.

	Minute	Small	Medium	Medium-large	Large	$\bar{X}$	S^2
	1.98	2.17 SBM	2.81 TAA	5.80	4.39	3.43	2.66
	1.35	1.80 DP	3.19 OSL	2.49	2.88	2.34	0.58
	2.64	3.68 P	3.59 ST	4.83	4.55	3.86	0.75
	1.70	3.70 M	4.91 OR	2.45	4.38	3.43	1.78
	1.99 M	2.70 CZ	3.21 MM	3.45	2.80	2.83	0.32
$\bar{X}$	1.93	2.81	3.54	3.80	3.80	3.18	
S^2	0.22	0.75	0.66	2.18	0.77		1.31

Considering the problems of diet broadly, insectivorous feeding is probably related to narrow niche and omnivorous habits to a niche that is relatively broad. Herbivorous and carnivorous modes of feeding are difficult to classify, involving diverse and often conflicting physiological functions. To illustrate, herbivorous rodents usually have at least four pairs of highly functional chewing molars and two pairs of highly functional gnawing incisors, but the extensive loss of teeth from the primitive dental formula emphasizes the shifting in niches and adaptive zones that has occurred. Variations in teeth are excluded from consideration here, although they are intimately and directly related to mode of feeding (the actual mechanics of feeding are largely unknown in mammals). Most Recent animals remain essentially unstudied with respect to tooth variation.

Insectivorous mammals, by and large, have low overall variation (e.g., shrews, bats, *Tupaia*). Definitely omnivorous are the opossum *(Didelphis)*, monkeys and man, the rat *(Rattus)*, the skunk *(Mephitis)*, and the bear *(Ursus)*. In their groups these mammals are moderately to highly variable, if *Didelphis* is considered variable (in some places it appears to be highly variable—Bader, 1955). Generally herbivorous mammals (such as rodents, rabbits, artiodactyls) vary from low to high in CV value but are frequently highly variable in cranial and body dimensions. Seemingly, the Carnivora are lower on the average in cranial variation than the herbivores. The data appear generally consistent with the hypothesis that width of niche varies with CV value; several related problems warrant additional study.

Domestication, Inbreeding, and Sexual Preponderance of High Variation

Generally, domestic mammals sampled are more variable than wild mammals, a phenomenon several authors have previously observed (Lee and Pearson, 1897; Alpatov and Boschko-Stepanenko, 1928; Latimer, 1936; Stockhaus, 1965; and others). In mammals considered domestic, or somewhat independent of natural ecological factors, it is interesting that in *Homo, Cavia, Felis*, and *Equus* cranial breadth is especially high in variations. As might be expected, variability in uncategorized dogs is extremely high (Stockhaus, 1965), but markedly lower in inbred strains (boxer, for example). Bader (1956) found that inbreeding of *Mus* did not markedly lower the variability of his samples in comparison to wild animals. Probably neither of these examples adequately reveals effects of natural mammalian inbreeding. For one thing, the effects of domestication, although apparently accelerant to increased variability, are poorly understood in relation to the theoretically inhibitory effect on variation of inbreeding. Also, *Mus* is apparently not so variable as *Canis* (wild or domestic) and may have been long stabilized in numerous characters prior to its use in experimentation.

Generally, those who have studied variability in mammalian sexes state that a preponderance in variability in one sex does not occur consistently (Pearson and Davin, 1924; Schultz, 1926; and numerous others). Table 1 categorizes mammals, listed in Long (1968), as wild or domestic, and compares variation between the sexes of mammals in which the male averages larger, or smaller. This is done for all available samples including two of *Canis lupus* and several subspecies of *Rangifer tarandus* and *Martes americana*. In *Rangifer*, data involving only two measurements are available and in *Martes* only one. The standard errors of the CV's of males and females for six characters were used to determine significant differences.

In the wild mammals, whether males or females exceed the opposite sex in size, there is as yet no significant basis for attributing greater variability to one sex in mammals as a group. In domestic mammals males definitely tend to vary more than females, irrespective of whether males are larger or smaller. The samples in Table 1 are somewhat biased in including among the wild mammals two samples of *Canis lupus* and several subspecies of *Martes americana* (only skull lengths), samples of *Homo*, and two of *Oryctolagus* (not "dwarfs") (see Long, 1968). That the variabilities of the six characters are more or less correlated is another source of bias. Even so, that males differing significantly in CV values between sexes are more variable in 10 tests, whereas females are more variable in none, points to the conclusion that domestic mammals generally vary more in the male sex, and that those characters of the female sex are less mutable (χ^2 table yields $P <$ one per cent that the ratio 10:0 is attributable to chance).

Frequency Distributions for Coefficients of Variation

For a given measurement, frequency distributions of mammalian CV's generally show skewed curves, which rise abruptly in the range of low variation (Fig. 1). Lack of correlation of subsidiary lengths and mathematical definitions of CV (see Long and Frank, 1968) might effect lower mean variation, or especially modal variation, in measurements of complex structures such as length of skull. Where correlation of component bones is positive and significant (such as interorbital breadth), the variation of the sum is somewhat increased. Curves of most of the six measurements show sharp, high peaks. Maxillary toothrow, with a high modal frequency, is least skewed of the six measurements. Zygomatic breadth is also high in

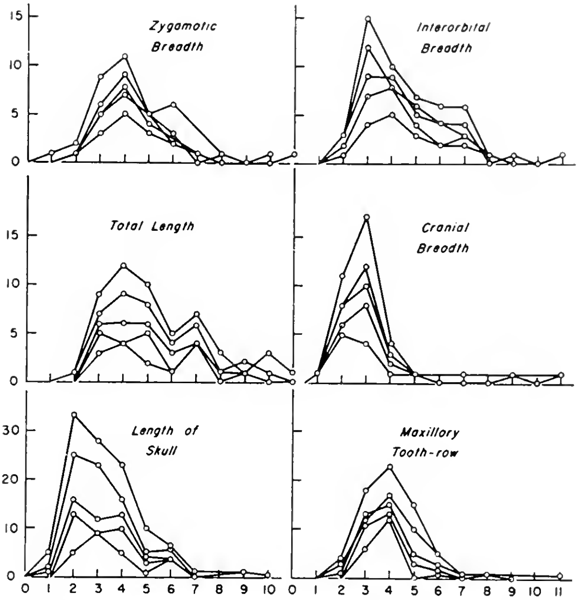

Fig. 1. Frequency distributions for coefficients of variation of wild mammals. Abcissas are CV values, ordinates are frequencies. See text for further explanation.

modal frequency, and also does not show a conspicuously skewed curve. The curve for total length is not conspicuously peaked, but is skewed strongly nevertheless.

It should be noted that the curves are not drawn from the same nor entirely different animals, availability of the data of wild animals being the only criterion of usage. The uppermost curve of each graph in Figure 1 represents all possible samples, within kinds and of each sex or of both sexes. The next lower curve represents taxa or kinds, the next species, and then genera. The lowermost curve represents families. The lower curves are made up from the data yielding the upper curves, and where possible, of means of the more subdivided data. Thus, the CV for total length in *Ornithorhynchus* is utilized in all curves for total length, but the curve for cranial breadth based on data of families incorporates a mean of the mean CV for *Sorex* (derived from the mean of the specific values) and the CV for *Blarina brevicauda* (mean of both sexes). The use of means permits a more reliable interpretation of the lower curves, whereas the biasing effected by "stacking" a higher taxonomic category with a poor sample of its true variability may lower the reliability of that interpretation. The upper and lower curves *agree* essentially in showing skewedness and low modal values. The curves reveal that, in relation to the mode, high values for CV are more often found than low values.

Concerning total length of skull, few CV's were less than 1.5, and the mode is low, not exceeding 2.5. Few values are greater than 6.5 (the abundance compares with those considered less than 1.5). Values exceeding 5.5 are uncommon (see Fig. 1).

Concerning maxillary toothrow, few values are less than 2.5, and the mode is high, about 4.0. Few values are greater than 6.5 (Fig. 1).

Concerning total length of head, body, and tail in representative mammals, one value was obtained that was less than 2.5, and values less than 3.5 were not uncommon. The mode is high, about 4.0 or 5.0, but few values exceed 8.5 (Fig. 1).

Concerning cranial breadth, the curve falls abruptly, tailing off to high values. Values below 1.5 are infrequent, but those approximately 2.0 are common. The mode is about 3.0. Few values exceed 4.5 (Fig. 1).

Concerning zygomatic breadth, few values are less than 2.5. The mode is high, about 4.0, but variation exceeding 6.5 is uncommon (Fig. 1).

Concerning interorbital breadth, few values are less than 2.5 and few exceed 7.5, but some were surprisingly high. Most values are about 3.0 or 4.0. Interorbital breadth approaches length of toothrow and zygomatic breadth in high variability.

Considering wild placental species (not utilizing all the horses and *Eumetopias*), the mean CV's with rather high standard deviations for all available species for each measurement are as follows: cranial length, 3.21 ± 1.40 (N, 51); maxillary toothrow, 3.99 ± 1.09 (N, 37); total length, 5.31 ± 1.96 (N, 31); cranial breadth, 3.05 ± 1.24 (N, 27); zygomatic breadth, 3.95 ± 1.34 (N, 30); interorbital breadth, 4.36 ± 1.51 (N, 32).

The means slightly exceed the modes, as would be expected of the skewed distributions.

SUMMARY

Patterns of variation observed in 96 mammals indicate that larger mammals are generally more variable among wild placentals. There are significant correlations of taxonomic position and amount of variation for several linear measurements of mammals, especially of placentals. A high amount of intercorrelation of variations of the six measurements is noted. Concerning variation and problems of weight, bats are low and some marine mammals are high in variation. Insectivorous mammals are generally low in variation, and omnivores are often high. Herbivores vary greatly in CV value, and tend to exceed carnivores. In wild species, neither sex shows a significant preponderance of high CV's, but in domestic mammals the males were more variable in 10 tests. Domestic mammals show moderate to high variations. Coefficient of variability values of wild taxa are skewed right, with mean CV's and modes varying from approximately 2.5 to 5.3.

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MIGRATION IN THE GUANO BAT, TADARIDA BRASILIENSIS

BY

E. LENDELL COCKRUM

Between September, 1952, and September, 1967, a total of 162,892 guano bats, *Tadarida brasiliensis mexicana* (Saussure), were banded in Arizona and adjacent regions by persons associated with the Department of Biological Sciences at the University of Arizona. Most of these were taken in a few caves, but smaller numbers were captured in a variety of situations including roosts in buildings, under bridges, and in mine tunnels, as well as in mist nets set over water. Appendices 1 and 2 and Table 1 summarize the majority of these banding activities and Figure 1 shows the geographic distribution of the banding sites.

MATERIALS AND METHODS

All of the bands used in this study were furnished by the Bat Banding Office, Fish and Wildlife Service, U.S. National Museum, Washington, D.C. Various sizes and styles of bands were used; mostly we employed the size 0 standard bird band, but others used included sizes 1, 1B, and 2 of the standard bird band, a few of the rounded-end style, and a few lipped bands. See Herreid *et al.* (1960) for a discussion of these band styles and their relative merits. All were applied to the forearm. Some bands were color-coded for use at specific localities. Anodized bands provided various colors that would remain evident for several weeks to years. Just how long the color remained evident depended upon how much the bat chewed on the band. This in turn seems to involve two factors, band application technique and variations in the reaction of individual bats to a band. Poorly applied bands (too tight, too loose, crooked) caused irritation, infections, and swellings and growths that sometimes covered the whole band.

Even when bands were apparently well applied, some individuals reacted by chewing at the band. On many occasions, after a large banding operation, bats would be observed landing in the cave, making vocal noises and chewing on the newly applied band. Especially with the size 0 bands, such chewing soon obliterated one or more numbers on the band. For example, a female banded at Silverbell (locality 28) on May 10, 1963, and recovered at Eagle Creek (locality 24) on June 5, 1963, had already so chewed the band that one number was not legible. Bats recovered one or more years after banding often had so chewed the band that three or more numbers were illegible, and, in some cases, holes were worn completely through the band.

This condition plus the appearance of the forearm of certain unbanded bats leads to the conclusion that many bands are actually removed by the bats. In other cases, swelling, irritation, and infection resulting from such chewing may

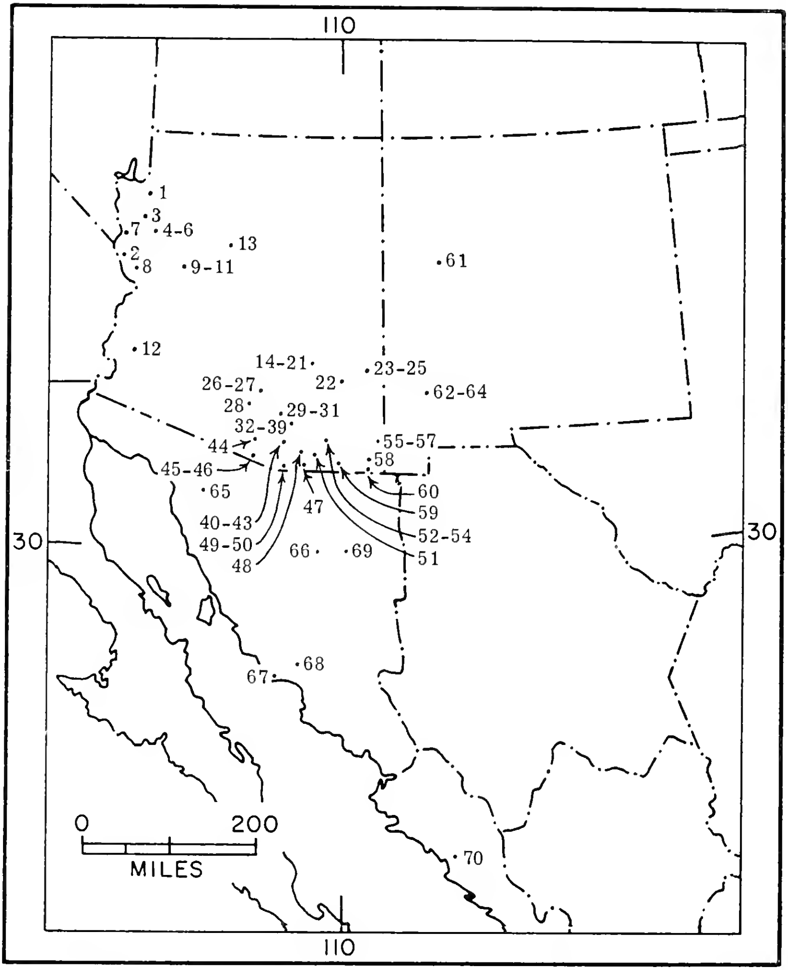

FIG. 1. Map showing geographic distribution of the banding sites of *Tadarida brasiliensis*. Numbers correspond to those listed in Appendices 1 and 2, and used in text.

have caused the death of certain individuals. If these conjectures are true, then recovery data in this study cannot be used to construct meaningful mortality tables. Guano bats appear to be much more aggressive and persistent in their attempts to remove bands than are other species banded in southern Arizona, although some *Eptesicus fuscus* and *Myotis velifer* and a few *Macrotus waterhousii* also chewed bands extensively.

Many different techniques of capture were used in this study. Most bats were captured with various modifications of the Constantine bat trap (Constantine, 1958). Light-weight versions, using vertical monofilament nylon strands held in place by brads spaced at intervals of three-quarters of an inch

TABLE 1.—SUMMARY OF NUMBERS OF *Tadarida brasiliensis* BANDED, ARRANGED BY THE MAJOR TYPES OF HABITATS FROM WHICH TAKEN.

Water			Mine or Cave			Building or bridge		
Locality	Males	Females	Locality	Males	Females	Locality	Males	Females
1	0	1	2	0	8	13	3	680
4	8	2	3	1	1	14	1	4
5	4	0	7	4	7	15	11	1
6	0	2	8	820	1,502	16	56	30
11	6	169	9	662	347	17	5	4
12	10	0	10	1	0	18	10	15
23	2	2	24	10,902	77,324	19	465	350
29	3	0	25	12	305	20	0	41
30	20	1	26	98	292	21	10	12
32	19	8	27	29	67	22	1	0
35	52	51	28	533	4,003	31	7	36
36	2	3	37	222	554	33	13	12
43	23	2	39	39	8	34	16	60
44	1	6	40	21	92	38	0	1
45	1	2	41	0	1	42	221	1,041
46	3	8	61	1,714	1,137	49	27	22
47	0	2	65	868	1,305	50	17	29
48	1	1	66	19,155	21,639	52	10	100
49	0	2	70	7,700	3,900	53	269	551
55	569	317	71	7	0	54	2	0
56	3	0	----	------	------	58	215	1,101
57	9	3	----	------	------	59	131	3
60	1	0	----	------	------	62	59	91
67	45	25	----	------	------	63	1	0
68	0	205	----	------	------	64	147	102
69	1	4	----	------	------	----	------	------
	783	816		42,788	112,492		1,697	4,316

on wooden frames made of pine boards (two by two inches) of appropriate lengths, were assembled in the field on many occasions. Plastic collecting baskets were positioned at the bottom of the trap or, when the trap had to be suspended above the ground, long funnels were made of four mil sheet plastic. Experience showed that funnels with a small throat size became clogged when the trap was placed in a dense flight. No such troubles were encountered when utilizing steep-sided funnels having throat diameters in excess of 24 inches. Retaining cages of sufficient number and size to avoid suffocation of the bats are necessary. Various kinds were used, all with open tops. Some were made at the trapping site, utilizing lumber and hardware cloth. Typically these included a plastic sheet along the upper edge of the inside of the cage to prevent bats from crawling out or, in large cages, baffles of plastic hanging down into the cage to prevent bats from flying out; others were long narrow tubs of sheet plastic supported by side poles and end frames. For smaller operations, 20 gallon plastic garbage cans, with a number of large holes cut in the sides, lined with a hardware cloth insert, and with a hole cut in the lid leaving about four inches of rim, were found to be useful.

DESCRIPTION OF ROOSTS AND POPULATIONS

Based upon such factors as season of the year and composition of the population present, various types of roosts are recognized:

(1) *Maternity Colonies,* containing primarily adult females and young of the year that appeared to have been born there; (2) *Summer Male Roosts*; (3) *Transient Roosts*; and (4) *Winter Roosts* (Villa-R. and Cockrum, 1962:58). A given locality may house successively in the same year different types of roosts that are made up of different individuals. Specific examples of this were seen at Carbo, Sonora (locality 66), and at the railroad bridge near Continental, Arizona (locality 42).

FIG. 2. A modified Constantine bat trap at the mouth of Eagle Creek Cave, Greenlee Co., Arizona (locality 24). Photograph by Bruce Hayward.

Maternity Colonies

Maternity colonies exist in a number of different situations. Small colonies are known from crevices in bridges, in mine tunnels, in attics and crevices in buildings, and in natural caves. Large maternity colonies exist in Eagle Creek Cave (locality 24), Silverbell Cave (locality 23), and Cueva del Tigre (locality 66).

Eagle Creek Cave (Figs. 2 and 3) is in the eastern canyon wall of Eagle Creek. The entrance is approximately 100 feet above the present stream level and is a vertical slit roughly 24 feet wide and 65 feet high. Inside, the cave opens into a single, large football-shaped chamber that is approximately 288 feet long, 65 feet wide, and 100 feet tall. Some wide, deep, chimney-like crevices in the ceiling provide additional roosting space for the bats. This cave has been known as a "guano cave" for many years and formerly biennial accumulations of guano were routinely removed and sold.

The cave is not readily accessible, even by vehicles with four-wheel drive—especially during the seasons of high water. It is 4.2 miles down the narrow valley of Eagle Creek. The walls of the canyon are 400 to 500 feet high and are sheer or nearly so. The stream meanders from one canyon wall to the other and thus must be forded many times. The course of the stream varies from year to year. In the dry season (usually March to June) it has little running water, but in the rainy season (July to September) is a raging torrent. During the times of run-off of rain and melting snow in the headwaters region (winter and early spring), flooding conditions exist, washing out most of the "road." The relative inaccessibility of this cave results in a minimal disturbance to the population by vandals but does impose difficulties in studying the bats.

This cave is occupied by bats only during the warmer parts of the year. A few are present by early April. The population increases during April, May, and early June, until, by late June, 25 to 50 million bats are present. Estimates are based on computation of area covered by roosting bats and counts of numbers hanging in a number of sample areas. After the young reach adult size, the population decreases so that only a few thousand are present in mid-September, and by mid-October all are gone. Pertinent field notes follow.

On April 3, 1961, Russell Davis and Bob Neal visited this cave. They reported (field notes): "The only bats present [estimate, 500] occupied a fissure at the highest point in the ceiling."

On April 13, 1963, William J. McCauley visited the cave. He reported (field notes): "The large crack in the ceiling of the Eagle

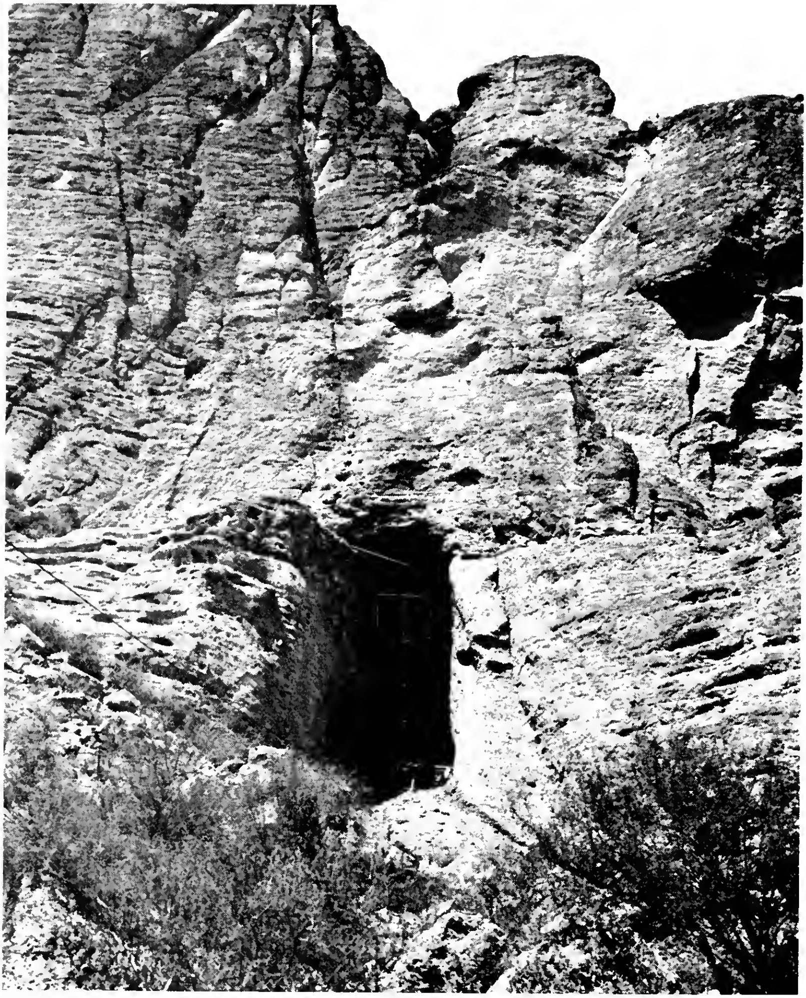

FIG. 3. Entrance to Eagle Creek Cave, Greenlee Co., Arizona (locality 24). Photograph by Bruce Hayward.

Creek Cave appeared to be filled with *Tadarida* and the population was beginning to overflow onto the horizontal ceiling of the main cave room. A number of bands could be seen but colors were not clearly discernible at that distance (75 feet and greater). Due to the sun being more directly in line with the cave entrance than at other times when the cave has been visited, the lighting in the cave was better and it was possible to see that the crack in the ceiling continues upward at least 60-70 feet above the level of the ceiling.

TABLE 2.—SUMMARY OF NUMBERS BANDED AND IN-PLACE RECOVERIES OF *Tadarida brasiliensis* AT EAGLE CREEK CAVE, ARIZONA.

				Recoveries								
	Banded			Total			In place			Foreign		
Date	Males	Females	Ratio	Males	Females	Ratio	Males	Females	Ratio	Males	Females	Ratio
August 19, 1958	26	100	21:79	0	0		0	0		0	0	
June 28, 1959	28	1,710	2:98	0	4	0:100	0	1	0:100	0	3	0:100
June 25, 1961	2,900	12,450	19:81	3	17	15:85	0	10	0:100	3	7	30:70
June 23, 1962	3,198	19,964	14:86	10	122	8:92	6	112	5:95	4	10	28:72
June 5, 1963	3,800	33,700	10:90	74	418	15:85	36	355	9:91	38	63	38:62
June 2, 1964	750	8,400	8:92	19	90	19:81	10	80	11:89	9	10	47:53
June 27, 1964	150	1,000	13:87	53	400	12:88	39	386	9:91	14	14	50:50
Totals	10,852	77,324	12:88	159	1,051	14:86	91	944	9:91	68	107	39:61

The highest part of the crack visible is still fairly wide and it appears that the crack continues considerably beyond that point. The areas of the ceiling and walls of the main cave room observed to be solidly occupied by bats last June were stained so that sharp lines of demarcation were clearly seen. It was clear that the crack in the ceiling could hold as large a population as could all of the area of ceiling wall ordinarily occupied in June. There was no evidence of young bats already born and it was conjectured that the cave might still be serving as a Spring Transient Locality with the animals presently occupying it destined to move to caves still further north before parturition. Bats were in motion flying in the usual direction; clockwise as seen from below. Ammonia odor was lighter than that observed in June, 1962, at the extreme south end of the main room. Dermestids were absent, or at least not obviously present in the guano."

TABLE 3.—ANALYSIS, BY SEX AND TIME LAPSE, BETWEEN BANDING AND IN-PLACE RECOVERIES OF *Tadarida brasiliensis* AT EAGLE CREEK CAVE, ARIZONA.

Time lapse at time of recovery	Females			Males		
	No.	No. banded	Per cent	No.	No. banded	Per cent
Same year	208	8,400	0.0247	16	750	0.0213
One year	537	66,114	0.0081	56	9,898	0.0056
Two years	179	34,124	0.0053	14	6,126	0.0023
Three years	20	14,260	0.0001	5	2,954	0.0018

Apparently most of the gravid females arrive at this colony within a few days before their young are born. For example, on June 1, 1964, the population in the Eagle Creek Cave was estimated to be less than 100,000. During the early morning return flight, many more bats came in than had left so that the population was estimated at about 250,000. Many bats were hanging in a part of the cave not occupied the previous day. Again on the night of June 2, even more bats came in so that about 1,000,000 were present on June 3.

A total of 88,176 guano bats have been banded at this cave (Table 2). Because most were banded in June, they were adults at least one year old that had spent the winter elsewhere and had moved into the cave during the weeks preceding banding. No special efforts were made to band individuals of a given sex so that the sex ratios of bats banded probably represents that of the whole population. Note that the ratio of those banded, 12 males to 88 females, compares favorably to the ratio in total recoveries, 14 males to 86 females. However, adult males banded at the cave do not

TABLE 4.—SUMMARY OF NUMBERS BANDED AND IN-PLACE AND FOREIGN RECOVERIES OF *Tadarida brasiliensis* AT SILVER CREEK BRIDGE, ARIZONA.

Date	Banded		Recoveries								
			Total			In place			Foreign		
	Males	Females	Males	Females	Ratio	Males	Females	Ratio	Males	Females	Ratio
May 20, 1961	65	238	2	4	33:67	0	1	0:100	2	3	40:60
May 21, 1961	1	20	0	0							
May 22, 1961	5	38	1	14		1	12		0	2	0:100
May 24, 1961	2	22	0	0							
May 27, 1961	11	43	11	25		11	25		0	0	
August 7, 1961	35	186	25	51	33:67	25	50	33:67	0	1	0:100
September 10, 1961	8	194	17	54		17	53		0	1	0:100
October 1, 1961	33	205	10	38		8	35		2	3	
June 17, 1962	43	197	4	11		4	8		0	3	0:100
August 15, 1962	0	0	0	4		0	4		0	0	
August 19, 1962	1	0	0	0							
May 24, 1962	11	11	0	0							
Totals	215	1,154	70	201		66	188		4	13	

return in the same ratio as do the adult females. The in-place recovery ratio is nine males to 91 females, whereas the foreign recovery ratio is 39 males to 61 females. A possible explanation is that a large percentage of the males in the colony are yearlings, born in the colony the preceding summer and thus not subject to banding at Eagle Creek. However these males would have been subject to banding at other locations during the preceding autumn, winter, and spring months.

An analysis of in-place recoveries by time lapsed before recovery is given in Table 3. Movements shown by the foreign recoveries is given in a later section of this paper.

Other smaller maternity colonies have been found in caves (localities 8, 61), bridge crevices (locality 13), and a mine tunnel (locality 28).

Summer Male Roosts

Few roosts of this type were studied. Many, perhaps most, of these roosts consist of small groups of 10 to 300 individuals. The roost examined on July 23, 1963, in the attic of St. Patrick Church, Bisbee, Arizona (locality 59), is the largest such colony observed. Approximately 1300 guano bats were present of which 134 (131 males, three females) were captured. The females showed no obvious signs of having borne young that year.

Transient Roosts

In the early part of the year and again in late summer and in autumn, guano bats occupy a variety of roosts on a temporary basis. Some appear to be occupied by a given group of bats for only a few (possibly only one) days, with another group being present a few days later. Examples of such roosts include: crevices in bridges (localities 14-21, 31, 42, 49, 50, 52, 53, 54, 58); mine tunnels (localities 26, 27, 37, 40, 41); buildings (localities 33, 34, 38, 62, 63, 64), and natural caves (locality 39). Populations in such roosts vary widely in numbers and sex ratios (Table 4).

Winter Roosts

No major winter roosts were found in the course of this study. The volcanic cave, Cueva Montelarga, 17 mi. W Pericos, Sinaloa, was thought to be a winter roost when first discovered in late January, 1963. Visits to this cave in December of 1963 and early January of 1964, however, revealed that no guano bats were present.

TABLE 5.—SUMMARY OF NUMBERS BANDED AND IN-PLACE RECOVERIES OF *Tadarida brasiliensis* AT CABBO, SONORA.

						Recoveries								
	Total		Banded			Total			In place			Foreign		
Date	Number	Ratio	Males	Females	Ratio	Males	Females	Ratio	Males	Females	Ratio	Males	Females	Ratio
January 30, 1962*	2,000	80:20				5	0	100:0	5	0	100:0	0	0	
January 30, 1963	5,000					4	3	57:43	3	3	50:50	1	0	100:0
February 15, 1963	5,000	96:04	1,650	50	97:03	37	2	95:05	28	2	93:07	9	0	100:0
February 17, 1958[1]	2,200													
February 23, 1962*	5,000	69:31												
March 3, 1962	100,000	61:39												
March 7, 1960	15,000	54:46	5,398	4,550	54:46	23	8	74:26	23	8	74:26	0	0	
March 15, 1963	100,000	74:26	3,000	1,100	73:27	120	5	96:4	111	2	98:02	9	3	75:25
March 21, 1964	100,000	59:41	2,850	2,000	59:41	83	18	82:18	68	8	90:10	15	10	60:40
March 24, 1962*	100,000	85:15				2	0	100:0	2	0	100:0	0	0	
March 30, 1963	70,000	42:58	540	860	39:61	96	10	91:9	92	8	92:08	4	2	66:34
April 8, 1960	75,000	51:49	1,000	1,000	50:50	144	61	70:30	144	61	70:30	0	0	
April 11, 1958	200,000	50:50												
April 11, 1963		52:48	300	300	50:50	99	66	60:40	91	57	61:39	8	9	47:53
April 18, 1959	500,000	25:75	420	1,297	24:76	16	12	57:43	14	6	70:30	2	6	25:75
April 21, 1962*	1,500,000	29:71				1	0	100:0	1	0	100:0	0	0	
April 26, 1963	500,000	20:80	181	2,369	7:93	34	37	48:52	31	35	47:53	3	2	60:40
May 20, 1963		13:87	100	900	10:90	46	81	36:64	42	78	35:65	4	3	57:43
May 26, 1962*	3,000,000	3:97												
June 23, 1962*	2,500,000	4:96												
July 1, 1963	100,000	6:94	83	1,000	8:92	21	63	25:75	20	51	28:72	1	12	8:92
July 2, 1961						3	115	3:97	3	114	3:97	0	1	0:100
July 18, 1960	200,000	3:97	94	2,906	3:97	0	53	0:100	0	53	0:100	0	0	
July 21, 1961						0	36	0:100	0	36	0:100	0	0	
August 7, 1959	2,500,000	39:61	500	800	38:62	0	1	0:100	0	1	0:100	0	0	
August 26, 1962*						0	1	0:100	0	1	0:100	0	0	
September 21, 1963	2,500,000	29:71	263	850	24:76	1	5	17:83	1	3	25:75	0	2	0:100
September 23, 1962*	20,000													
October 21, 1965	1,000													
October 23, 1962*	0													
November 3, 1963	1,000					5	0	100:0	4	0	100:0	1	0	100:0
November 7, 1959	10,000	61:39	2,350	1,500	61:39	7	2	78:12	7	2	78:12	0	0	
November 12, 1957[2]	200	25:75												
November 23, 1961*	1,000	89:11												
November 30, 1958	5,000		426	157	73:27	0	1	0:100	0	0		0	1	0:100
December 23, 1961*	5,000	57:43												
Totals			19,155	21,639	47:53	447	580	56:44	690	529	57:43	57	51	53:17
Grand totals:			40,794			1,027			1,219			108		

* From Mitchell (1963); [1] from field notes of Roger Carpenter; [2] from notes notes of D. G. Constantine.

As bats were being banded at the Pericos locality on March 2, 1963, an unusual behavior of captives was noted. Males were much more active than the females; thus bats taken from a freshly filled retaining cage tended to be primarily males, whereas primarily females remained in the cage. A gross examination revealed that males were reproductively active and that vaginal plugs were present in many females. In contrast to their behavior during most other banding operations, females reacted to the touch of the banders by crouching down, not by aggressive biting and attempts to escape.

Multi-use Roosts

The localities listed above fall rather clearly into a given type of roost. A few localities serve, in season, as transient roosts and as a maternity colony. One such locality that was visited many times during this study is a volcanic tube cave, Cueva del Tigre, 14.9 mi. SSE Carbo, Sonora. It was in this cave that Henry Mitchell carried out a year-round survey of the cave environment as part of his study of the respiratory physiology of certain molossid bats (Mitchell, 1963).

Table 5 summarizes visits to this cave, estimates of population size, and information on bandings, recoveries, and sex ratios. Note the low population in the winter months with, in general, more males present than females. Males predominate through mid-March. By late June and July, when the population reaches a maximal size, females make up most of the population.

In all, 3240 guano bats were recovered in place. Most of these involved a single recapture of a given individual, often a year or more after the time of banding. Such recoveries give little insight into the question as to how "loyal" a bat is to a given transient roost or maternity colony. However, a few individuals were recaptured in place three or more times (Table 6). This demonstrates that a given individual will utilize a given temporary roost both in the spring and again in the autumn (Silver Creek, St. David) as well as in successive years in the same season. This "loyalty" to the use of transient roosts persists in spite of the bats being physically removed and released at another place. The Silver Creek, Arizona, populations were utilized along with *Myotis velifer* and *Antrozous pallidus* in a series of homing experiments (Davis, 1966). For example, 65 female *Tadarida* taken at Silver Creek on May 20, 1961, all were released five miles southwest of the site. None returned the same or the following night, although one returned the third night (May 22),

TABLE 6.—PARTIAL LIST OF IN-PLACE RECOVERIES OF *Tadarida brasiliensis* TAKEN MORE THAN ONCE.

Original capture	1st recapture	2nd recapture	3rd recapture
Carbo, Sonora (males)			
April 18, 1959	April 9, 1960	July 2, 1961	
November 6, 1959	March 7, 1960	March 15, 1963	
March 7, 1960	April 21, 1962	April 11, 1963	
March 7, 1960	February 13, 1963	April 11, 1963	
March 7, 1960	April 9, 1960	May 20, 1963	
March 7, 1960	February 15, 1963	March 30, 1963	April 11, 1963
April 9, 1960	February 15, 1963	March 21, 1964	
April 9, 1960	March 30, 1963	April 11, 1963	March 21, 1964
April 9, 1960	March 20, 1963		
April 9, 1960	March 15, 1963	March 21, 1964	
February 15, 1963	March 15, 1963	March 30, 1963	April 11, 1963
Carbo, Sonora (females)			
April 9, 1960	July 18, 1960	July 21, 1961	
Silver Creek, Arizona (females)			
May 20, 1961	October 10, 1961	June 17, 1962	August 5, 1962
May 20, 1961	September 10, 1961	June 17, 1962	
September 10, 1961	June 17, 1962	June 4, 1963	
St. David, Arizona (males)			
June 22, 1959	March 27, 1960	May 28, 1960	August 27, 1960
June 1, 1959	July 24, 1959	May 28, 1960	August 27, 1960
July 24, 1959	March 27, 1960	May 28, 1960	September 23, 1961
St. David, Arizona (females)			
June 1, 1959	June 22, 1959	October 1, 1960	April 15, 1961
June 1, 1959	June 24, 1959	July 24, 1959	May 28, 1960
June 22, 1959	May 28, 1960	September 3, 1960	
July 24, 1959	May 28, 1960	August 22, 1960	
Eagle Creek, Arizona (males)			
June 5, 1963	June 2, 1964	June 27, 1964	
Eagle Creek, Arizona (females)			
June 24, 1951	June 23, 1962	June 4, 1963	
June 23, 1962	June 4, 1963	June 27, 1964	

three by May 27, and 14 others returned one or more times in the following 18 months, even though each recapture was followed by a release some distance from the roost. For example, a female released 5 mi. SW Silver Creek on May 20, 1961, was recaptured on May 27 and released at Maricopa, Pinal County. It was again recaptured at Silver Creek on September 10, 1961, and released at Tucson (100 miles northwest), was captured again on October 1, 1961, and again released at Tucson, and finally was recaptured at Silver Creek on June 17, 1962. Six others of this group showed three or more such recaptures. Twelve of 65 males reacted in a similar manner. One male, banded and released 5 mi. SW Silver Creek on May 20, 1961, was recovered on August 7, 1961, and released 10 mi. SW Silver Creek; it was recovered on September 10 and again released 10 mi. SW Silver Creek; recovered again on October 1, 1961, and released at Benson (60 miles northwest); recovered again on June 12, 1962, and released at Tucson (100 miles northwest); and finally recovered on August 5, 1962.

Foreign Recoveries

In all, 539 guano bats have been recovered at points other than the site of banding. Most (all but 22) of these were recovered by persons actively collecting bats or involved in bat banding activities. Thus, in spite of an intensive publicity campaign designed to enlist the cooperation of the general public in reporting captured banded bats, less than four per cent of the foreign returns came from that source. Foreign returns are summarized in Tables 7 and 8. A complete breakdown of these recoveries, giving time and date of banding and recovery, is available from the author on request.

DISCUSSION

Most of the foreign recoveries represent individuals retaken only a single time (Table 7). However, fourteen individuals were retaken twice (Table 8) and some of these clearly indicate movement back and forth between transient roosts. Added to information gained from an analysis of movements (see maps, Figs. 4-7) and of roost types, the following sequence of movements appears to characterize the migration of guano bat populations in Arizona. Most spend the winter months (December and January) in Mexico, presumably at locations south of Pericos, Sinaloa. Some, mainly males, winter as far north as Carbo, Sonora, and a few probably winter in the lower valleys of Arizona. In late February and early March, breeding occurs in Sinaloa and Sonora. In March, April, May, and June subpopulations move progressively northward, occupying successively a series of transient roosts. Males appear to move more rapidly than females (see sex ratios of bats taken at Carbo, Sonora, during these months, Appendix 1). During May and early June a large number of females arrive in northern Sonora and southern Arizona. By mid-June to early July, when gestation occurs, most females have congregated in a relatively few maternity colonies (e.g., Eagle Creek, 25 million; Carbo, three million; Powerline Cave, 8,000 to 10,000; Perkinsville, 3,000; Galts Cave, 5,000). During this time males generally occur in smaller colonies, consisting primarily of males.

Probably not all males migrate northward, for Alfred Gardner (field notes) observed some 40,000 guano bats in a cave near Comitán, Chiapas, on June 23, 1964. All examined were male.

After the young reach adult size, the maternity colonies rapidly break up (but are not abandoned by all bats) and, in late August, September, and early October, a number of transient roosts are occupied in Arizona and northern Sonora. During this time, popula-

TABLE 7.—SUMMARY OF FOREIGN RECOVERIES OF *Tadarida brasiliensis*. LOCALITIES LISTED ON TOP OF TABLE ARE THE POINTS AT WHICH BATS WERE BANDED; LOCALITIES ON LEFT ARE THE PLACE OF RECOVERY. THE NUMBERS INDICATE THE NUMBER OF RECOVERIES OF EACH SEX AT A GIVEN LOCALITY (FOR EXAMPLE, 1-0 MEANS ONE MALE AND NO FEMALES RECOVERED).

Banded / Recovered	Powderline Cave	Perkinsville	Coolidge Dam	Eagle Creek	Plantsite	Silverbell	Tucson	Beehive	Continental	Benson	St. David	SWRS	Bisbee	Silver Creek	Galts Cave	Silver City	Tajitos	Carbo	Guaymas	Pericos	
Topock	1-0																				1-0
Perkinsville						0-1															0-1
Coolidge Dam				1-16																	1-16
Eagle Creek			0-6		0-2	2-23			0-4	0-2	0-1	3-0		2-7	3-0	1-4	0-4	52-54		3-2	64-109
Plantsite				0-2																	0-2
Duncan				1-1																	1-1
Safford			1-0	0-6																	1-6
Phoenix						0-1															0-1
Silverbell				0-20					4-25							2-0	0-1	2-17			8-43
Tucson				1-1		1-0															2-1
Beehive							1-0					1-1									1-2
Rita				0-1																	0-1
Continental				2-6		0-37												0-3			2-46
Benson				0-1																	0-1
Bowie				0-1																	0-1
St. David				0-1														0-1			0-2
SWRS												1-0						2-0			3-0
Bisbee																		2-0			2-0
Silver Creek				0-9							0-1							0-2			0-12
Monte Vista				1-0																	1-0
Galts Cave			2-0	10-1					1-0									2-0			15-1
Cliff				0-1																	0-1
Gila				0-1																	0-1
Truth or Consequences															0-1						0-1
Silver City				1-0																	1-0
Lordsburg				0-1																	0-1
Las Cruces				0-1																	0-1
Tijatos				0-14		2-20												1-6		2-0	5-40
Carbo		1-1		40-24		0-4	0-1		0-4			3-0	1-0	2-5	1-0	2-0			1-0	13-7	64-46
Guamuchal																				1-0	1-0
Marquipo				0-1																	0-1
Novolata				0-1																	0-1
Pericos								1-2						1-0							2-2
	1-0	1-1	3-6	57-110	0-2	5-85	1-1	1-2	5-33	0-2	0-2	8-1	1-0	5-12	4-1	5-4	0-5	61-83	1-0	16-7	

TABLE 8.—FOREIGN RECOVERIES OF *Tadarida brasiliensis* THAT WERE TAKEN MORE THAN ONCE.

Banded	1st recovery	2nd recovery
	Males	
1 Carbo (April 18, 1958)	SWRS (July 16, 1959)	Carbo (November 6, 1959)
1 Carbo (February 15, 1963)	Eagle Creek (June 4, 1963)	Carbo (March 21, 1964)
1 Carbo (February 15, 1963)	Eagle Creek (June 4, 1963)	Carbo (March 21, 1964)
1 Eagle Creek (June 5, 1963)	Galts Cave (June 21, 1963)	Eagle Creek (June 27, 1964)
	Females	
1 Carbo (March 7, 1960)	Silverbell (May 10, 1963)	Carbo (March 21, 1964)
1 Silver Creek (March 21, 1961)	Eagle Creek (June 24, 1961)	Silver Creek (October 1, 1961)
1 Eagle Creek (June 23, 1962)	Silverbell (May 10, 1963)	Eagle Creek (June 27, 1964)
1 Continental (May 3, 1963)	Silverbell (May 10, 1963)	Continental (June 11, 1963)
1 Continental (May 3, 1963)	Silverbell (May 10, 1963)	Continental (May 16, 1963)
4 Silverbell (May 10, 1963)	Continental (May 16, 1963)	Silverbell (June 10, 1963)
1 Silverbell (May 10, 1963)	Continental (May 16, 1963)	Tajitos (September 6, 1963)

tion samples reveal sex ratios approaching 50:50 in most roosts. By mid-October, most bats have left Arizona and are occupying transient colonies in Sonora.

The details of flight compositions and patterns as well as distances covered in a given flight are not known. The spectacular increase in the population at the maternity colony at Eagle Creek in early June of 1964 already has been discussed. A similar spectacular increase in the population at the cave near Carbo, Sonora, was observed by Henry Mitchell (1963:38) and William J. McCauley (field notes). No bats were present in the cave on March 24, 1962, but by the morning of March 25 approximately 100,000 were present (85 per cent of those examined were males).

Some recoveries indicate that rapid flights over relatively long distances are possible (Table 9). One female moved 175 miles in no more than four nights (averaging 43.8 miles per night); two others covered 85 miles in no more than two nights (42.5 miles per night). Two females and one male traveled 765 miles in no more than 39 nights (averaging 19.6 miles per night). Since exact times of departure and arrival are not known, these probably represent minimal values. Glass (1959:544) reported movements of approxi-

TABLE 9.—MOVEMENTS OF INDIVIDUAL *Tadarida brasiliensis* SELECTED TO SHOW RATE OF FLIGHT DURING MIGRATION. SEE TEXT FOR DISCUSSION.

No.	Banding locality	Date	Recovery locality	Date	Distance	Night	Miles/Night
			Males				
1	Beehive (no. 37)	October 6, 1957	Pericos (no. 70)	November 14, 1957	765	39	19.6
1	Carbo (no. 66)	May 20, 1963	Eagle Creek (no. 24)	June 3, 1963	255	14	18.2
1	Eagle Creek (no. 24)	June 5, 1963	Galts Cave (no. 61)	June 21, 1963	180	16	11.2
6	Pericos (no. 70)	March 2, 1963	Carbo (no. 66)	April 11, 1963	335	40	8.4
1	Guaymas (no. 67)	April 1, 1959	Carbo (no. 66)	April 18, 1963	120	17	7.1
1	SWRS (no. 55)	June 3, 1963	Eagle Creek (no. 24)	June 26, 1963	75	23	3.3
			Females				
1	Continental (no. 42)	May 16, 1963	Carbo (no. 66)	May 20, 1963	175	4	43.8
2	Benson (no. 52)	June 1, 1963	Eagle Creek (no. 24)	June 3, 1963	85	2	42.5
6	Eagle Creek (no. 24)	June 5, 1963	Silverbell (no. 28)	June 10, 1963	130	5	26.0
1	St. David (no. 53)	June 22, 1959	Eagle Creek (no. 24)	June 28, 1959	95	4	23.7
2	Beehive (no. 37)	October 6, 1957	Pericos (no. 70)	November 14, 1957	765	39	19.6
2	Carbo (no. 66)	May 20, 1963	Eagle Creek (no. 24)	June 3, 1963	255	14	18.1
1	Eagle Creek (no. 24)	June 5, 1963	Galts Cave (no. 61)	June 21, 1963	180	16	11.2
2	Silverbell (no. 28)	June 10, 1963	Carbo (no. 66)	July 1, 1963	210	20	10.5
1	Eagle Creek (no. 24)	June 5, 1963	Carbo (no. 66)	July 1, 1963	255	25	10.2
3	Continental (no. 42)	June 11, 1963	Carbo (no. 66)	July 1, 1963	175	20	8.7
1	Silverbell (no. 28)	May 10, 1963	Carbo (no. 66)	June 13, 1963	210	34	6.2
1	Silverbell (no. 28)	June 10, 1963	Tajitos (no. 65)	June 28, 1963	105	18	5.5
1	Silverbell (no. 28)	May 10, 1963	Carbo (no. 66)	June 28, 1963	210	49	4.3
1	Silver Creek (no. 58)	May 20, 1961	Carbo (no. 66)	July 3, 1961	160	44	3.6

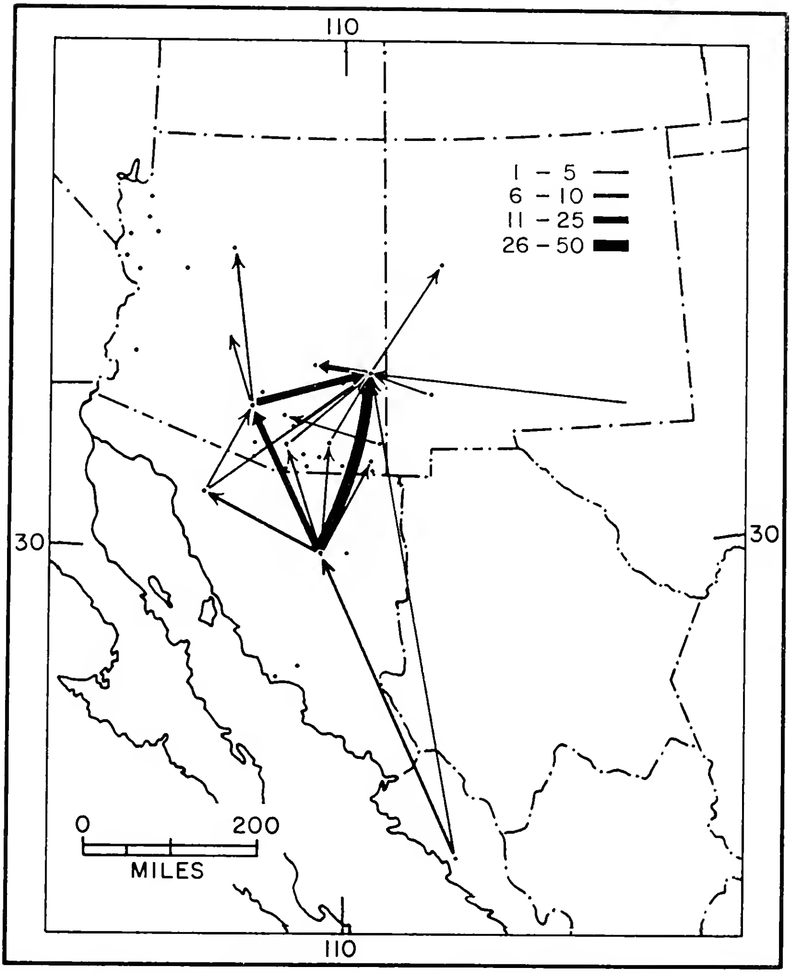

Fig. 4. Map showing northward movements of banded female *Tadarida brasiliensis.*

mately 500 miles (from Selman's Cave, Oklahoma, to Carlsbad Caverns, New Mexico). Four bats made the trip in 12 nights (an average of about 42 miles per night) and one in 13 nights (an average of about 38 miles per night). Again, these represent minimal values.

Some females, but no males, have been recovered moving southward in the late spring (Table 9). For example, three females banded at Continental, Arizona, on June 11, 1963, were retaken in the maternity colony at Carbo on July 1, and a female banded at

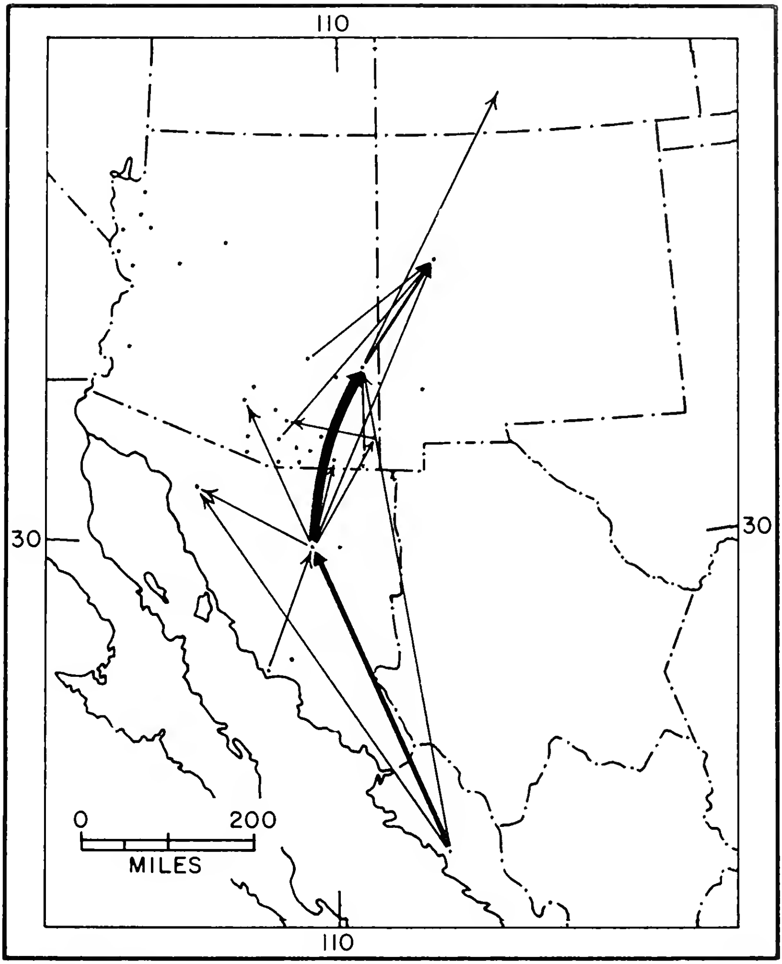

FIG. 5. Map showing northward movements of banded male *Tadarida brasiliensis.*

Silverbell, Arizona, on June 10, 1963, was taken at Tajitos, Sonora, on June 28. The significance of these movements is not known. However, at least some were not gravid and showed no obvious signs of recent parturition at the time of recapture. Perhaps the stresses of the original capture and banding had caused a miscarriage (a situation observed at times in guano bats and more commonly in other species) and the migration to a northern maternity colony was not completed. Glass (1959:544-545) has reported a similar southward movement of a female, of some 400 miles, when

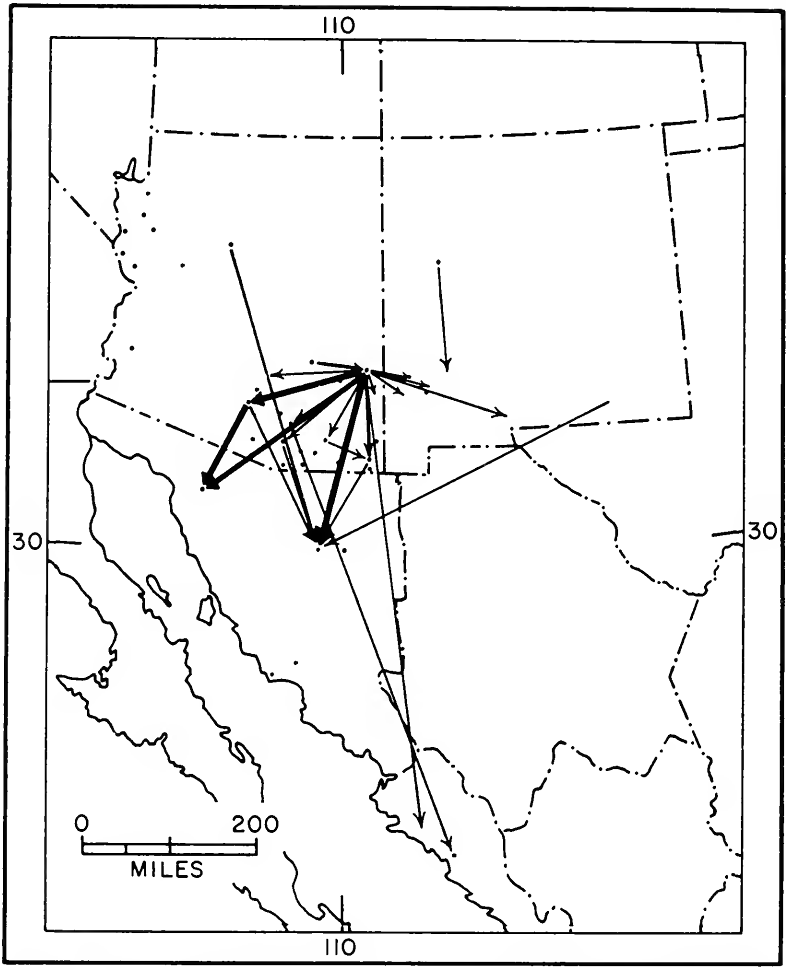

FIG. 6. Map showing southward movements of banded female *Tadarida brasiliensis.*

the time of the year coincided "with the peak of reproductive and nursing activity, when females might be expected to be most sedentary."

The guano bat, *Tadarida brasiliensis* Geoffroy, has been recorded from localities as far north as Medford, Oregon, and Lincoln, Nebraska (Hall and Kelson, 1959:206), southward through the southern United States, Mexico, Central America and, in South America, at least to Chimpay, Rio Negro, Argentina (Schwartz, 1955:108). It also occurs on most of the islands in the Caribbean

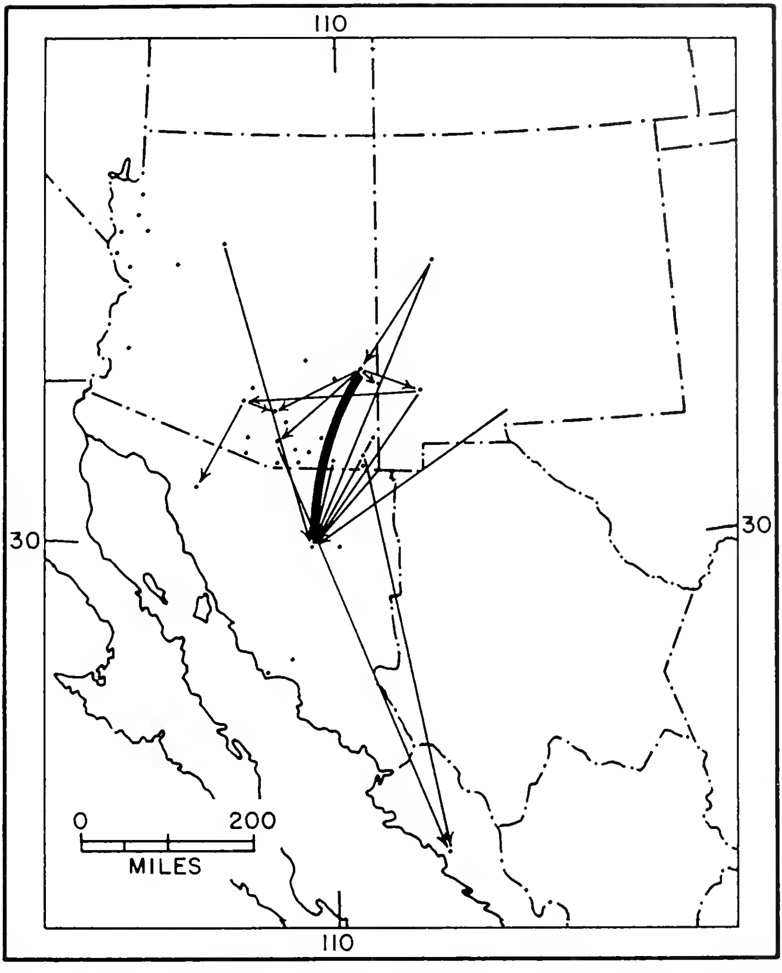

FIG. 7. Map showing the southward movements of banded male *Tadarida brasiliensis.*

(Hall and Kelson, *loc. cit.*). As currently understood the species is divisible into a number of races (Schwartz, *op. cit.*), but the interrelationships of the various populations within the species complex are poorly known. The discovery that at least some of the populations of the north temperate portion of this range are migratory has led to even further confusion concerning these relationships.

In recent years all guano bats in the southwestern United States and Mexico have been referred to a single subspecies, *Tadarida brasiliensis mexicana* (Saussure). Large numbers of these bats have been banded in Oklahoma (Bryan Glass and associates), Texas (Davis *et al.*; Eads *et al.*), New Mexico (see Constantine, 1967:54, for list), and California (Albert J. Beck, Philip Leitner, and others). One of the surprising aspects of this study was that none of the bats banded in Arizona was recovered in California or in the Oklahoma-Texas region. Further, none of the bats banded in western Arizona were recovered in eastern Arizona (or vice versa). In fact, only one of the bats banded in western Arizona was retaken at other than the point of banding and it demonstrated only a local movement. These facts, coupled with an analysis of the literature reports of the seasonal distribution of populations (Villa-R. and Cockrum, 1962), and the banding results reported by others leads to the conclusion that four or more behaviorally (and possibly genetically) separate populations of *Tadarida brasiliensis mexicana* occur in the western United States during the summer months (see map, Fig. 8).

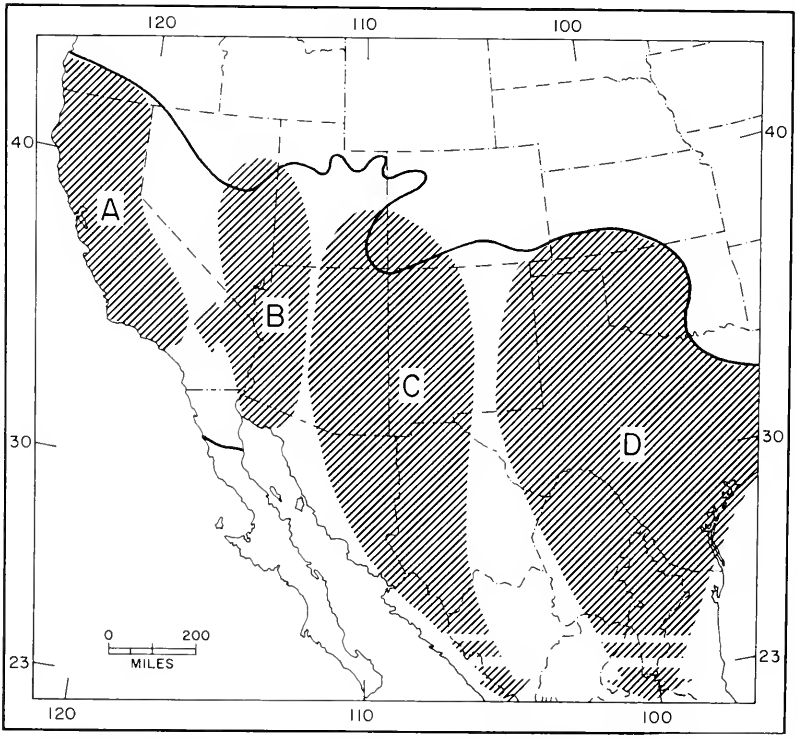

FIG. 8. Map showing approximate limits of behaviorally (and probably genetically) separate groups of *Tadarida brasiliensis mexicana* (Saussure) in the southwestern United States. Group A performs only local movement; group B migrates only a short distance; groups C and D migrate, in separate flyways, distances in excess of 1000 miles. See text for discussion.

Group A, inhabiting southern Oregon and California, probably is composed of resident populations. They appear to perform only local seasonal movements as argued by Benson (1947). At that time, Christensen (1947) had concluded, on the basis of observations at Carlsbad Caverns, New Mexico, that *T. b. mexicana* was migratory. Benson argued, on the basis of observations in California, that *mexicana* probably was not migratory and stressed the necessity for banding studies to clarify the situation. At this point it appears that the two groups of *Tadarida* behave differently. California populations appear to make only local seasonal movements; Carlsbad populations do appear to perform long movements (Constantine, 1967).

Group B, inhabiting western Arizona, southern Nevada, and at least southeastern California along the Colorado River probably does migrate, but not southward into Sonora and Sinaloa. Perhaps these bats move southward into Baja California, or perhaps westward into the low interior valleys of southern California. In any case, they appear to be absent in Nevada, Arizona, and extreme southeastern California during the winter months and none has been recovered in Sonora or Sinaloa. Extensive field work, especially in the winter months, is needed to clarify the status of these populations.

Group C, inhabiting central and eastern Arizona as well as western New Mexico, appears to have a well-developed fly-way through Sonora and Sinaloa, west of the Sierra Madres. A map (Fig. 8) combining all of the movements found in this study demonstrates many of the features of this fly-way.

Group D involves the populations of central and eastern New Mexico, western Kansas, Nebraska, Texas, and adjacent portions of Mexico. Constantine (1967) reported movements to and from Carlsbad Caverns, New Mexico. With few exceptions, these involved movements within the area ascribed here to Group D. None of the exceptions (Eagle Creek Cave, Arizona, and Carbo, Sonora, as also reported above in this paper) involved movements in the same season. The findings of Davis *et al.* (1962:320) further support this concept as do the findings of Glass (1958, 1959) for bats banded in Oklahoma.

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APPENDIX 1

SUMMARY OF *Tadarida brasiliensis* BANDED, 1952-1965. LOCALITY NUMBERS CORRESPOND TO THE NUMBERS ON FIGURE 1 AND TO THE DETAILED LOCALITY DATA GIVEN IN APPENDIX 2.

Locality	Type of habitat	Date	Males	Females
Arizona: Mohave County				
1. Red Lake	Water hole	July 8, 1963	0	1
2. 5 mi. NE Topock	Sink hole	May 13, 1961	0	8
3. Jim Kane Mine	Mine	September 9, 1961	1	1
4. 1 mi. N Kingman	Water tank	July 15, 1959	0	2
		October 17, 1961	1	0
		April 18, 1962	7	0
5. SE Kingman	Water tank	September 26, 1961	4	0
6. SSE Kingman	Water tank	July 16, 1960	0	1
		August 8, 1961	0	1
7. Davis Dam	Crevices	September 17, 1960	4	2
8. Powerline Cave	Cave	August 16, 1960	80	157
		June 23, 1961	0	119
		July 25, 1962	740	826
		July 2, 1963	0	400

Locality	Type of habitat	Date	Males	Females
9. Burro Creek	Mine tunnel	March 27, 1960	0	3
		April 19, 1960	657	344
		June 6, 1961	2	0
		April 25, 1962	3	0
10. Lower Burro Creek	Mine tunnel	April 28, 1962	1	0
11. Alamo Crossing	Water tank	July 30, 1963	6	169
Arizona: Yuma County				
12. Kofa Game Refuge	Water tank	April 23, 1959	10	0
Arizona: Yavapai County				
13. Perkinsville	Railroad bridge	July 13, 1963	3	680
Arizona: Graham County				
14. Bridge no. 1	Highway bridge	March 11, 1961	1	4
15. Bridge no. 2	Highway bridge	March 11, 1961	1	1
		April 20, 1963	10	0
16. Railroad bridge	Railroad bridge	March 11, 1961	56	30
17. Bridge no. 5	Highway bridge	March 11, 1961	4	3
		March 17, 1961	1	1
18. Bridge no. 7	Highway bridge	March 11, 1961	9	14
		March 18, 1961	1	1
		February 25, 1961	2	1
19. Bridge no. 9	Highway bridge	March 11, 1961	242	161
		March 17, 1961	83	13
		September 10, 1961	0	62
		April 20, 1963	138	113
20. Bridge no. 10	Highway bridge	August 9, 1961	0	41
21. Bridge no. 22	Highway bridge	April 20, 1963	10	10
22. Safford	Building	June 21, 1959	1	0
Arizona: Greenlee County				
23. Pump station	Eagle Creek	August 18, 1958	2	2
24. Eagle Creek	Cave	August 19, 1958	26	100
		June 28, 1959	28	1710
		June 24, 1961	2900	12450
		June 23, 1962	3198	19964
		June 5, 1963	3800	33700
		June 2, 1964	750	8400
		June 27, 1964	200	1000
25. Plantsite, Morenci	Railroad tunnel	August 20, 1958	7	210
		June 13, 1959	5	95
Arizona: Pinal County				
26. Picacho 3-hole	Mine tunnel	August 25, 1955	98	284
		May 6, 1958	0	7
		May 21, 1960	0	1
27. Picacho drive-in	Mine tunnel	April 29, 1955	0	1
		August 25, 1955	3	36
		October 9, 1955	9	13
		October 16, 1955	0	1
		May 6, 1958	1	1
		May 3, 1959	0	6
		October 3, 1959	3	6
		August 28, 1960	0	1
		September 18, 1960	0	2
Arizona: Pima County				
28. Silverbell	Mine tunnel	May 10, 1963	380	2903
		June 10, 1963	133	1000
		May 1, 1964	20	100

Locality	Type of habitat	Date	Males	Females
29. Rillito	Irrigation ditch	July 14, 1958	3	0
30. Sabino Canyon	Stream	July 21, 1958	9	0
		June 2, 1961	1	0
		June 4, 1961	3	0
		June 8, 1961	1	1
		June 30, 1961	5	0
		July 12, 1961	1	0
31. Cañon del Oro	Highway bridge	May 3, 1959	1	9
		May 30, 1959	3	22
		April 9, 1960	1	0
		June 18, 1960	2	1
		June 19, 1960	0	1
		September 24, 1960	0	1
		October 1, 1960	0	1
		October 14, 1960	0	1
32. NE Tucson	Pond	April 17, 1954	10	0
		April 20, 1954	0	8
		April 22, 1954	9	0
33. Tucson	Building	November 4, 1953	13	12
34. University of Arizona campus	Building	June 29, 1955	6	39
		July 1, 1955	6	21
		July 24, 1955	3	0
		March 11, 1960	1	0
35. Gravel pit, Tucson	Water hole	June 10, 1958	0	6
		June 12, 1958	15	8
		June 13, 1958	22	25
		June 16, 1958	11	4
		June 24, 1958	1	4
		June 27, 1958	2	3
		July 10, 1958	1	1
36. Valencia Road, Tucson	Water hole	May 12, 1958	2	2
		May 21, 1958	0	1
37. Beehive Mountain	Mine tunnel	April 11, 1955	26	0
		September 6, 1955	38	140
		May 12, 1956	17	89
		May 13, 1956	8	21
		May 19, 1956	0	3
		September 27, 1956	8	13
		October 2, 1956	4	2
		September 24, 1957	3	8
		October 6, 1957	91	99
		April 24, 1958	6	22
		April 27, 1958	1	4
		April 29, 1958	4	7
		May 2, 1958	7	15
		May 4, 1958	0	6
		May 7, 1958	0	3
		May 11, 1958	0	1
		May 14, 1958	0	3
		August 16, 1958	2	3
		August 24, 1958	1	38
		September 20, 1958	0	2
		October 5, 1958	0	1
		May 3, 1958	0	4
		May 30, 1958	1	32
		September 10, 1959	0	2
		September 20, 1959	5	36
38. San Xavier Mission	Building	May 2, 1954	0	1
39. Saguaro Nat'l Monument	Cave	March 7, 1960	39	0

Locality	Type of habitat	Date	Males	Females
40. Helmet Peak	Mine	October 1, 1952	1	1
		March 28, 1953	0	1
		April 9, 1953	1	0
		April 17, 1953	1	18
		April 24, 1953	10	9
		May 10, 1953	0	31
		August 3, 1953	0	1
		April 24, 1954	3	4
		June 26, 1954	1	9
		April 11, 1955	1	9
		April 30, 1955	0	1
		May 1, 1955	1	3
		May 2, 1955	2	5
41. Twin Buttes	Mine	April 17, 1953	0	1
42. Continental	Railroad bridge	May 3, 1963	78	441
		May 16, 1963	43	476
		June 5, 1963	100	5
		June 11, 1963	0	124
43. Madera Canyon	Water hole	May 23, 1958	6	0
		May 26, 1958	0	1
		April 2, 1959	17	1
44. Fresnal Canyon	Water hole	August 1, 1961	0	5
		August 2, 1961	1	1
45. NW Sasabe	Water hole	June 10, 1962	1	2
46. Garcia's Represso	Water hole	July 15, 1958	3	6
		July 24, 1958	0	2
Arizona: Santa Cruz County				
47. Lochiel	Water hole	June 6, 1958	0	2
48. Patagonia	Water hole	June 8, 1961	1	1
49. Hayward's bridge	Bridge	March 27, 1960	3	3
		September 6, 1960	22	16
		September 11, 1960	0	1
		August 28, 1961	2	2
50. Davis' bridge	Bridge	March 27, 1960	3	3
		April 3, 1960	7	18
		October 15, 1960	1	0
		November 6, 1960	0	1
		April 15, 1961	4	6
		April 3, 1963	2	1
Arizona: Cochise County				
51. Canello	Water hole	June 17, 1960	0	2
52. Benson	Highway bridge	September 25, 1961	0	2
		June 1, 1963	10	98
53. St. David	Highway bridge	June 1, 1959	41	146
		June 22, 1959	160	160
		June 24, 1959	14	17
		July 8, 1959	3	4
		July 24, 1959	21	74
		March 27, 1960	6	8
		April 3, 1960	2	0
		May 28, 1960	12	70
		July 3, 1960	3	4
		July 4, 1960	1	1
		July 17, 1960	0	2
		June 23, 1960	0	4
		August 6, 1960	0	1
		August 18, 1960	1	3
		August 22, 1960	2	1

Locality	Type of habitat	Date	Males	Females
		August 27, 1960	2	32
		September 3, 1960	1	10
		October 8, 1960	0	1
		April 15, 1961	0	1
		May 7, 1961	0	3
		September 10, 1961	0	1
		June 13, 1962	0	8
54. St. David	Highway bridge	March 27, 1960	1	0
		May 28, 1960	1	0
55. Southwestern Research Station	Swimming pool	May, 1955 (2)	13	3
		June, 1955 (56)	56	28
		July, 1955 (1)	1	0
		August, 1955 (6)	34	7
		September, 1955 (9)	86	86
		October, 1955 (23)	101	78
		November, 1955 (2)	2	3
		March, 1956 (1)	1	1
		April, 1956 (4)	4	0
		May, 1956 (12)	21	5
		June, 1956 (13)	33	14
		July, 1956 (10)	15	1
		August, 1956 (3)	5	0
		September, 1956 (19)	35	23
		October, 1956 (12)	25	32
		November, 1956 (4)	7	5
		February, 1957 (3)	4	4
		March, 1957 (6)	2	7
		June, 1958 (6)	12	4
		July, 1958 (9)	39	3
		September, 1958 (3)	9	7
		October 15, 1958 (3)	2	0
		November 30, 1958	1	0
		June 27, 1959	12	3
		July 30, 1959	47	0
		May 24, 1963	2	0
		March 28, 1964	0	1
56. Portal	Water hole	July 2, 1958	1	0
		July 3, 1958	2	0
57. South Cave Creek	Stream	June 2, 1955	1	0
		July 11, 1958	3	1
		July 21, 1958	5	1
		August 21, 1958	0	1
58. Silver Creek	Highway bridge	May 20, 1961	65	238
		May 21, 1961	1	20
		May 22, 1961	5	38
		May 24, 1961	2	22
		May 27, 1961	11	43
		August 7, 1961	35	186
		September 10, 1961	8	194
		October 1, 1961	33	205
		June 17, 1962	43	197
		August 19, 1962	1	0
		May 24, 1963	11	11
59. Bisbee	Building	July 23, 1963	131	0
60. 10 mi. E Douglas	Water tank	April 1, 1961	1	0
New Mexico: Valencia County				
61. Galts Cave	Cave	July 21, 1963	1714	1137

Locality	Type of habitat	Date	Males	Females
New Mexico: Grant County				
62. Silver City, no. 1	Building	September 1, 1962	0	2
		September 5, 1962	15	12
		September 17, 1962	36	71
		September 19, 1962	8	6
63. Silver City, no. 2	Building	September 8, 1961	1	0
64. Silver City, no. 3	Building	October 29, 1962	64	46
		October 30, 1962	60	38
		October 31, 1962	5	11
		November 6, 1962	18	7
Mexico: Sonora				
65. Tajitos	Mine	June 28, 1963	3	4
		September 5, 1963	863	1300
		October 5, 1963	2	1
66. Carbo (see Table 5)	Cave	Various	19155	21639
67. Guaymas	Water hole	March 28, 1959	2	0
		March 31, 1959	26	0
		April 1, 1959	2	4
		April 19, 1960	1	0
		April 20, 1960	13	21
		July 22, 1961	1	0
68. Matorrena	Water hole	July 26, 1960	0	105
		July 27, 1960	0	100
69. Moctezuma	Water hole	August 5, 1961	1	4
Mexico: Sinaloa				
70. Pericos	Cave	March 2, 1963	7700	3900
Mexico: Chiapas				
71. Comitán	Cave	June 23, 1964	7	0

APPENDIX 2

DETAILED LOCALITY DATA, ASSOCIATED SPECIES, AND NAMES OF PRINCIPAL BANDERS OF *Tadarida brasiliensis* REPORTED IN APPENDIX 1.

Arizona: Mohave County

1. Mist net over water hole in Red Lake area, about 35 mi. N Kingman; netted July 8, 1963, 1 *Tadarida brasiliensis* and 1 *Pipistrellus hesperus* (Bill Musgrove).
2. Sink hole, 5 mi. NE Topock, near old railroad bed; sink hole opening about 30 feet in diameter, 40 feet deep, larger at bottom than top, and with 15 foot overhang; May 13, 1961, about 300 *Tadarida brasiliensis* in crevices; July 31, 1961, maternity colony of 400 to 500 *T. brasiliensis* (Bill Musgrove).
3. Jim Kane mine, 17 mi. NW Kingman, short tunnel about 100 feet deep; September 24, 1961, about 40 *Antrozous pallidus* and 3 *Tadarida brasiliensis* present (Bill Musgrove).
4. Mist net over water hole near rock cliffs, 1 mi. N Kingman, 3400 ft.; July 15, 1959, 31 *Pipistrellus hesperus*, 13 *Eptesicus fuscus*, 2 *Antrozous pallidus*, and 2 *T. brasiliensis*; October 17, 1961, 3 *T. brasiliensis*, 7 *Myotis californicus*, 1 *Antrozous pallidus*; April 18, 1962, 7 *T. brasiliensis*, 1 *Lasiurus cinereus*, 1 *Pipistrellus hesperus*, 1 *Antrozous pallidus*, 1 *Eptesicus fuscus* (Bill Musgrove).
5. Mist net over water hole, 1.5 mi. SE Kingman about 3300 ft.; September 26, 1961, 2 *Pipistrellus hesperus*, 4 *T. brasiliensis*, 1 *Myotis californicus*, 1 *Myotis thysanodes*, 6 *Antrozous pallidus*, 1 *Tadarida macrotis* (Bill Musgrove).

6. Mist net over water tank at windmill, 4.5 mi. SSE Kingman, about 4000 ft.; nets set for 28 nights between July 11, 1959 and July 6, 1962; only 3 *T. brasiliensis* taken during this time, but 1 *Plecotus townsendii,* 13 *Myotis subulatus,* 14 *Myotis volans,* 5 *Myotis thysanodes,* 9 *Myotis evotis,* 31 *Myotis californicus,* 39 *Antrozous pallidus,* 253 *Eptesicus fuscus,* and 486 *Pipstrellus hesperus* were also taken (Bill Musgrove).
7. Slits and crevices in Davis Dam across Colorado River; September 17, 1960, estimated 10,000 *Myotis yumanensis* and 10,000 *T. brasiliensis*; April 9, 1961, nothing; April 15, 1962, estimated 500 *T. brasiliensis* and 3500 *Myotis yumanensis* (Bill Musgrove).
8. Volcanic tube on W slope Chemehuevi Mtns., 8 mi. E Site 6 and 62 mi. SW Kingman; cave 75 by 100 feet, ceiling 25 feet high, opening 20 by 8 feet; outside temperature 86°F on August 16, 1960, 88°F to 108°F on July 2, 1963; August 16, 1960, estimated 2000 *T. brasiliensis*; July 10, 1961, about 8000 *T. brasiliensis*; April 15, 1961, nothing; July 25, 1962, about 10,000 *T. brasiliensis*; July 2, 1963, about 8000 *T. brasiliensis.*
9. Mine tunnel, about 3½ mi. E Burro Creek bridge on highway 93; March 27, 1960, about 500 *T. brasiliensis,* 1 *Macrotis waterhousii*; April 19, 1960, about 3000 *T. brasiliensis,* 25 *Myotis velifer,* 1 *Macrotus waterhousii*; July 16, 1960, 793 *Myotis velifer,* 7 *Myotis californicus*; August 7, 1960, 1 *Myotis velifer*; May 17, 1961, 102 *Myotis velifer,* 1 *Plecotus townsendii*; April 28, 1962, 30 *Plecotus townsendii,* 22 *Myotis velifer,* 3 *Tadarida brasiliensis* (Bill Musgrove, E. L. Cockrum).
10. Mine tunnel near Burro Creek, 2¾ mi. below bridge over Kaiser Spring Wash on highway 93; this tunnel visited 10 times between May 17, 1961 and April 7, 1963; *Macrotus waterhousii* and *Myotis velifer* present in numbers but only 1 *T. brasiliensis* was seen (April 28, 1962) (Bill Musgrove).
11. Mist net over water hole in Bill Williams River at Alamo Crossing; July 30, 1963, 178 *T. brasiliensis,* 6 *T. femorosacca,* 1 *Myotis velifer,* 1 *Myotis yumanensis,* 1 *Antrozous pallidus,* 1 *Macrotus waterhousii* (Bill Musgrove).

Arizona: Yuma County

12. Mist net over Horse Tank, Kofa Game Refuge; April 28, 1959, 10 *T. brasiliensis,* 2 *Eptesicus fuscus,* 1 *Antrozous pallidus* (E. L. Cockrum).

Arizona: Yavapai County

13. Railroad bridge, ½ mi. N Perkinsville; June 30, 1960, maternity colony estimated at 3000 *T. brasiliensis* (Bruce Hayward); July 13, 1963, maternity colony estimated at 3000 *T. brasiliensis* (Robert Schwab and Russell Davis).

Arizona: Graham County

14.-21. Crevices in series of highway bridges on old U.S. highway 80 east of Coolidge Dam; (locality 14) 26.4 mi. E Coolidge Dam, (15) 4 mi. E Coolidge Dam, (16) just 50 yards S of no. 15, (17) 22.7 mi. E Coolidge Dam, (18) 21.1 mi. E Coolidge Dam, (19) 18.1 mi. E Coolidge Dam, (20) 16.8 mi. E Coolidge Dam, (21) 2.6 mi. E Coolidge Dam; these bridges visited five times between February 25, 1961 and July 20, 1965. *Antrozous pallidus* present in warm months, *T. brasiliensis* present in spring and autumn (Russell Davis, Bruce Hayward, E. L. Cockrum).

22. Attic abandoned church, 3.7 mi. S Safford; June 21, 1959, 1 *Myotis velifer,* 1 *T. brasiliensis* (G. Bradshaw, Bruce Hayward, E. L. Cockrum).
23. Mist net over Eagle Creek, 1 mi. N Pump Station and *ca.* 5 mi. W Morenci, 3600 ft.; August 18, 1958, 4 *T. brasiliensis* (Alfred Gardner, E. L. Cockrum).
24. Cave, E wall of Eagle Creek Canyon, 4.2 mi. S Pump Station and 4 mi. S and 2.3 mi. W Morenci, 3500 ft.; (E. L. Cockrum, Wm. J. McCauley, Russell Davis, Bill Musgrove, Bruce Hayward, Gordon Bradshaw, Alfred Gardner, and about 30 others—see Table 5).

25. Abandoned railroad tunnel, ½ mi. S of East Plant Site, Morenci; August 20, 1958, about 500 *T. brasiliensis*; June 13, 1959, about 1000 *T. brasiliensis*; June 21, 1959, 1 *T. brasiliensis*, 5 *Myotis yumanensis*.

Arizona: Pinal County

26. Mine tunnel, SE corner Picacho Mtn. about 3 mi. SE Picacho, *ca.* 2200 ft.; visited 33 times between April 16, 1955 and October 15, 1960; up to 4000 *Myotis velifer* in summer, up to 500 *T. brasiliensis* in August, up to 100 *Macrotus waterhousii* (E. L. Cockrum, Gordon Bradshaw, Bruce Hayward, Alfred Gardner, Anthony Ross, and others).
27. Group of three mine tunnels, SW corner Picacho Mtn. about 2½ mi. SSE Picacho, *ca.* 2200 ft.; visited 22 times between July 28, 1955 and July 31, 1960; up to 42 *Antrozous pallidus*, 3000 *Myotis velifer*, 15 *Macrotus waterhousii*, 400 *Tadarida brasiliensis* (same investigators as under no. 26).

Arizona: Pima County

28. Mine tunnel and associated natural cave in "Old Silverbell" mine; May 27, 1958, 300 *Tadarida brasiliensis*; July 10, 1962, several hundred *T. brasiliensis*; May 10, 1963, 20,000 *T. brasiliensis*, 300 *Myotis velifer*; June 10, 1963, 10,000 *T. brasiliensis*, 3000 *Myotis velifer*; September 13, 1963, nothing; May 1, 1964, 1000 *T. brasiliensis* (Gordon Bradshaw, Russell Davis, Robert Schwab).
29. Mist net over irrigation ditch, 1 mi. S and 1 mi. W Rillito; July 14, 1958, 1 *Pipistrellus hesperus*, 3 *Eptesicus fuscus*, 3 *Tadarida brasiliensis*, 14 *Tadarida femorosacca*, 2 *Antrozous pallidus* (E. L. Cockrum).
30. Mist nets over various water holes in Sabino Canyon; netted 40 nights between July 21, 1958, and August 24, 1962; totals—1 *Choeronycteris mexicana*, 1 *Leptonycteris sanborni*, 3 *Myotis californicus*, 294 *Pipistrellus hesperus*, 138 *Eptesicus fuscus*, 1 *Lasiurus cinereus*, 1 *Plecotus townsendii*, 7 *Antrozous pallidus*, 22 *Tadarida brasiliensis*, 30 *T. femorosacca*, 6 *T. macrotis*, 8 *Eumops perotis* (Alfred Gardner, E. L. Cockrum, Bruce Hayward, Thomas J. Cox, Stephen Cross, Bill Musgrove).
31. Crevices under highway bridge over Cañon del Oro, 10 mi. NNW Tucson; visited 26 times between May 3, 1959, and August 5, 1962; in May to September up to 50 *Antrozous pallidus;* in May and June and September and October up to 50 *T. brasiliensis* (E. L. Cockrum, Bruce Hayward, Gordon Bradshaw, Russell Davis, and others).
32. Mist net over pond 2 mi. E, 7 mi. N Tucson; only *T. brasiliensis* taken on dates indicated (E. L. Cockrum).
33. Crevice between two buildings, downtown Tucson; November 4, 1953, about 50 *T. brasiliensis* (Lee Beatty).
34. In crevices in Library Building and Old Main Building on University of Arizona campus, Tucson (E. L. Cockrum).
35. Mist net over water hole in gravel pit, S end Cottonwood Lane, Tucson; netted eight nights between June 10, 1958, and July 10, 1958; totals—1 *Myotis yumanensis*, 8 *Myotis velifer*, 57 *Eptesicus fuscus*, 17 *Antrozous pallidus*, 106 *T. brasiliensis*, 37 *T. femorosacca* (Alfred Gardner).
36. Mist net over water hole, S side of Valencia Road, just west of Santa Cruz River, Tucson; netted six nights between April 29, 1958, and June 9, 1958; totals—14 *Myotis velifer*, 15 *Eptesicus fuscus*, 4 *Lasiurus cinereus*, 1 *Plecotus townsendii*, 5 *Tadarida brasiliensis* (Alfred Gardner).
37. Mine tunnel, W slope Beehive Mtn., Tucson Mtns.; visited 69 times between April 11, 1955, and September 23, 1961; *T. brasiliensis* present April and May and August to October, usually less than 100 but April 29, 1955, about 10,000 were present; *Myotis velifer* present about same time (E. L. Cockrum, Alfred Gardner, Gordon Bradshaw, Bruce Hayward, and others).

38. Under eaves of buildings at San Xavier Mission, SSW Tucson; about 50 *T. brasiliensis* present (E. L. Cockrum).
39. Cave in Box Canyon, Saguaro National Monument; August 5, 1958, 2000 *Myotis velifer*; August 15, 1959, 2000 *Myotis velifer*, 500 *T. brasiliensis*; March 7, 1960, 50 *T. brasiliensis*; May 11, 1960, 150 *Leptonycteris sanborni*, 35 *Myotis velifer*, 15 *Plecotus townsendii*; August 24, 1960, 2 *Leptonycteris sanborni*, 3000 *Myotis velifer*, 15 *Plecotus townsendii*, 500 *T. brasiliensis* (Alfred Gardner, E. L. Cockrum, Bruce Hayward).
40. Mine tunnel, S side Helmet Peak, 18 mi. S and 7 mi. W Tucson, 3500 ft.; visited 97 times between October 1, 1952, and May 30, 1962; *T. brasiliensis* (up to 50) March to June and August to October, *Myotis velifer* (up to 3000) April to October, *Macrotus waterhousii* (up to 50), *Antrozous pallidus* (night roost) April to October (same investigators as listed in no. 37).
41. Mine tunnel, S side W Butte of Twin Buttes, 21 mi. S and 5½ mi. W Tucson, 3500 ft.; visited 32 times between April 17, 1963, and May 20, 1962; usually nothing or only 10 to 20 *Antrozous pallidus* and 10 to 20 *Myotis velifer* present; only 1 *T. brasiliensis* seen (same investigators as no. 37).
42. Railroad bridge, 4.5 mi. S Continental; maternity colony for *T. brasiliensis* and *Eptesicus fuscus*; July 8, 1962, 1000 *T. brasiliensis*, 60 *Eptesicus fuscus*; August 8, 1962, 3000 *T. brasiliensis*, 40 *Eptesicus fuscus*; August 15, 1962, 5000 *T. brasiliensis*; March 31, 1963, 100 *T. brasiliensis*, 1 *Eptesicus fuscus;* April 3, 1963, 15 *T. brasiliensis*; May 3, 1963, 530 *T. brasiliensis*, 16 *Eptesicus fuscus*; May 8, 1963, nothing; June 5, 1963, 200 *T. brasiliensis*; June 11, 1963, 500 *T. brasiliensis*; April 24, 1964, none; June 25, 1965, 300 *T. brasiliensis*, 30 *Eptesicus fuscus* (Russell Davis, Stephen Cross, Robert Schwab, E. L. Cockrum).
43. Mist net over pond, mouth Madera Canyon, 4400 ft.; May 23, 1958, 1 *Myotis velifer*, 4 *Pipistrellus hesperus*, 6 *Eptesicus fuscus*, 2 *Lasiurus cinereus*, 8 *T. brasiliensis*; May 26, 1958, 4 *Pipistrellus hesperus*, 12 *Eptesicus fuscus*, 1 *Lasiurus cinereus*, 1 *T. brasiliensis*; April 2, 1959, 1 *Eptesicus fuscus*, 18 *T. brasiliensis*; April 10, 1959, 2 *Myotis velifer*, 1 *Myotis volans*, 1 *Pipistrellus hesperus*, 1 *Eptesicus fuscus*, 3 *Lasiurus cinereus*, 1 *Antrozous pallidus*, 6 *Tadarida brasiliensis*; April 15, 1959, 1 *Eptesicus fuscus*, 1 *Tadarida brasiliensis* (Alfred Gardner, E. L. Cockrum).
44. Mist net over pool in Fresnal Canyon, W slope Baboquivari Mtns.; August 1, 1961, 7 *Myotis velifer*, 8 *Eptesicus fuscus*, 1 *Antrozous pallidus*, 5 *T. brasiliensis*; August 2, 1961, 3 *Myotis velifer*, 1 *Myotis californicus*, 6 *Pipistrellus hesperus*, 12 *Eptesicus fuscus*, 2 *Tadarida brasiliensis* (Thomas Cox, Jaime Maya).
45. Mist net over pond in Los Encinas Wash, 8 mi. NW Sasabe, 3950 ft.; 5 *T. brasiliensis*, 8 *T. femorosacca*, 2 *Eumops underwoodi*.
46. Mist net over Garcia's Represso, 2 mi. E Sasabe; July 15, 1958, 13 *Eptesicus fuscus*, 6 *Antrozous pallidus*, 9 *T. brasiliensis*, 11 *Eumops underwoodi*; July 24, 1958, 5 *Myotis velifer*, 1 *Pipistrellus hesperus*, 1 *Eptesicus fuscus*, 4 *Antrozous pallidus*, 2 *T. brasiliensis*, 4 *T. femorosacca*, 7 *Eumops underwoodi* (A. L. Gardner).

Arizona: Santa Cruz County

47. Mist net over water hole, 3 mi. N Lochiel, June 6, 1958, 2 *Myotis velifer*, 4 *Eptesicus fuscus*, 1 *Lasiurus cinereus*, 2 *T. brasiliensis* (Alfred Gardner).
48. Mist net over water hole, 6.8 mi. N Patagonia; June 7, 1961, 1 *Myotis californicus*, 6 *Myotis keenii*, 1 *Pipistrellus hesperus*, 4 *Eptesicus fuscus*, 1 *Lasiurus borealis*, 1 *Antrozous pallidus*, 2 *T. brasiliensis* (E. L. Cockrum and others).

49. "Hayward's Bridge," crevices in bridge on old U.S. highway 89, near U.S.-Mexico border at Nogales; visited 39 times between March 27, 1960, and April 3, 1963; *Myotis velifer, Eptesicus fuscus,* and *T. brasiliensis* (Bruce Hayward, Russell Davis, Gordon Bradshaw, E. L. Cockrum and others).
50. "Davis Bridge," crevices in old highway 82 bridge across Santa Cruz R, NE Nogales; visited 21 times between March 20, 1960, and April 29, 1964; *Myotis velifer, Eptesicus fuscus, Antrozous pallidus,* and *T. brasiliensis* (same investigators as no. 49).

Arizona: Cochise County

51. Mist net over stock pond, 2.2 mi. SE Canello, 5000 ft.; 3 *Myotis velifer,* 1 *Myotis keenii,* 3 *Eptesicus fuscus,* 3 *Lasiurus cinereus,* 1 *Antrozous pallidus,* 2 *T. brasiliensis* (Bruce Hayward).
52. Whetstone Overpass of U.S. 80 over railroad, about 1.6 mi. W Benson, 4000 ft.; July 18, 1961, about 500 *T. brasiliensis*; September 25, 1961, 200 *T. brasiliensis,* 10 *Antrozous pallidus*; June 1, 1963, 125 *T. brasiliensis,* 10 *Antrozous pallidus* (Russell Davis, Robert Schwab).
53. Crevices in highway bridge, S St. David, 3800 ft.; visited 56 times between June 1, 1959, and May 24, 1963; *Eptesicus fuscus* (up to 110), *Antrozous pallidus* (up to 150) and *T. brasiliensis* (up to 360) (mainly Russell Davis, but also E. L. Cockrum, Bill Musgrove, Bruce Hayward, Gordon Bradshaw and others).
54. Crevices in highway bridge, S St. David, 4000 ft.; visited 33 times between March 27, 1960, and May 24, 1963; *Myotis velifer* (1), *Eptesicus fuscus* (up to 75), *Antrozous pallidus* (up to 45), *T. brasiliensis* (up to 3) (same investigators as in no 53).
55. Mist net over swimming pool, 5360 ft.; Southwestern Research Station, Cave Creek Canyon, Chiricahua Mtns.; netted 315 nights between May 29, 1955, and March 28, 1964 (mainly by Ellen Ordway, but many others involved).
56. Mist net over Represso, 1 mi. WNW Portal, 4900 ft.; netted three nights, total—1 *Myotis californicus,* 2 *Myotis volans,* 2 *Myotis keenii,* 32 *Pipistrellus hesperus,* 13 *Eptesicus fuscus,* 2 *Lasiurus cinereus,* 3 *Plecotus phyllotis,* 1 *Plecotus townsendii,* 3 *T. brasiliensis* (Larry Commissaris).
57. Mist net over pools in S fork Cave Creek 5400 ft.; Chiricahua Mtns.; netted 28 nights between June 2, 1955, and August 21, 1958; totals—16 *Choeronycteris mexicana,* 34 *Myotis volans,* 3 *Myotis thysanodes,* 50 *Myotis evotis,* 39 *Myotis californicus,* 3 *Myotis subulatus,* 117 *Pipistrellus hesperus,* 81 *Eptesicus fuscus,* 2 *Lasionycteris noctivagans,* 17 *Lasiurus cinereus,* 2 *Lasiurus borealis,* 18 *Plecotus townsendii,* 12 *Plecotus phyllotis,* 46 *Antrozous pallidus,* 12 *T. brasiliensis* (Larry Commisaris, Ellen Ordway, E. L. Cockrum, and others).
58. Crevices in highway bridge over Silver Creek, on U.S. 80, NE Douglas, 4500 ft.; visited 27 times between April 1, 1961, and May 24, 1963; up to 60 *Myotis velifer,* 1 *Eptesicus fuscus* (1 time only), 30 *Antrozous pallidus,* 350 *T. brasiliensis* (Russell Davis).
59. Attic of St. Patrick Church, Bisbee, 5300 ft.; July 23, 1963, about 200 *Eptesicus fuscus,* 1300 *T. brasiliensis* (E. L. Cockrum).
60. Mist net over concrete cattle tank, 10 mi. E Douglas, on Guadalupe Canyon road, 4500 ft.; April 1, 1961, 1 *Plecotus townsendii,* 1 *T. brasiliensis* (Russell Davis).

New Mexico: Valencia Co.

61. Galts Cave, about 7200 ft.; about 15 mi. S San Rafael; June 24, 1963, 5000 to 10,000 *T. brasiliensis*; July 21, 1963, 5000 *T. brasiliensis* (Robert Schwab).

New Mexico: Grant County

62.-64. In crevices in attic of buildings in Silver City, 5900 ft.; autumn transient colonies of *T. brasiliensis* (Bruce Hayward).

Mexico: Sonora

65. Mine tunnels (Mina de la Virgen), Tajitos; June 13, 1963, "several million" *T. brasiliensis*; June 28, 1963, 5000 *Leptonycteris sanborni*, 500 *Macrotus waterhousii*, 40 *Antrozous pallidus*, 500 *Tadarida brasiliensis*; August 30, 1963, 20,000 *Leptonycteris sanborni*, 50,000 *T. brasiliensis*; September 5, 1963, 50 *T. brasiliensis*; October 5, 1965, 10 *Macrotus waterhousii*, 50 *Myotis velifer*, 5 *Antrozous pallidus*, 1 *Tadarida brasiliensis* (Robert Schwab, E. L. Cockrum, Russell Davis, Robert Baker).

66. Volcanic tube, la Cueva del Tigre, 14.9 mi. SE Carbó; visited 32 times between November 12, 1967, and October 21, 1965 by many different persons (see Table 7 for results).

67. Mist net over fresh water ponds on N shore, Bocachimpampa Bay, NW Guaymas, 20 ft.; March 28, 1959, 1 *Leptonycteris sanborni*, 12 *Macrotus waterhousii*, 5 *Pipistrellus hesperus*, 2 *T. brasiliensis*; March 31, 1959, 1 *Lasiurus ega*, 26 *T. brasiliensis*, 1 *T. macrotis*; April 1, 1959, 6 *T. brasiliensis*; April 19, 1960, 10 *Macrotus waterhousii*, 10 *Pipistrellus hesperus*, 5 *Lasiurus ega*, 1 *T. brasiliensis*; April 20, 1960, 1 *Lasiurus ega*, 24 *T. brasiliensis* (Alfred Gardner, Bruce Hayward, E. L. Cockrum, Anthony Ross, and others).

68. Mist net over water hole, 2 km. SW Matorrena (NE Guaymas); July 26, 1960, 4 *Antrozous pallidus*, 108 *T. brasiliensis*, 1 *T. femorosacca*, 3 *Eumops underwoodi*; July 27, 1960, 5 *Myotis velifer*, 1 *Pipistrellus hesperus*, 1 *Antrozous pallidus*, 100 *T. brasiliensis*, 1 *T. femorosacca*, 3 *Eumops underwoodi* (Alfred Gardner).

69. Mist net over stock tank, 11 mi. W Moctezuma, 5 *T. brasiliensis* (Thomas Cox).

Mexico: Sinaloa

70. La Chinacatua, Cueva Montelargo, 17 mi. W Pericos; March 2, 1963, 5000 *Chilonycteris psilotis*, 10,000 *Pteronotus davyi*, 100,000 *Tadarida brasiliensis* (E. L. Cockrum, Wm. J. McCauley, Alfred Gardner, Russell Davis, and others).

Mexico: Chiapas

71. Cueva la Trinitaria, 19 km. SE Comitán; June 23, 1964, 40,000 *T. brasiliensis* (Alfred Gardner).

INTRASPECIFIC POPULATION STRUCTURE OF THE SPECIES PAPPOGEOMYS CASTANOPS

BY

ROBERT J. RUSSELL

Comparatively little is known about species in a multidimensional system. Complex intraspecific population structure and relationships have not, so far as I know, been described in detail for any mammal. In the course of recent taxonomic studies of the pocket gopher, *Pappogeomys castanops,* I became interested in the intraspecific relationship of populations consisting of groups of subspecies. These populations, here called subspecies clusters, seen to behave as units, and, thereby, play an important role in the evolution and differentiation of the species. I was especially interested in the way in which these populations were distinguished and the way in which they originated. The complex relationships between them involve the essential feature of populations of a species in a multidimensional system—interbreeding and, therefore, gene flow between populations. Restriction of gene flow results in divergence, and, ultimately, in the formation of separate species. A range of intraspecific compatability was found to exist between the populations of *Pappogeomys castanops.*

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ANALYSIS OF VARIATION

Intraspecific variation in *Pappogeomys castanops* occurs mainly in external and cranial dimensions. Color distinctions have developed in some populations, but most of these pocket gophers are characterized by approximately the same range of variation in pigmentation. Differences in qualitative morphological traits between the populations were not observed. On the basis of geographic variation in quantitative characters, Russell (1968:621-691) recognized 25 subspecies. At the time that geographic variation was analyzed, it was noted that the subspecies did not differ from each other either in the same combination of characters or to the same degree. Thus, the variation characterizing the species was found to be heterogeneously distributed throughout the range of *P. castanops*. Moreover, critical comparison of the subspecies, disclosed, as expected, that geographical adjacent subspecies closely resembled one another morphologically, and, therefore, could be grouped into geographic clusters. Each subspecies cluster differed from other such clusters in the same traits and usually to the same degree (see Figs. 2-13).

The subspecies cluster is here recognized as a secondary division on the population level within the species. Evidence obtained in this study suggests that the subspecies cluster tends to be permanent over relatively long periods of time and that it evolves as a population unit. Therefore, the subspecies cluster has great significance as a unit of evolution, especially in relation to divergent trends within the species. The recognition of subspecies clusters and the analysis of the complex relationships between them provide a better understanding of intraspecific trends in evolution.

In *Pappogeomys castanops,* six subspecies clusters and two geographic isolates are recognized on the basis of distribution of geographic variation. These populations have been given letter designations A through H. The geographic distribution of the clusters and isolates are depicted in Figure 1, and include the following subspecies: (A) geographic isolate, *P. c. parviceps*; (B) subspecies cluster including *P. c. consitus, P. c. perexiguus,* and *P. c. surculus*; (C) subspecies cluster including *P. c. subnubilus, P. c. elibatus, P. c. planifrons,* and *P. c. peridoneus*; (D) subspecies cluster including *P. c. goldmani* and *P. c. rubellus*; (E) subspecies cluster including *P. c. excelsus, P. c. subsimus, P. c. jucundus, P. c. sordidulus,* and *P. c. ustulatus*; (F) subspecies cluster including *P. c. clarkii, P. c. pratensis, P. c. perplanus, P. c. simulans,* and *P. c. castanops*; (G) geographic isolate, *P. c. hirtus*; (H) subspecies cluster including *P. c. bullatus, P. c. tamaulipensis, P. c. angusticeps,* and *P. c. torridus.*

Several of the subspecies included in subspecies clusters may actually be geographic isolates. If so, they evidently have only recently become isolated, and have not developed significant distinctions from the other taxa in the subspecies cluster to which they are assigned. For instance, *P. c. torridus* of population H is probably now isolated from *P. c. angusticeps* to the east, and *angusticeps* is separated from *P. c. bullatus* to the south by the Rio Grande. The Rio Grande probably serves only as a filter barrier for these pocket

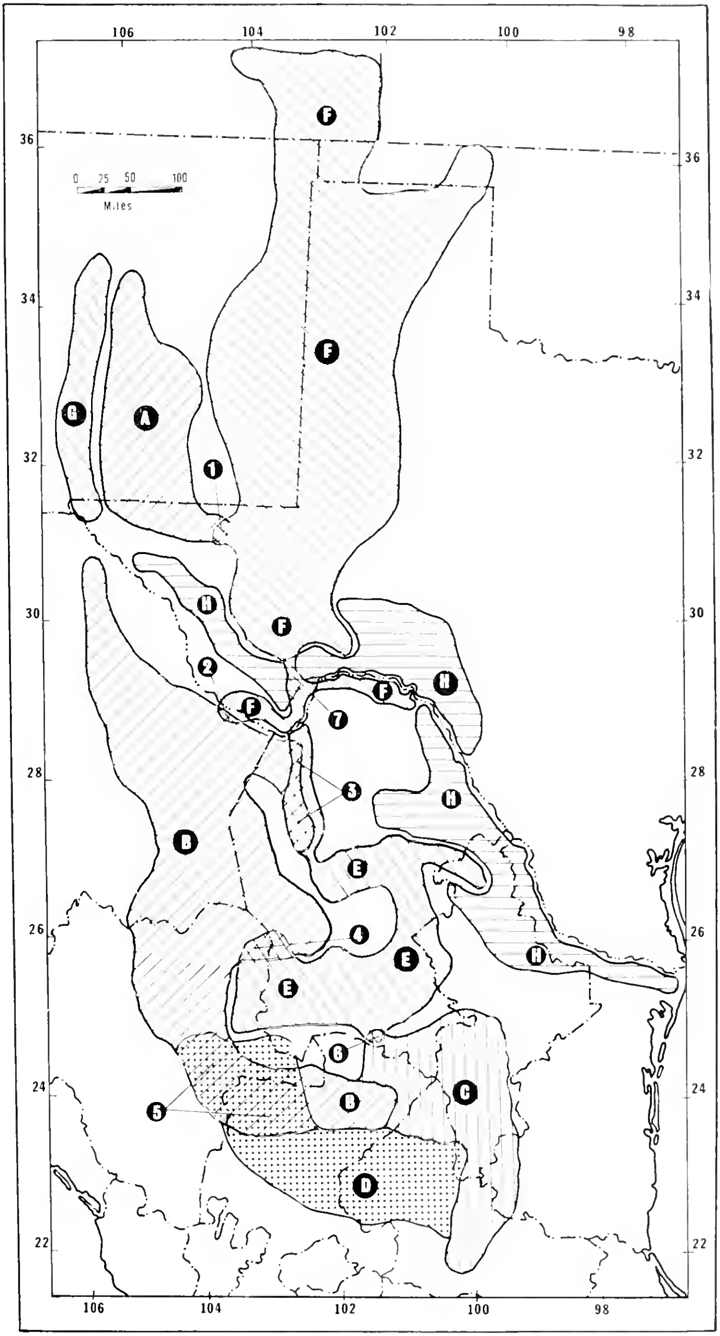

FIG. 1. Distribution of intraspecific populations of *Pappogeomys castanops* depicting subspecies clusters and geographic isolates (A-H) and the areas where either sympatry (1-6) or secondary intergradation (7) occurs. For detailed explanation, see text.

gophers; therefore, gene flow is only reduced, not totally restricted. In population F, records of occurrence indicate that *P. c. clarkii* probably no longer has contact with either *P. c. pratensis* to the north or with *P. c. sordidulus* to the south (a subspecies of population E). Also in population E, *P. c. ustulatus* evidently has become isolated recently from *P. c. jucundus* to the west.

The subspecies that comprise any one of the population clusters cannot be reduced to one taxon owing to the wide range of variation that is heterogeneously distributed among the included subspecies. The range of variation characterizing a subspecies cluster yields high coefficients of variation, suggesting that the sample is heterogeneous. Since variation due to sex and age has been eliminated, the significantly high coefficiency must be ascribed to taxonomic variation of the geographic races that make up the population cluster. It should be pointed out, however, that neither the population clusters nor the geographic isolates are at once obvious. Only after careful analysis of subspecific variation was I able to define these population units.

Twelve metric characters were analyzed. The result is represented by histograms in Figures 2-13. Ten of the characters are cranial dimensions and two are external dimensions.

Condylobasal length (see Figure 2).—Of the characters studied, condylobasal length was found to have the greatest range of variation. On the basis of this character, populations of *Pappogeomys castanops* fall into two distinct and sharply defined groups, one characterized by short skulls including populations A, B, and C, and the other characterized by long skulls including populations E, F, G, and H. Population D is intermediate, both morphologically and geographically (see map, Fig. 1), between the two divergent groups.

Of populations A, B, and C, population C, although it occurs in a relatively small geographical area compared with B, has a much greater range of variation in condylobasal length. Also population B, a subspecies cluster, yields slightly more variation than population A, an isolated subspecies.

Comparison of populations E, F, G, and H reveals that both E and F (both subspecies clusters) are about equally variable and that G, a single isolated species, shows, as expected, considerably less variation than the subspecies clusters. Of these populations, the skull of H is significantly shorter, overlapping the range of variation developed in the group with shorter skulls (A, B, and C).

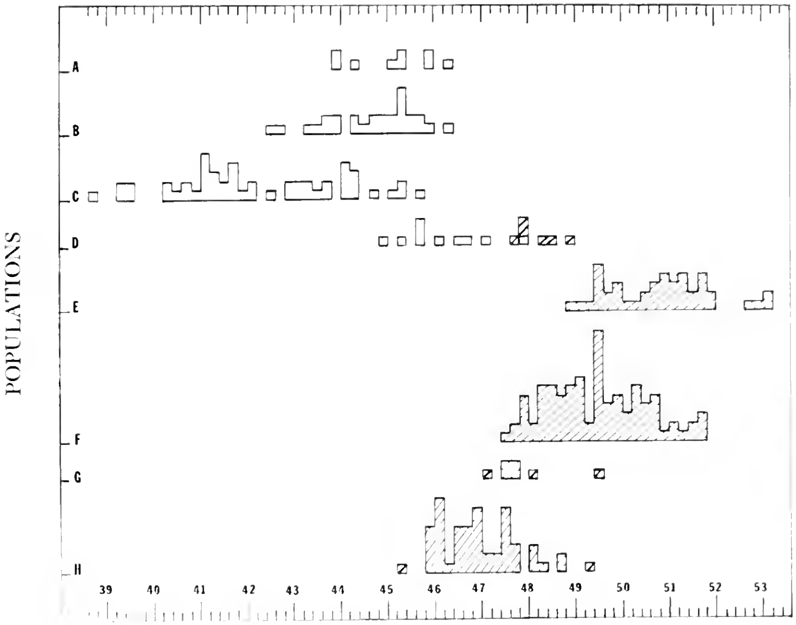

FIG. 2. Histograms of condylobasal length (mm.) in intraspecific populations of *P. castanops*.

The highest degree of distinction in condylobasal length of E, F, G, and H, as compared with A, B, and C, is developed in population E. Populations F, G, and H show progressively less distinction, although all but H fail to overlap the maximum range of variation developed in A, B, and C.

Length of palate (see Figure 3).—Length of palate is separated into two distinct groups—one characterized by a short palate, including populations A, B, and C, and one characterized by a long palate, including populations E, F, G, and H. Population D is characterized by a range of variation that overlaps both the maximum variation of C and the minimum variation of E, and, as in condylobasal length, this character provides dimensions intermediate between the shortest measurements of the palate in population C and the longest in E.

Compared with populations A, B, and C, population E is the most distinct. Indeed, there is no overlap in the ranges of minimum-maximum variation, a significant fact considering that the geographic ranges of B and C are contiguous with that of E. Only slight overlap obtains between populations A, B, and C and

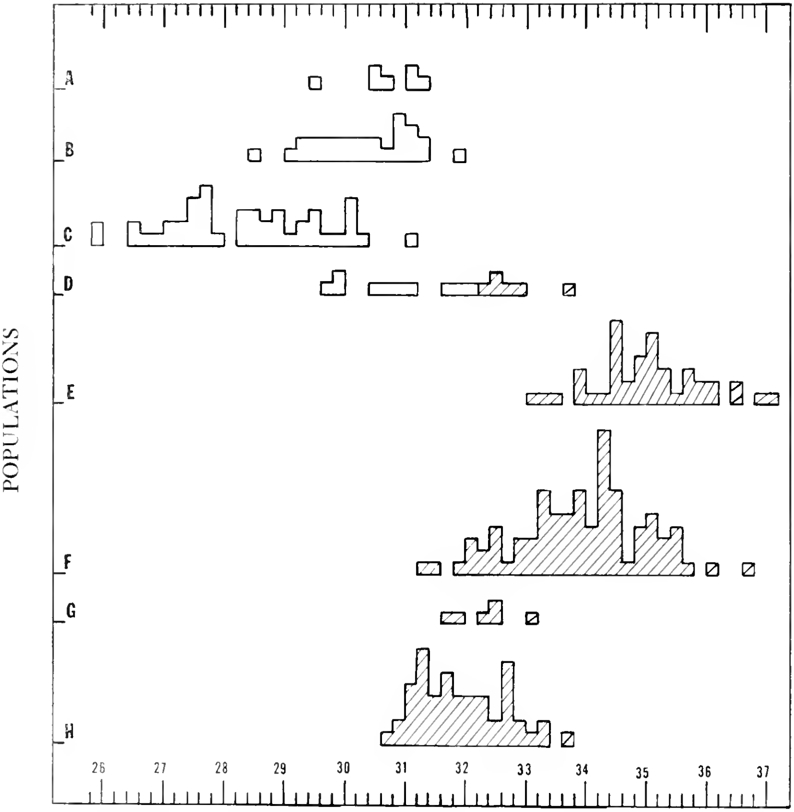

FIG. 3. Histograms of length of palate (mm.) in intraspecific populations of *P. castanops*.

populations F and G; only populations A and B are in geographic contact with F and G. The least distinction is developed in population H in comparison with A, B, and C. In this case, a significant proportion of the smaller individuals of population H have palates no longer than those at the maximum range of variation in A, B, and C.

Of the group with short palates, population C has a greater range of variation than does either A or B, and, of the group with long palates, population F provides the greatest range of variation. The range of variation in population H is less than that of E and F, and although H broadly overlaps F, there is only slight overlap with E.

Palatofrontal depth of skull (see Figure 4).—The populations show less distinctiveness in palatofrontal depth than they do in condylobasal length and palatal length; the same pattern of variation is evident but with less of a degree of difference and with decidedly more overlap between populations. Major population groups within the species can not be separated readily on the basis of this character.

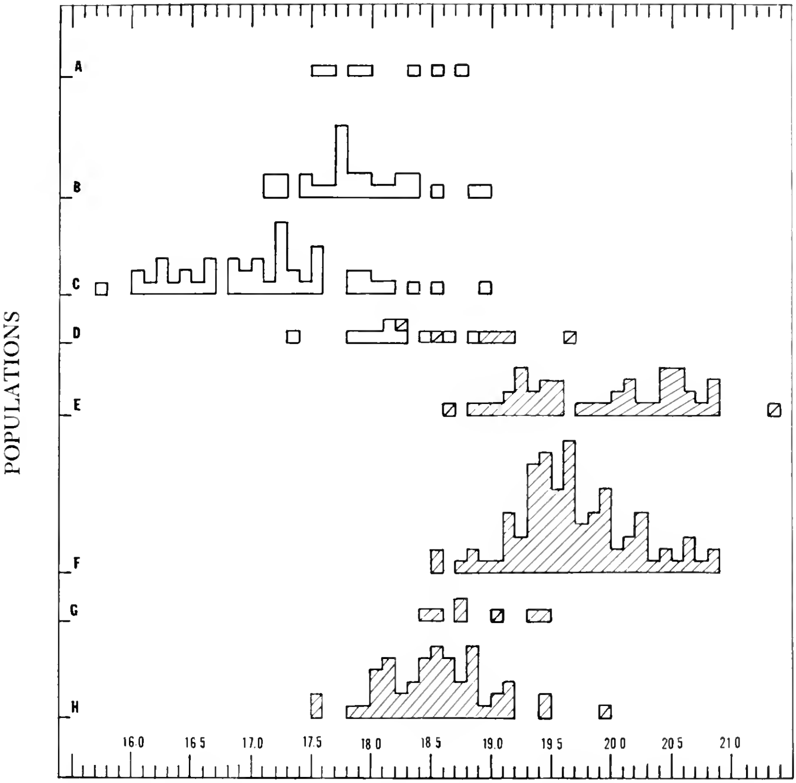

FIG. 4. Histograms of palatofrontal depth of skull (mm.) in intraspecific populations of *P. castanops*.

Even so, the shallowest skulls are found in populations A, B, and especially C, and the deepest skulls in populations G and H, and especially E and F. The variations of populations E and F differ little from each other in this character; both are significantly larger than population H. As in other features, the greatest degree of difference is found between populations C and E, but, in this case, populations C and F are equally distinct. Geographically and morphologically, populations E and C are linked by population D, which links the two extremes. The greatest range of variation of

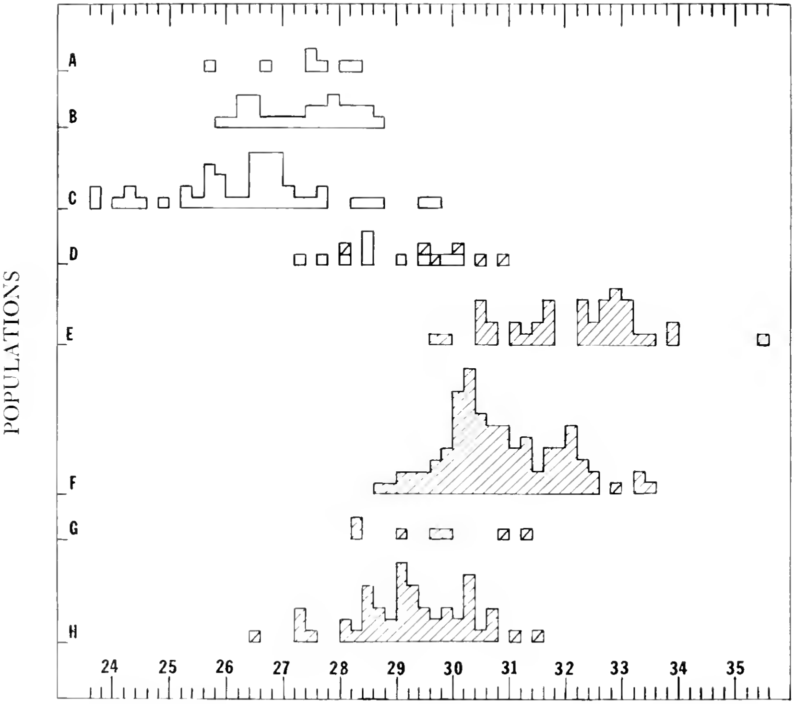

FIG. 5. Histograms of greatest zygomatic breadth (mm.) in intraspecific populations of *P. castanops*.

any single population is developed in population C. Population H more broadly overlaps A, B, and C than any of the other populations with deep skulls.

Zygomatic breadth (see Figure 5).—Zygomatic breadth, measured across its greatest distance, depicts the same pattern as observed in other characters; however, the degree of overlap between population H and populations A, B, and C is greater than in either condylobasal length, length of palate, or palatofrontal depth. Regardless, the narrowest skulls are developed in populations A, B, and especially C, and the broadest in populations E, F, and G, and to a lesser degree H. Population D provides an intergrading series between E and C, both of which overlap slightly in their ranges of variation in this trait.

Zygomatic breadth is especially useful in separating populations A and B from populations F and G. All four occur in geographically adjacent regions (see map, Fig. 1). Population B also occurs adjacent to the range of population C, and both are clearly distinguished in this character. The greatest range of variation was observed in population C, in which the range of variation exceeds both the minimum and maximum variation of populations A and B.

Squamosal breadth (see Figure 6).—The distinctiveness of the populations is not so clearly defined in squamosal breadth as it is by zygomatic breadth, but the same pattern of population variation emerges. Indeed, the patterns between these two measurements of cranial breadth are quite similar. The narrowest skulls are characteristic of populations A, B, and C, and the broadest skulls are found in populations E, F, G, and H. The greatest extremes in minimum-maximum breadth, as in zygomatic breadth, are developed in populations C, E, and F, respectively. As in other dimensions, the two groups are connected by the intermediate and overlapping range of variation found in population D.

The overall trend in divergence is apparent in Figure 6; however, squamosal breadth is useful taxonomically only in separating

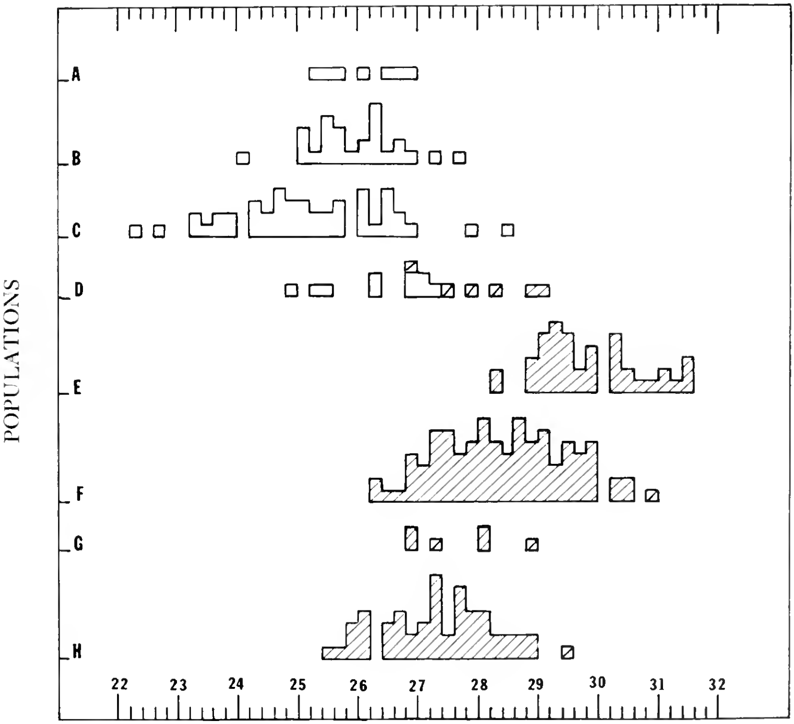

FIG. 6. Histograms of squamosal breadth (mm.) in intraspecific populations of *P. castanops*.

population E from A, B, and C; only a slight overlap in minimum-maximum dimensions occurs (with C) between these particular populations. The distinctions between populations F and H are less developed in this character and the minimum of the ranges of variation in both populations broadly overlap the maximum ranges of variation of populations A, B, and C.

The highest degree of variation obtained in any one population, once again, was found in population C, and, as in zygomatic breadth, the range of variation in C exceeds both the minimum and maximum variation in A and B.

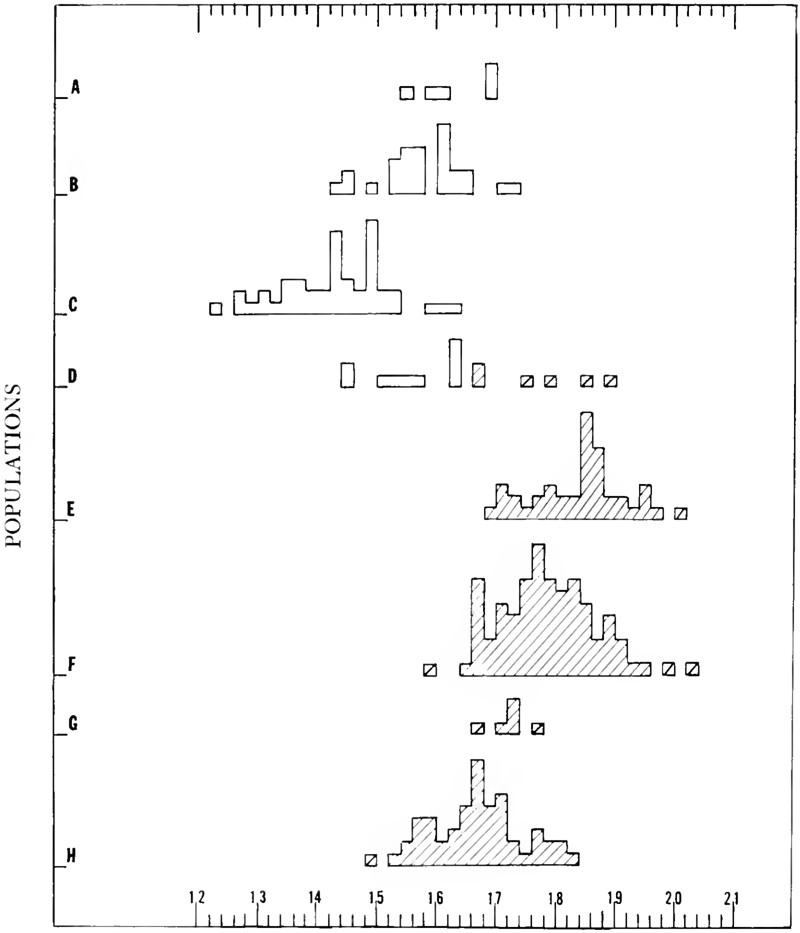

FIG. 7. Histograms of length of nasals (mm.) in intraspecific populations of *P. castanops.*

Length of nasals (see Figure 7).—The pattern of population variation noted in the preceding characters is weakly developed in length of nasals. As usual, the shortest nasals are developed in populations A, B, and C, and the longest nasals are in E, F, G, and H, but the degree of overlap is more extensively developed than usual. Population D provides an intermediate range of variation between the two groups.

The distinction between the two groups in length of nasals is more highly developed between population C and population E than between other populations of the two groups. The lack of overlap in the ranges of variation of this character in C and E is significant in view of the fact that they occupy adjacent geographic ranges. Only slight overlap occurs between B and E, which also occur in adjacent geographic areas. The distinction between these adjacent populations also is reflected in population D, where the intergrading series includes samples referable to the small group of subspecies on the lower end of the gradient and some referable to the large group of subspecies on the upper end of the gradient, without overlapping. This is the only example where the range of variation of population D exceeds that of population C.

Population F and especially H are less clearly distinguished from A, B, and C, and all five populations broadly overlap in variation. Distinctions between A, B, and C, and F, G, and H are poorly defined.

Length of rostrum (see Figure 8).—The populations have developed the same pattern of variation in length of rostrum as developed in other cranial dimensions. The shortest rostra are characteristic of populations A, B, and C and the longest rostra in E, F, G, and H. As in other characters, population D indicates intergradation between the two groups.

Differences among the populations with short rostra (A, B, and C) is not great, with the exception of A, which has developed longer rostra than usual for the group. Also, in the populations with long rostra (E, F, G, and H), the differences are not significant, except in population H, which has decidedly shorter rostra. Even so, the range of variation in H broadly overlaps that of E, F, and G as well as A, B, and C.

Difference in length of rostrum between the two groups, therefore, is especially significant between populations B and C of the small group and E and F of the large group. In fact, there is no overlap between B-C and E in the samples available to me, and

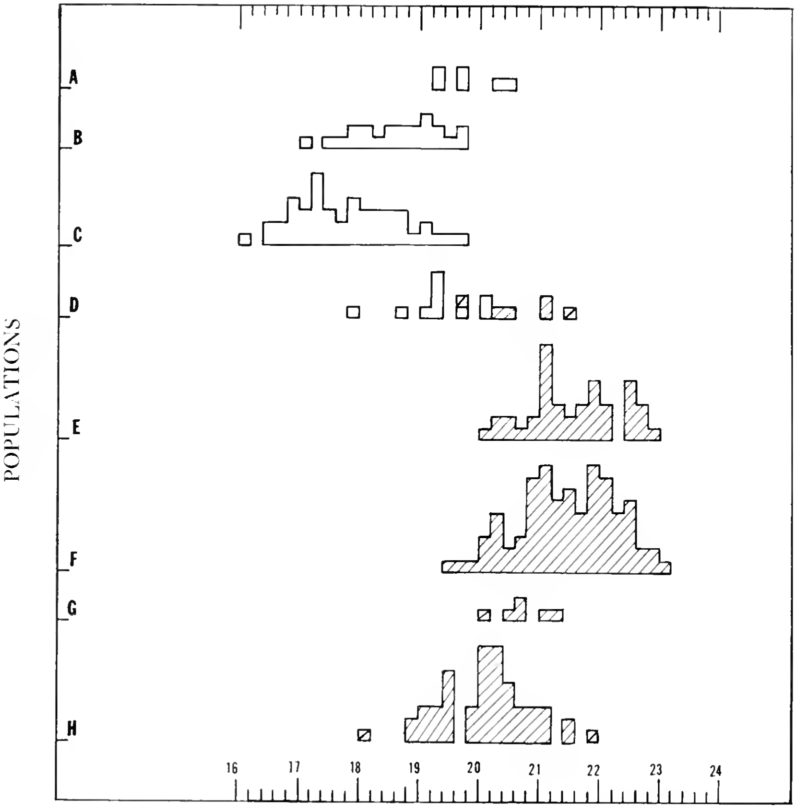

FIG. 8. Histograms of length of rostrum (mm.) in intraspecific populations of *P. castanops*.

only slight overlap between B-C and F. The overlap between A and F-G is noteworthy because these three populations have adjacent ranges. Of course, population H is not in geographic contact with any of the small populations (A, B, and C).

The minimum-maximum range of variation between populations C, D, F, and H is comparable, being only slightly greater in population H.

Breadth of rostrum (see Figure 9).—The narrowest rostra are characterized by populations A, B, and C, and the broadest by E, F, G, and H, especially E and F. As in other dimensions, population D yields a range of variation intermediate between the small and large groups, and, unlike some of the other characters, the variation of the representatives of the two groups that comprise population D broadly overlap.

Although the two groups show a tendency toward divergence in breadth of rostrum, the trend is not so strongly developed in this character as in other measurements. Therefore, broad overlap is observed in the minimum-maximum ranges of variation of the two groups. The greatest degree of difference between the two groups occurs between populations C and E. Less distinction and more overlap than usual is found between the contiguous populations A-B and E-F, although those populations of F that have actual geographic contact with populations of both A and B are composed of individuals that provide the upper range of the variation ascribed to F. In the usual pattern, population H is decidedly smaller than F and especially E, but, in breadth of rostrum, H completely over-

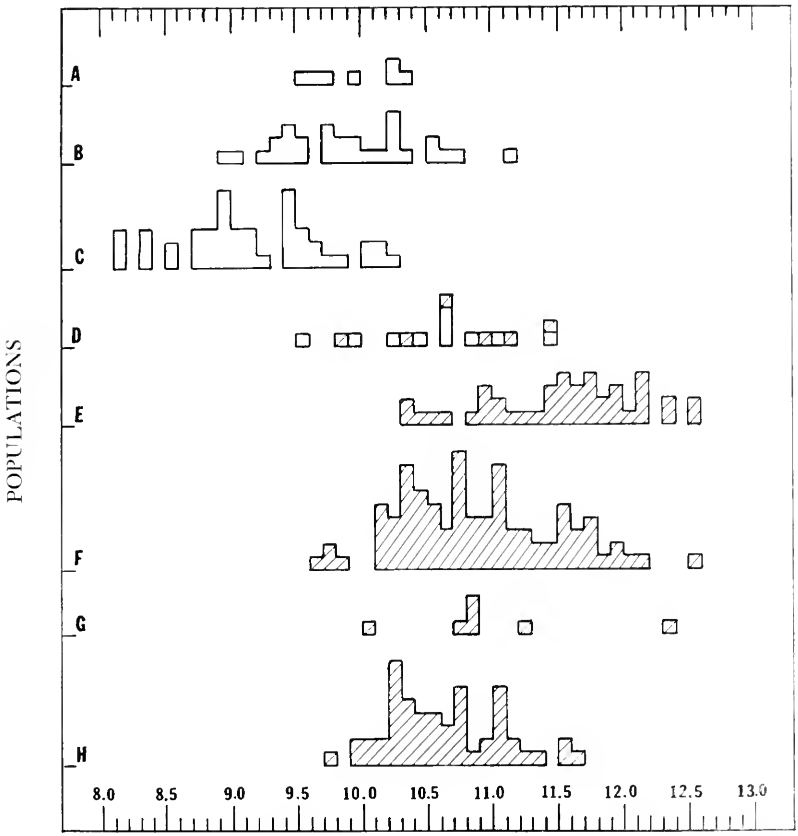

FIG. 9. Histograms of breadth of rostrum (mm.) in intraspecific populations of *P. castanops*.

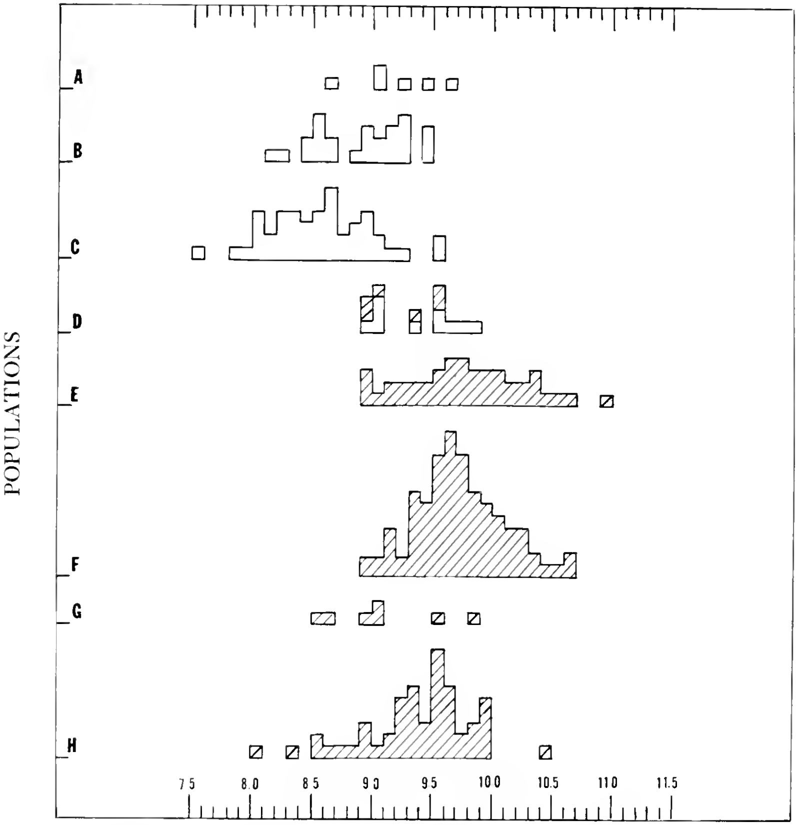

FIG. 10. Histograms of alveolar length of maxillary toothrow (mm.) in intraspecific populations of *P. castanops*.

laps F and broadly overlaps E. However, individuals of population H do not obtain so great a breadth as the largest in E, F, or G.

Population B of the small group has a greater maximum variation than either A or C. Unusually broad rostra are developed in local populations in the northern (Chihuahua) part of the range of population B.

Alveolar length of maxillary toothrow (see Figure 10).—The populations studied differ less in length of maxillary toothrow than any other cranial feature, except for breadth of braincase. Even though the distinctiveness of each population is minimal, the same pattern of variation developed in other cranial features emerges. Although broadly overlapping in range of variation, the populations with the shortest toothrows tend to be A and especially B and C.

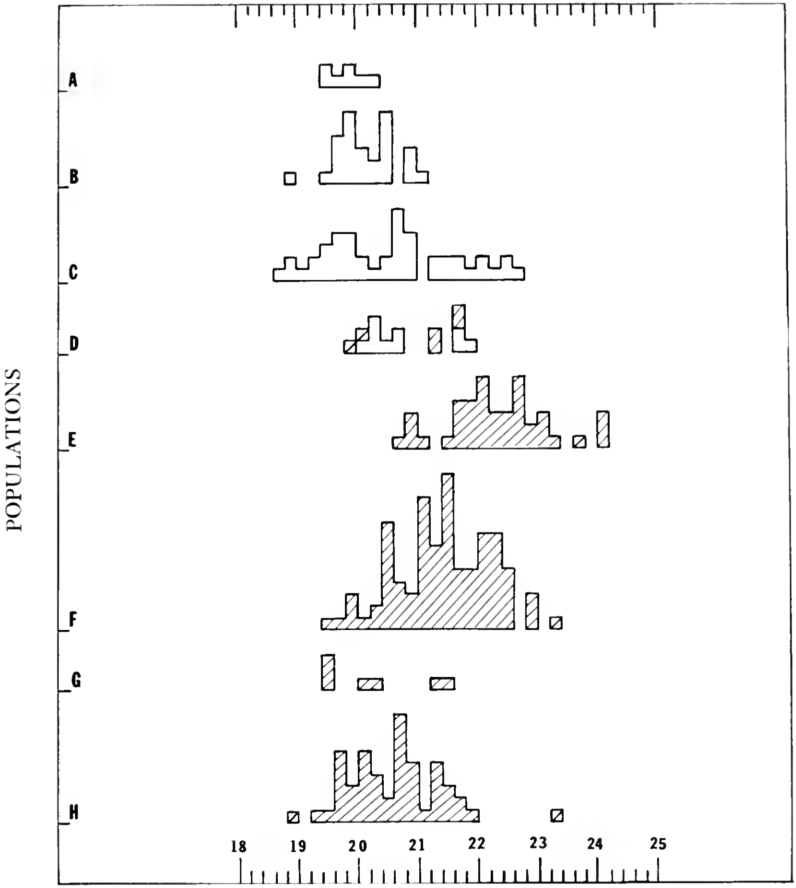

FIG. 11. Histograms of breadth of braincase (mm.) in intraspecific populations of *P. castanops.*

The greatest degree of overlap of populations A, B, and C is with populations G and H. Those with the longest toothrows are E and F. In population D, representatives of the two subspecies groups intergrade completely, with no indication of divergence.

As is usually the case, the smallest individuals are found in population C and the largest in population E. Also, the highest degree of distinction occurs between populations B-C and E-F. In this feature, population H, rather than C, yields the highest degree of variation.

Breadth of braincase (see Figure 11).—Significant overlap is developed in breadth across the braincase between all the populations except A, a geographic isolate, and E. The congruity of the populations in this feature largely obscures the characteristic pattern of variation noted in most other cranial characters analyzed; however, a tendency toward divergence still can be ascertained by comparing population E with populations A, B, and C. The braincase in populations A, B, and C is not significantly narrower than other populations (F, G, and H); rather, there is a weakly defined trend toward a broader than usual braincase in population E. Yet broad overlap occurs with other populations. Aside from population E, breadth of braincase averages slightly greater in population F as compared with the other populations.

Although some difference is developed between the geographically adjacent populations C and E, the intergrading series D shows no tendency toward divergence. Both populations C and H show a greater range of variation than the other populations; but that of H is due entirely to one individual, which has a considerable broader braincase than is usual for that population.

Length of head and body (see Figure 12).—Two external dimensions were analyzed, length of head and body and length of hind foot. Both show a considerable range of variation when lumped in subspecies clusters, although length of hind foot sometimes distinguishes two or more of subspecies included within the subspecies clusters. Total length is especially variable owing to the high degree of individual variation of the length of tail in these pocket gophers. The length of head and body (total length less length of tail) is a much more reliable character in the study of geographic variation, and the population relationships of subspecies clusters are defined more clearly in length of head and body than in other external features in this species.

The pattern observed in most of the cranial dimensions is evident in length of head and body; but, the range of overlap between most populations is great, especially observed in populations A, B, and C when compared with F, G, and H. There is no significant difference among populations A, B, and C of the small group or F, G, and H of the large group. However, there is a weakly developed, but nonetheless clearly defined, trend toward larger size in population E of the large group.

The tendency toward large size in population E is noteworthy because this population has evidently had longer contact with the small group (C, D, and especially B) than have other populations of the large group (F, G, and H). This difference suggests a trend

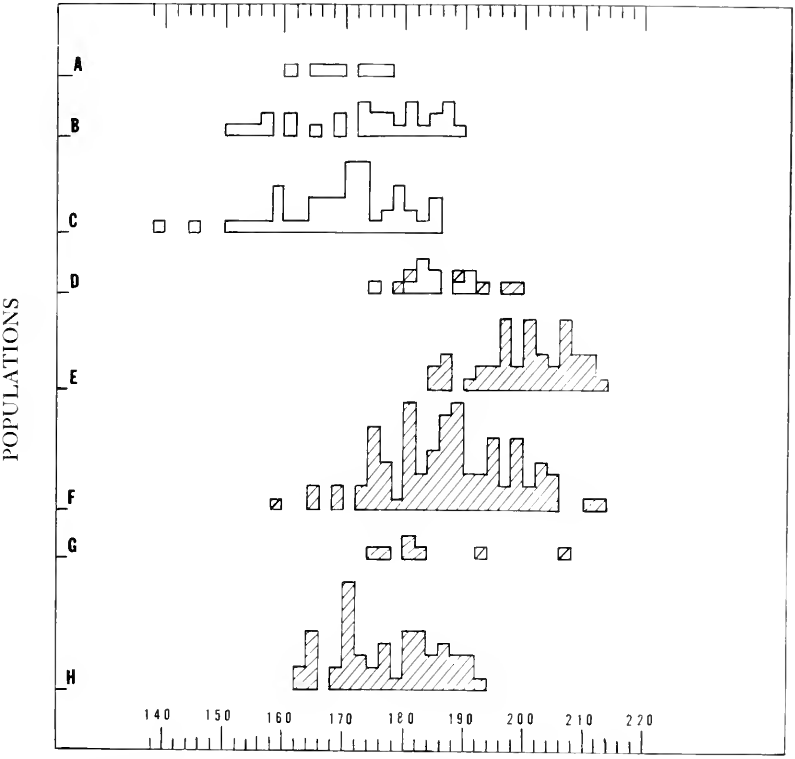

FIG. 12. Histograms of length of head and body (mm.) in intraspecific populations of *P. castanops*.

toward larger size in population E. Moreover population D, which includes an intergrading series between population E and C, clearly is intermediate between these two populations. For instance, gophers in population D are greater in maximum size than those of population H, which is the population least distinguished from A, B, and C.

The smallest individuals, as in most cranial characters, are found in population C and the largest in E. The greatest range of variation was observed in population F.

Length of hind foot (see Figure 13).—Length of hind foot was recorded in whole numbers; hence, this accounts for the even spacing between bars in the histograms. However, when a particular variable occurred at a higher frequency than could be conveniently recorded in the diagram, the bar was doubled, or in one case (F) tripled, by duplicating the bar behind the initial one with as many

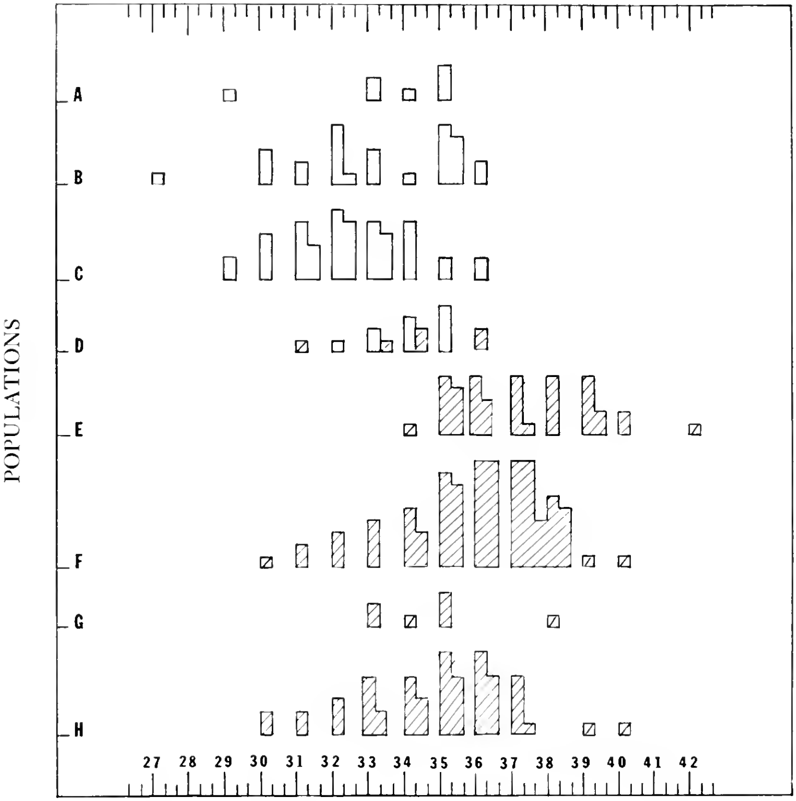

FIG. 13. Histograms of length of hind food (mm.) in intraspecific populations of *P. castanops*.

squares as necessary. The same system was used in population D, where two subspecies, one from each of the major groups, are included in the same subspecies cluster; however, in this case each is distinguished in the diagram by difference in shading.

Variation in length of hind foot shows an overall pattern that resembles in general that of length of head and body excepting that it is not so strongly developed. No significant difference could be ascertained between populations A, B, and C or populations F, G, and H. Moreover, the distinction between the small group (A-C) and the large group (E-H) is weakly developed. Only in population E, as in length of head and body, is there a tendency toward deviation from the other populations in that there is a poorly defined trend toward greater length of the hind foot, emphasized in comparison with other populations of the large group by the lack of extreme measurements at the minimal range of variation. This suggests that selection is favoring divergence in population E by elimination of smaller-sized individuals. Unlike length of head and body, population H shows no tendency toward distinctiveness.

There is a tendency in all populations for development of a relatively wide range of variation in length of hind foot. In most populations, individuals are recorded that are characterized by an extreme measurement separated by a significant hiatus from the main body of the population. This is especially noted in populations A, B, E, G, and H.

POPULATION STRUCTURE

Analysis of geographic variation in *Pappogeomys castanops* discloses a complex relationship between populations and groups of populations. One of the fundamental disclosures is that subspecies may be grouped into intraspecific population units, here called subspecies clusters. Each subspecies cluster has a well-defined geographic range, and, of course, all of the individual and mutually exclusive ranges of the subspecies of each cluster are contiguous. The analysis of variation in the preceding section shows that all of the subspecies that comprise a cluster are characterized by a similar pattern of variation. This suggests that the subspecies of a particular cluster occur under fairly uniform environmental conditions throughout the geographic range occupied by that cluster. Therefore, the populations of the cluster are subjected to the same or similar selection pressures resulting in the strong resemblance of patterns of variation among the member subspecies of a cluster.

The fact that the subspecies of a cluster do differ significantly from each other, usually in combinations of several features (see Russell, 1968:621-691), offers evidence suggesting that the direction and intensity of selection is not precisely the same everywhere within the range of the cluster. Hence, divergence on a minor scale is occurring among the subspecies of a cluster, allowing perhaps for a more precise adaptation to environmental optima from place to place over the geographic range of the cluster. Evidently, the environmental conditions and, concomitantly, the selective pressures vary between the different subspecies clusters. The interaction of these evolutionary agents have produced significant divergence between the subspecies clusters. As to be expected, the degree of divergence between particular subspecies clusters varies, being greater in some cases than in others. It is of interest to note that the differences between subspecies clusters are greater than the differences between the subspecies of a cluster.

Therefore, intraspecific population structure in *Pappogeomys castanops* is organized into population units greater in scope than the subspecies. These population units consist of two or more subspecies that are characterized by a unique pattern of variation, occupy a specific geographical range, and evidently evolved as a unit. No doubt, the subspecies clusters of *Pappogeomys castanops* have some degree of constancy in time because they have developed distinctive characteristics.

Population units below the level of subspecies include local populations and demes. The variation and relationships of these small units are not analyzed in this report for lack of appropriate data. Huge collections, including samples from all places of occurrence, would be necessary for a detailed study of this sort; to my knowledge, none has been made.

Not all subspecies are united into clusters. In *Pappogeomys castanops*, two are clearly geographic isolates. In analyzing the geographic variation of the species, the isolated subspecies were treated along with the subspecies clusters; however, their range of variation is not so great as that of the clusters and their distinctiveness is not so sharply defined. In both cases, the geographically isolated subspecies could have been assigned to one of the neighboring subspecies clusters (geographic isolate A to cluster B and geographic isolate G to cluster F) without difficulty. Probably, each originated in the not-too-distant past from (or along with) the subspecies group with which the closest relationship exists. However, the geographically isolated subspecies are discrete population units owing to the lack of gene flow with neighboring populations, and, therefore, deserve to be analyzed separately. Considering long range evolution, however, I do not regard them to be as important as the subspecies cluster because they have neither the store of variability nor the potential for mutation of the larger population units.

The four subspecies of one cluster, population H (see preceding section), actually may be a collocation of geographic isolates. Certainly the Rio Grande restricts gene flow between *P. c. bullatus* and *P. c. angusticeps*, and mountains at least restrict, if not prevent, gene flow between *P. c. angusticeps* and *P. c. torridus*. Geographically intermediate populations between *P. c. bullatus* and *P. c. tamaulipensis* of the lower Rio Grande Valley have not been secured. However, all four subspecies are closely related, and, therefore, are treated as a subspecies cluster. Isolation, if it exists, is probably of recent origin.

The sharp discontinuity between subspecies clusters, relative to that between subspecies of a cluster, is especially noteworthy. The subspecies clusters meet along narrow zones or belts of intergradation as indicated in Figure 1. The abrupt shift from one characteristic range of variation to a different and equally characteristic range of variation indicate secondary zones of intergradation where the ranges of subspecies clusters abut. Secondary zones of intergradation suggest secondary contact after prior geographic isolation. On the other hand, zones of contact between subspecies of the same cluster are characteristic of primary zones of intergradation that have developed in the absence of geographic isolation (not shown in Fig. 1, but see Russell, 1968:622). Evidently, the member subspecies of a cluster have developed while in geographic contact and not while isolated, at least not while isolated for significant periods of time.

There seems to be no restriction to gene flow between contiguous subspecies of the same cluster, thus contributing to the cohesiveness of the population unit. To the contrary, evidence suggests that there is some restriction to gene flow between subspecies clusters, more in some cases than in others. For instance, no evidence of intergradation could be found between subspecies clusters E and H where their ranges meet in north-central Coahuila; however, secondary intergradation occurs between clusters H and F in the vicinities of Sanderson and Dryden, southwestern Texas (see Russell, 1968:632). Reduction of gene exchange between adjacent subspecies clusters would be advantageous in promoting local adaptation by preventing the destruction of advantageous gene combinations through the introgression of foreign genes. The unique gene combinations of each subspecies cluster are maintained, therefore, by the low incidence of gene introgression. Whether there is selection against intergrades in the secondary zones of intergradation or some restriction to interbreeding between individuals of different subspecies clusters is not known; however, I would suppose that the former is more likely the case.

Even so, owing to the intraspecific population structure, a situation exists that lends itself to the ready establishment of reproductive isolation between subspecies clusters. If lengthy geographic isolation occurs, the already divergent populations may develop biological isolating mechanisms that will severely restrict or prevent interbreeding once the isolated populations have re-established contact. Evidently, such is the case between populations A, B, and C and populations E, F, G, and H in *Pappogeomys castanops.* As pointed out in a preceding publication (Russell, 1968:623-627 and 769-771), there are a number of places (points 1, 2, 3, 4, 5, and 6 on Fig. 1) where the ranges of these two groups are sympatric with no evidence of interbreeding, and in these areas they behave as full species.

That populations A, B, and C are referable to the same species as populations E, F, G, and H is established by a chain of interbreeding populations between population C and E. However, this can be demonstrated in only one geographic area—southwestern San Luis Potosi, northern Zacatecas, and eastern Durango. The intergrading populations consisting of two subspecies, *P. c. rubellus* and *P. c. goldmani,* are included here in population D, which in most characters (see Figs. 2-13) clearly depicts the intermediate relationship between the two distinctly different subspecies clusters (populations C and E) that it connects. Save for gene flow between the populations in this area, the two groups of subspecies could be recognized as two separate, albeit closely related, species. Russell *(loc. cit.),* recognizing these distinctions, assigned the populations to one of two subspecies-groups: populations A-C to the *subnubilus*-group (unshaded histograms) and E-H to the *excelsus*-group (histograms with diagonal lines in Figs. 2-13). Population D, the intergrading series, includes two subspecies, one *(P. c. goldmani)* referable to the *excelsus*-group and the other *(P. c. rubellus)* referable to the *subnubilus*-group.

Examination of Figures 2-13 reveal that those populations of the *excelsus*-group that are in contact with populations of the *subnubilus*-group have developed the greatest degree of difference. In contrast, subspecies cluster H, which has no contact with the populations of the *subnubilus*-group, has developed the least degree of differentiation. Moreover, subspecies cluster E, which has probably been in contact with the *subnubilus*-group longer than any other populations of the *excelsus*-group (see discussion beyond), is characterized, considering the entire cluster, by the highest degree of differentiation. This example of character displacement (see Brown and Wilson, 1956:49-64) or character divergence (Mayr, 1963:82-86), suggests that the *excelsus*-group has responded to sympatry with the *subnubilus*-group by divergent evolution, resulting in an increase in cranial dimensions. Therefore, most cranial dimensions of populations G, F, and especially E are significantly larger than those of the *subnubilus*-group (see Figs. 2-9), usually with only slight overlap, or no overlap, in the respective ranges of variation.

On the other hand, most cranial distinctions between population H and the *subnubilus* populations are not great and usually are characterized by broad overlap in their ranges of variation. Evidently, since population H has had no contact with the *subnubilus*-group there has also been no selection pressure toward character divergence. Therefore, population H of the *excelsus*-group shows closer resemblance to the *subnubilus*-group than do adjacent populations of the *excelsus*-group.

Also, there is less resemblance between population H and populations E, F, and G of the *excelsus*-group than there is among E, F, and G. Indeed, as mentioned above, field data indicate that populations H and E may not interbreed where they are in contact in north-central Coahuila. Russell (1968:634) could find no evidence of intergradation between *P. c. bullatus* (subspecies cluster H) and *P. c. ustulatus* and *P. c. jucundus* (subspecies cluster E) in this area. However, population H does intergrade with population F both in northern Coahuila (Russell, *loc. cit.*) and in eastern part of the Trans-Pecos region of Texas (Russell, *op. cit.*: 632). Moreover, the subspecies *P. c. pratensis* of population F, occurring in the central part of the Trans-Pecos of Texas (point 7, Fig. 1), seems to have differentiated, judging from its characters, as the result of unrestricted gene exchange between ancestral stock of the small animals of population H and the large animals of population F that became sympatric in this area (see discussion beyond).

Populations A, B, and C of the *subnubilus*-group are less sharply differentiated in most features than those of the *excelsus*-group. Most of the contact with the *excelsus*-group occurs with populations A and B; population C, which occurs south of the mountainous barrier formed by the Sierra Guadalupe-Sierra Parras ranges in southwestern Coahuila, has only limited contact with population E of the *excelsus*-group. For example, contact occurs only in a few high passes in the mountains, as in Santo Domingo Cañon (point 6, Fig. 1). Hence, it is unlikely that there would be selection for character divergence in this population, and none is evident. Therefore, population C probably has remained little changed from its earlier Pleistocene ancestor; except, of course, for subspecific differentiation within the cluster.

It is at first surprising to find that the differences between populations A, B, and C are so weakly developed, especially in view of the broad contact of A and B with populations of the *excelsus*-group. One would expect population A and B to have developed some degree of character divergence, and, therefore, to have developed distinctive differences from population C. Such is not the case. Instead of in the *subnubilus*-group, character divergence has occurred in the *excelsus*-group, particularly in populations in the zone of sympatry.

Analysis of the species *Pappogeomys castanops* as a multidimensional system, reveals a complex population structure with a wide range of interpopulation relationships. At one extreme are the collection of demes and local populations that compose the subspecies. Such groupings are characterized by unlimited gene exchange, especially on the interdemic level. Next, subspecies are usually grouped into larger intraspecific population units, the subspecies cluster. Unrestricted gene flow through primary intergradation within the subspecies cluster results in a characteristic pattern of variation and degree of adaptation for the entire population unit. The relationship between subspecies clusters seems to vary in this species between nearly maximum rates of gene exchange (which evidently occurred in the differentiation of *P. c. pratensis*) down to what seems to be severely restricted gene flow (as between populations H and E). At any rate, the zones of contact between the subspecies clusters are evidently zones of secondary intergradation, and were established after periods of geographic isolation. At the other extreme, are the sympatric occurrence of populations of different subspecies clusters. There is no indication of interbreeding between these populations at most localities. Reproductive isolation in this non-dimensional system is probably due to the formation of biological isolating mechanisms. The nature of these is unknown, but both ecological and ethological mechanisms are indicated. Regardless, the sympatric populations behave as species in these areas. Correlated with their sympatric occurrence has been the development of considerable character divergence. Breakdown of the isolating mechanisms that prevent interbreeding between these sympatric populations occurs only in one area. There, two of the subspecies of the diverging groups do interbreed where their ranges are contiguous, resulting in gene introgression into adjacent populations of both subspecies-groups. At least two geographic isolates, with the possibility of several others (as mentioned above), are known. Taxonomically, both have been assigned subspecific status.

On the intraspecific level, the subspecies cluster in *Pappogeomys castanops* seems to be the most important population unit of evolution. Intraspecific divergence seems to occur on this level, including divergent trends that could lead in the future to the separation of the complex into two or more species if geographic isolation develops.

EVOLUTION OF INTRASPECIFIC POPULATION STRUCTURE

In order to reconstruct the evolutionary history of the complex population structure of *Pappogeomys castanops,* two sorts of data are vital. First, it is necessary to have a knowledge of current population structure, relationships, and geographic variation. Second, at least a general knowledge of the immediately past climatic changes in the area of distribution also is pertinent. One could argue that actual fossil evidence would be ideal for reconstructing the past history of the species. I disagree with this opinion, for two reasons: (1) we are concerned with the formation of intraspecific structure of a modern species, and thus we are dealing only with evolutionary changes in the terminal stage of the Pleistocene (Wisconsin and post-Wisconsin periods) and in the Recent, too short a time span, therefore, for fossil evidence to be of much value; (2) fragmentary fossils from widely scattered sites, even if available, would offer little evidence for solving the details of intraspecific population variation. Therefore, the development of the complex must be based on the interpretation of other data, and it is primarily a problem of neontology. Some idea of the formation of intraspecific population structure helps to appreciate the complex relationships of the species and also provides some notion as to how they may develop.

Pleistocene Changes in Climate and Environment

Late Pleistocene climatic changes and concomitant changes in the environment have had a direct effect upon the process of speciation and the patterns of distribution of living species. These climatic changes took place during the time of the last glacial advance (Wisconsin) in the northern part of the continent, and, of course, the climatic changes continued into the post-Wisconsin period. Evidence supporting trenchant environmental changes in the southwestern United States and northern México is from three sources: analysis of pollen profiles; analysis of contemporary distributions and ecologies; and, to a lesser extent, the distribution of late Pleistocene fossils.

During much of the Wisconsin glaciation of North America, and probably as late as the Cochran Readvance (see Dorf, 1960:342; and Hibbard, 1955:82-84), northern México and the southwestern United States experienced a cool, moist climate. Jaeger (1926) suggested that these pluvial cycles were characterized by the development of numerous lakes, many of large size, throughout the northern part of the Mexican Plateau (see Flint, 1947:476, for a brief discussion). Old stream courses, now dry, and the large number of old lake beds bear out Jaegers opinion.

Before the Wisconsin pluvial cycles, in the terminal stages of the Sangamon interglacial period, this region was evidently hot and dry, characterized in the main by desert environments. Hibbard (1960:22, 25) pointed out that the Sangamon interglacial stage terminated with a particularly arid interval just preceding the Wisconsin. Extensive deposits of caliche formed on the Great Plains (southwestern Kansas) at the close of the Sangamon, indicating a hot, dry climate. It is not unreasonable to suppose that aridity also developed over the major part of the region to the south and west at the same time. An abrupt shift to cool, moist climates of the Wisconsin stage followed the arid interval.

The most convincing evidence of the shift to cool, moist climates in northern México and the southwestern United States is afforded by palynological evidence. Wisconsin and post-Wisconsin fossil pollen sequences have been studied from many sites, especially from the northern part of this region by Martin (1963), Martin and Mehringer (1965), Hafsten (1961), and more recently by Wendorf (Symposium on Pleistocene and Recent Environments on the Central Great Plains, University of Kansas, October 26, 1968). Analysis of these fossil pollen records indicates that the region inhabited by *Pappogeomys castanops* was characterized by a cool, moist climate during the Wisconsin pluvial. The dominant vegetation was a boreal forest of pine, spruce, and fir. Evidently, during somewhat dryer subintervals, oak increased in abundance resulting in mixed pine-oak forests on dryer sites. The pluvial interval and its boreal environment lasted to the end of the Wisconsin, approximately 10,000-11,000 years BP. During the height of pluviation the evidence suggests that boreal forests were more or less continuous in both lowlands and highlands. Toward the close of the Wisconsin

(14,000 to 10,000 BP), the continuous boreal forests of the lowlands gave way to grasslands mixed with boreal woodlands.

In the post-Wisconsin, conditions became progressively more arid. Probably the trend toward aridity began in the southern part of the region and gradually advanced northward. As the climate became hot and dry, desert shrubs and forbs once again became dominant. On some sites, probably at higher elevations in the foothills of the mountains, grassland savannas of oaks and junipers replaced forests.

During the Wisconsin pluvial cycle, many northern species extended their ranges southward into northern México. For example, the remains of *Sorex cinereus* (Findley, 1953:635-636), *Synaptomys cooperi,* and an unidentified species of *Marmota* (see Jakway, 1958: 319, 321; Cushing, 1945:185) were recovered from Wisconsin deposits from San Josecito Cave in Nuevo León. At the present time, none of these mammals occur nearer the site of the cave than 800 miles to the north in the mountains of central New Mexico *(Sorex* and *Marmota).* Furthermore, these terrestrial species, restricted to relatively small home ranges, must have reached the area of the cave when the intervening area was favorable to their occurrence. In the case of the shrew, this would have necessitated a relatively cool and mesic environment according to Findley (*loc. cit.:* 636), although less mesic environments could have favored the two rodents. The postulation that *Sorex cinereus* enjoyed a continuous distribution in the pine-spruce forests throughout this region is substantiated by the occurrence of *Sorex milleri,* a living monotypic species endemic to higher elevations in the Sierra del Carmen of north-central Coahuila and the Sierra Madre Oriental in extreme southeastern Coahuila (see Baker, 1956:167-168). Findley (1955: 617) found *Sorex milleri* to be a close relative of *Sorex cinereus,* and he postulated that the southern segment of *S. cinereus,* that which expanded southward during the Wisconsin pluvial stage, became isolated in post-Wisconsin time and gave rise to *S. milleri.* The post-Wisconsin shift to aridity contributed, as Findley *(loc. cit.)* suggested, to the present disjunct distribution of *milleri.* The two small populations of *S. milleri,* therefore, are relics that have found refuge in isolated mountains.

Subsidiary, but important, evidence is provided by two other relics of this region, *Scalopus montanus* and *Cynomys mexicana.* Both species have restricted ranges in northeastern México (see Baker, *op. cit.:* 170, 202), and both species are geographic isolates, separated from the main range of their nearest relatives to the north and northeast. We may assume that both of these isolated populations reached the sites of their present occurrence by range extensions of the main body of their respective genera when environmental conditions were more mesic than now in the intervening areas. Both populations were left in isolation by the extirpation of the connecting populations with the post-pluvial trend to aridity. *Scalopus* is of particular interest in view of the restrictions of movement imposed by its fossorial adaptations. Moist, friable soils with suitable insect populations are necessary for its occurrence.

Also, the disjunct distributional patterns in northern México of *Eutamias dorsalis*, *Neotoma mexicana*, *Sigmodon ochrognathus*, *Microtus montanus*, *M. longicaudus*, *M. mexicanus*, and *M. pennsylvanicus* (see reports of Baker, 1956; Findley and Jones, 1960; Anderson, 1959, 1961; Findley and Jones, 1962) furnish additional information as to the effects of the post-Wisconsin shift to xeric conditions in the lowlands. All the aforementioned species are presently restricted to pockets of favorable habitat found at higher elevations in the isolated mountains of the region. No doubt the currently disjunct populations of each of these species enjoyed a more widespread and continuous distribution across the intervening lowlands during the more mesic pluvial stage.

The detailed investigation of *Sigmodon ochrognathus* by Findley and Jones (1960:462-469) revealed a distributional history that probably is characteristic of the other species listed above. These authors could find no significant differences among the many isolated populations of S. *ochrognathus* that they sampled, indicating to them that all of these isolated populations were recently connected by continuous distribution. Moreover, this species of *Sigmodon* is restricted ecologically to the oak forest zone. These data suggest that oak forest, and a more mesic environment, were widespread throughout the lowlands between the mountain ranges of this region synchronously with the uninterrupted distribution of the cotton rats.

In summary, the pre-Wisconsin climate of northern México and the southwestern United States was hot and dry with decidedly arid environments prevailing especially in the lowlands. The Wisconsin glacial period that followed was marked by a shift to cool, moist climates that supported more mesic environments. During the pluvial maxima, boreal forests of pine, spruce, and fir became the dominant vegetation in the lowlands. Fluctuating subcycles prob-

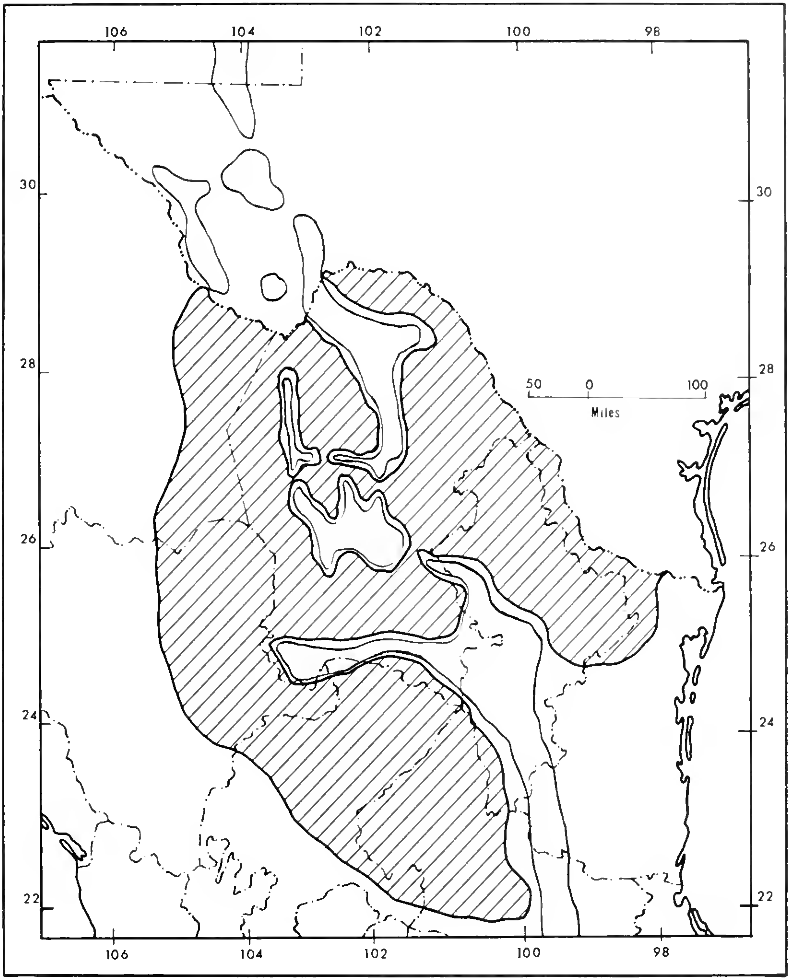

FIG. 14. Possible pattern of distribution of *P. castanops* in the early Wisconsin.

ably occurred during the pluvial period until the Wisconsin terminated. The post-Wisconsin was characterized by the progressive development of hot, dry climates, accompanied by a trend toward xeric environments. The return to arid conditions was thus marked by the rise to dominance of the desert flora and fauna that occurs in this region at the present time. This general history of northern México provides a model for analysis of microevolution in *Pappogeomys castanops*.

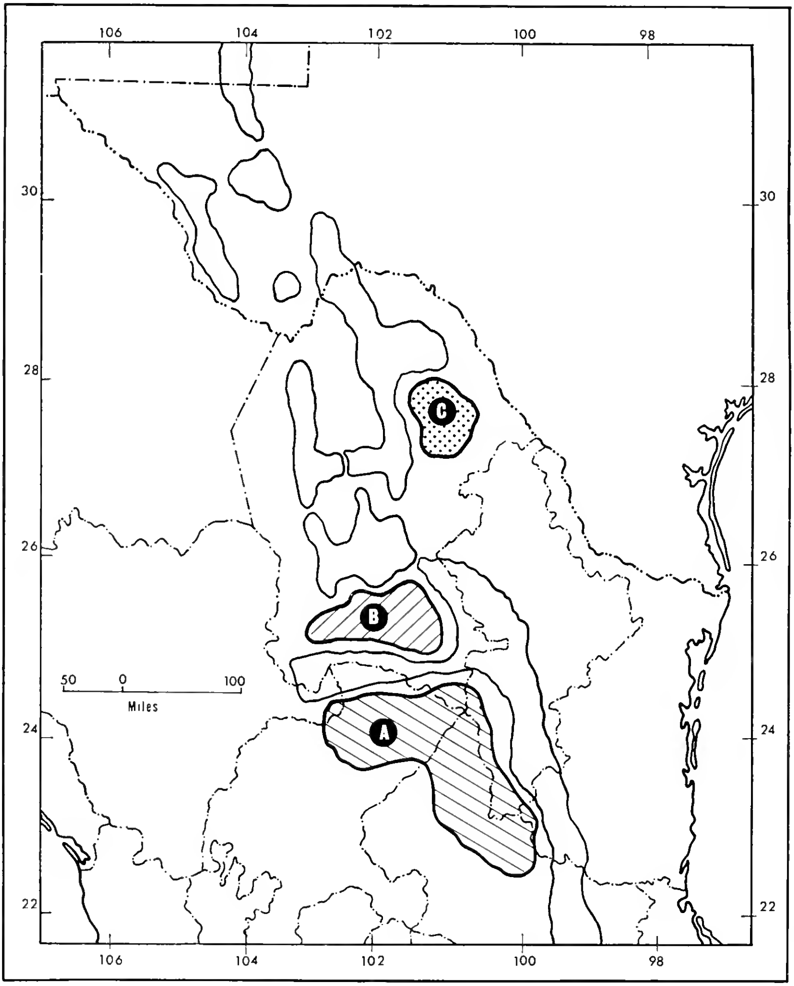

FIG. 15. Possible disjunct pattern of distribution of major populations (A-C) of *P. castanops* during the time of pluvial maximum in the Wisconsin.

Microevolution of Pappogeomys castanops

Remains of *Pappogeomys castanops* from the Wisconsin deposits of San Josecito Cave in Nuevo León, México (Russell, 1960:543) demonstrates the occurrence of the species in northeastern México in the late Pleistocene. In pre-Wisconsin times, this species probably enjoyed an extensive range in the lowlands of northeastern México as suggested in Figure 14. The extent of its distribution outside of northeastern México, if indeed it occurred elsewhere, is not known;

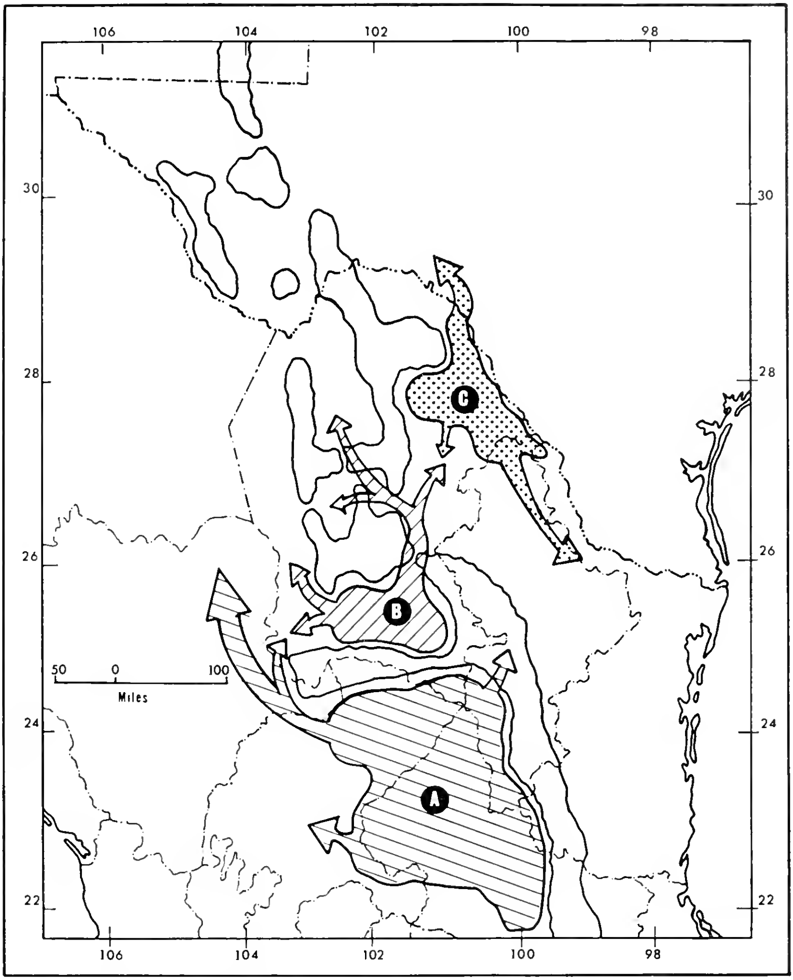

FIG. 16. Possible directions of emigration from the three major refugia in the early stages of post-Wisconsin time. Note initial points of contact between the populations A-B and B-C.

there is no evidence at this time of occurrence beyond the region indicated. The hot, dry climates at the close of the Sangamon would have favored the development of xerophytic vegetation, thus, providing adequate habitat for these pocket gophers.

The shift to cool, moist climates in the early stages of the Wisconsin would have been unfavorable to *Pappogeomys castanops*; and, as boreal vegetation from the north progressively replaced the

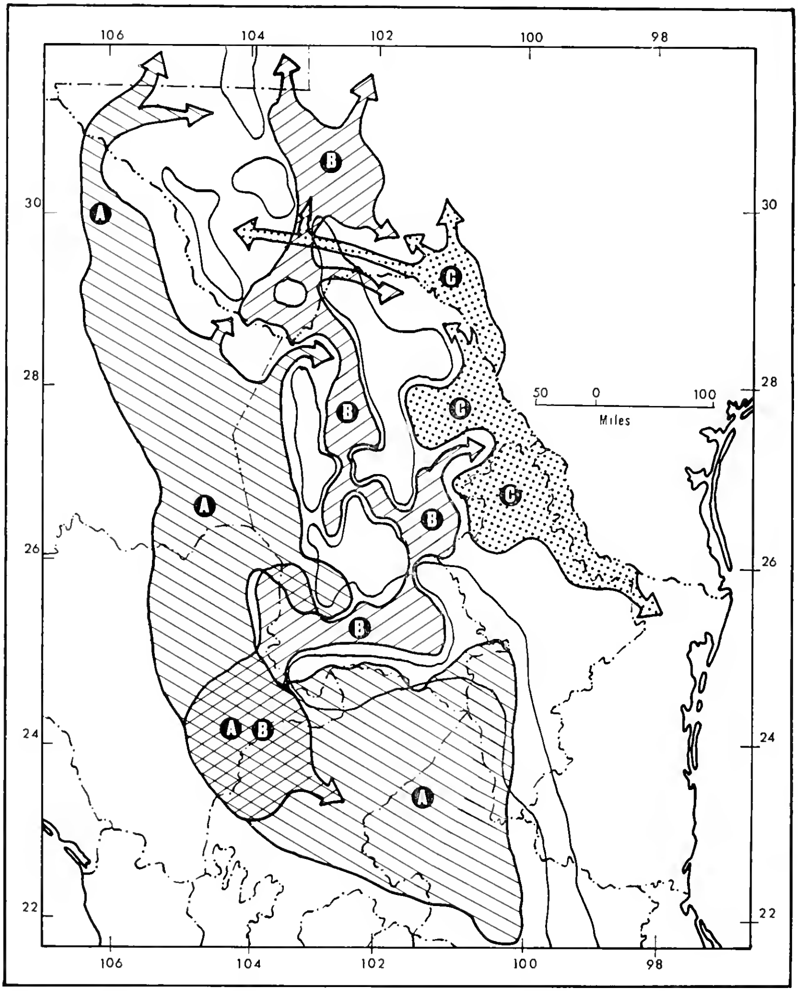

FIG. 17. Possible patterns of gene flow with continued emigration in post-Wisconsin time and the establishment of zones of sympatry in areas where intraspecific inter-breeding was restricted. Movements of populations in this final phase of post-Wisconsin readjustment has resulted in the superspecies complex that occurs at the present time (see Fig. 1).

xerophytic species in the lowlands, *Pappogeomys castanops* would have been forced out of most of the areas where it previously occurred. As a result of adverse conditions the range of this species decreased, finally fragmenting into isolated populations, restricted to small areas of preclimax conditions, at least during the height of the pluvial cycles. These refugia may have been located in the rain shadow of the higher mountains where drier environments prevailed. Although these areas probably did not offer optimum habitat, they did allow survival of the species. There is no way of knowing how many isolated populations existed; probably they varied in number and size, becoming less numerous as the Wisconsin pluviation continued. Current patterns of geographic variation and population structure suggest that there were at least three main refugia, which were located, in general, in the areas indicated in Figure 15. Refugia A and B were in the rain shadow of the Sierra Madre Oriental; refugium A was located to the south of the east-west oriented Sierra Guadalupe-Sierra Parras ranges, and refugium B was located to the north of the same escarpment. A third refugium (C) must have occurred on the low coastal plain somewhere to east of the sierras. Its exact location is not clearly discernible, and perhaps several refugia existed on the coastal plain rather than one. During the period of isolation, the disjunct populations evolved as separate systems. The small populations would have been favored by maximum rates of evolution, and, therefore, divergent evolution took place in a relatively short time. However, the period of isolation was not long, and reproductive isolation was not fully developed in all the isolated populations. Thus, the trend toward speciation was incomplete.

At the end of the Wisconsin with the return to arid conditions, the isolated populations of *Pappogeomys castanops* expanded their ranges out from the Wisconsin refugia. Contact was re-established between the isolated populations as their ranges became more widespread, as suggested in Figure 16. Wisconsin populations A and B probably first established contact on the elevated plains in northeastern Durango and southwestern Coahuila west of the Sierra Parras. Populations B and C evidently came into contact along the western limits of the coastal plain, probably in the area presently inhabited by *P. c. bullatus* and *P. c. ustulatus* (see Russell, 1968: 622). There is no evidence the Wisconsin population C moved westward in México. Also there is no evidence that Wisconsin populations B and C made contact during the time of range expansion; probably the high sierras of this area still functioned as a barrier to their dispersal.

Relationships between the descendants of these Pleistocene isolates indicates, that interbreeding was restricted when they made contact at the close of the Wisconsin and the incidence of crossbreeding was small. Reproductive isolation was especially well developed between Wisconsin populations A and B. Probably biological isolating mechanisms, developed while in isolation, functioned to severely reduce the incidence of cross-mating between these populations. As a response to intergroup competition in the areas of sympatry, especially between populations A and B, character divergence evolved, resulting in the distinctions between living descendants of these populations. As a result of reduced gene flow (or lack of it), each of the populations was able to maintain its unique features.

As arid conditions of post-Wisconsin time progressively moved northward, replacing the more mesic environments of the pluvial stage, the populations of *Pappogeomys castanops* expanded their ranges northward as suggested in Figure 17. At places where the ranges of populations A and B became contiguous they maintained reproductive isolation and did not interbreed. Indeed, a broad area of sympatry was developed between A and B in northeastern Durango and northern Zacatecas by the southwestward expansion of population B from Coahuila. Population B also extended its range northward into the Trans-Pecos of Texas, there making contact with northwestward-expanding segments of population C. In this area, (point 7, Fig. 1), potential isolating mechanisms between populations B and C failed to function, and the resultant interbreeding between the two units produced a population with intermediate features *(P. c. pratensis).* Further range extension to the north resulted in the present pattern of distribution depicted in Figure 1.

Wisconsin population A, therefore, gave rise to living populations A, B, and C depicted in Figure 1. Wisconsin population B gave rise to the modern populations E, F, and G, and Wisconsin population C to the modern population H. The characteristics and relationships of these populations are described in the aforegoing accounts.

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TAXONOMIC REVIEW OF THE GOLDEN MOUSE, OCHROTOMYS NUTTALLI

BY

ROBERT L. PACKARD

Golden mice (genus *Ochrotomys*) are rather unique, semi-arboreal cricetines in the neotomyine-peromyscine phyletic line. The single species, *Ochrotomys nuttalli,* occurs in the southeastern United States (see Fig. 1)—westward to eastern Texas, north as far as northern Kentucky and central Virginia, and south to central Florida. Ecologically, the distribution of these mice is closely correlated with that of the southeastern deciduous (oak-hickory) hardwoods and pine stands, or the Lower Austral and portions of the Upper Austral life-zones (Austroriparian and part of the Carolinian biotic provinces). Golden mice are found from lowland, heavily forested floodplains, to pine uplands where there is considerable underbrush, but seem most numerous in the former type of habitat. Considerable information has appeared recently on the biology of these mice (see McCarley, 1958; Layne, 1960; Rippy and Harvey, 1963; Packard and Garner, 1964; and Linzey and Linzey, 1967a, 1967b), but there has been only a single systematic revision (Osgood, 1909). This was based on 250 specimens from segments of the currently known geographic range, and two subspecies were recognized.

Golden mice were described by Harlan in 1832 as *Arvicola nuttalli,* with the type locality, Norfolk, Norfolk Co., Virginia. In 1841, Audubon and Bachman described *Mus (Calomys) aureolus* from oak forests of South Carolina. Baird, in 1858, followed Wagner (1843:51) in considering golden mice as belonging to the genus *Hesperomys* and stated (p. 468): ". . . I am impelled, by a strict regard for the law of priority, to change the expressive name of *aureolus,* hitherto applied exclusively to this species, for the less meaning one of *nuttalli.*" Bangs (1898), presumably following Trouessart (1897), placed the golden mice in the genus *Peromyscus.* When Osgood (1909) revised *Peromyscus,* he accorded golden mice subgeneric standing with the description of *Ochrotomys,* based on the numerous characters by which these mice differ from other peromyscoids.

Aside from the description of two new subspecies (*P. n. lewisi* Howell, 1939, and *P. n. flammeus* Goldman, 1941), no changes were made in the taxonomy of golden mice until Blair (1942) suggested that they might represent a distinct genus. However, Miller (1912, 1924), Miller and Kellogg (1955), and Hall and Kelson (1959) all followed Osgood's arrangement. Hooper (1958) concluded from his study of the male phalli in peromyscoids that golden mice should be accorded generic rank. More recently (Manville, 1961; Rinker, 1963; Hooper and Musser, 1964; Patton and Hsu, 1967), using different approaches, have strengthened the position that golden mice warrant generic recognition. There has been no recent analyses of geographic variation and synthesis of the available data bearing on the phylogeny of these mice. The objectives of this report are: (1) analyze variation in a population resulting from age, season, and sex; (2) record the amount of variation within and between populations; (3) comment on the systematic status and phylogeny of the golden mice.

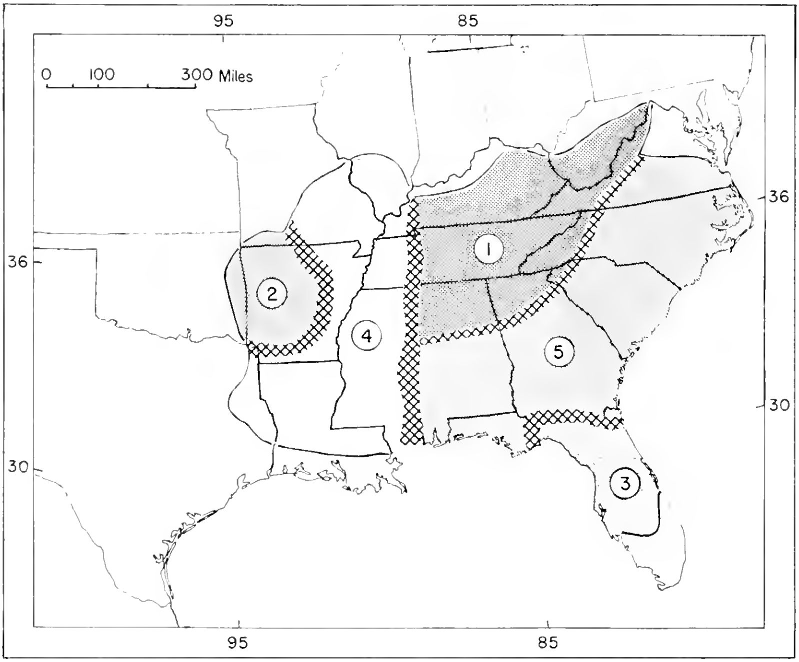

FIG. 1. Geographical distribution of subspecies of *Ochrotomys nuttalli*: *O. n. aureolus* (1); *O. n. flammeus* (2); *O. n. floridanus* (3); *O. n. lisae* (4); *O. n. nuttalli* (5). Cross-hatching indicates areas of intergradation.

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MATERIALS AND METHODS

This report is based on the study of approximately 825 museum specimens (skins, skulls, complete skeletons, and entire animals preserved in liquid, approximately two-thirds more specimens than were available to Osgood, 1909). Most specimens were accompanied with data relative to locality, date of capture, sex, and standard external measurements. In addition, live golden mice were captured and retained in the laboratory where breeding tests were conducted and behavioral data gathered.

Specimens were grouped for study by sex, age, and season of capture (when feasible). Because of the limitations placed on statistical analyses by extremely small sample sizes, specimens were regrouped into units for study of geographic variation. These units were selected on the basis of knowledge of habitat (the degree of uniformity), altitude, and general geographic relationship. As a result, composition of the groups were: (1) Florida Peninsula; (2) coastal plains of Louisiana, Mississippi, Alabama, and Florida (north of *ca.* 30° N latitude); (3) coastal plain, piedmont, and mountains of Georgia; (4) South Carolina; (5) coastal plain, piedmont, and mountains of North Carolina; (6) coastal plain, piedmont, and area of Amelia Court House, Virginia; (7) mountains of western Virginia, southeastern Kentucky, and eastern Tennessee; (8) Mississippi River Valley of southern Illinois and Missouri; (9) Arkansas (principally mountainous area); (10) eastern Texas. Measurements from classes 3 to 5 (see section on age), adults of both sexes, were programmed (according to the above listed localities) in a 7040 IBM

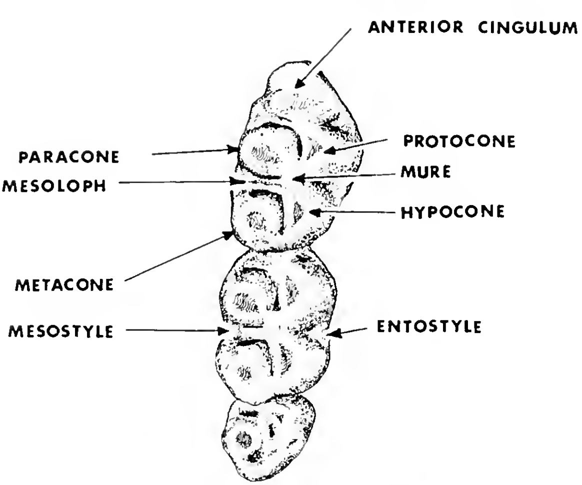

FIG. 2. Right upper molar row of *Ochrotomys nuttalli*, age three male, no. 1072 Stephen F. Austin State College, 2 mi. SW Bienville, Bienville Parish, Louisiana.

computer at this institution using the biomed simple data description, version of February 6, 1964, Health Sciences Computing Facility, University of California (Los Angeles).

External measurements used were those recorded by collectors plus body length, which was obtained by subtracting the length of the tail from the total length. Fifteen cranial measurements were analyzed in the study of non-geographic variation of a Texan population. Coefficient of variation was calculated for all measurements in the population studied and those that varied least were selected for comparing samples from different geographic areas. As a result, the following cranial measurements (see Packard, 1960:585, for description) were selected: condylobasal length; zygomatic breadth; depth of cranium; length of rostrum; alveolar length of maxillary toothrow; post-palatal length; least interorbital breadth; alveolar length of mandibular toothrow.

Some of the color notations refer to the Munsell Soil Color Charts (1954), whereas other terms used do not refer to any one standard. The names of cusps and ridges on the teeth (see Fig. 2) are those of Wood and Wilson (1936) and the enamel grooves and folds are those of Hershkovitz (1944) and Hooper (1952).

Secondary sexual variation was not found significant (see analyses of age and sexual variation and Fig. 3) and adult males and females were considered together in the analysis of geographic patterns.

NON-GEOGRAPHIC VARIATION

Non-geographic variation in *Ochrotomys* has been little studied. Aside from Osgood's (1909) revision and Hooper's (1957) study of variation in dental patterns, only cursory comments on this subject are in the literature. Important contributions in the development, growth, and molt of golden mice have been reported by Linzey and Linzey (1967a, 1967b) and Layne (1960). Blus (1966) contributed information on variation in litter size.

The largest sample available to me for study was 79 specimens of *O. n. flammeus* from Nacogdoches County, Texas. These were separated by sex, thence into age categories, and measured. Most specimens were captured between the months of February to May. All measurements were analyzed by the 7040 computer using the simple data description program previously mentioned.

VARIATION WITH AGE

Specimens of both sexes were grouped into five age categories as follows: (1) juvenile; (2) young or subadult; (3) young adult; (4) adult; (5) old adult (hereafter age categories will be referred to by number). Linzey and Linzey (1967b) pointed out that golden mice have a prolonged, but slow, growth rate. Thus, mice beyond 10 to 12 weeks of age do not change appreciably in size. My age categories were based first on morphological criteria and secondly were compared with the linear data on growth of Linzey and Linzey (1967b) and Layne (1960). External measurements (particularly length of tail) of mice of age group five compare favorably with those of individuals 48 weeks of age, age group four with mice 28 to 44 weeks old, age group three with those 16 to 28 weeks old, age group two with mice that were seven to 12 weeks old, and age group one with individuals less than seven weeks old. Linzey and Linzey's *(loc. cit.)* and Layne's *(loc. cit.)* growth data for external measurements (total length, body length, length of tail, length of hind foot) show a significant leveling in rate of increase between three to six weeks. Golden mice eight weeks old or older, while still growing at a rather slow but constant rate, changed little in size. Layne (1960) stated that cheekteeth are fully developed between four to five weeks. On this basis, my age one mice would be less than four to five weeks of age, whereas my age two mice would seemingly be five weeks old or older.

For purpose of comparisons of mice from different geographic areas, only individuals of ages three through five were used. In most cases, specimens in comparable pelages (having completed the post-juvenile molt, see Linzey and Linzey, 1967a) were used for geographic analyses.

Age 1.—Mice with M3 and m3 erupted to alveolar surface; cusps, styles, and lophs of other molars all distinct with little or no evidence or wear; all cranial sutures generally distinct with presphenoid-basisphenoid suture widely open; tympanic bullae rugose with mottled appearance; dentary bone rugose;

TABLE 1.—ANALYSIS OF VARIATION WITH AGE AND SECONDARY SEXUAL VARIATION OF *Ochrotomys nuttalli* FROM EASTERN TEXAS.

Variant	Sex	N	Range	Mean	SE	SD
	Age 1					
Total length	M	1	-----------	125.0	-----	-----
	F	1	-----------	109.0	-----	-----
Length of body	M	1	-----------	65.0	-----	-----
	F	1	-----------	60.0	-----	-----
Length of tail	M	1	-----------	60.0	-----	-----
	F	1	-----------	49.0	-----	-----
Length of hind foot	M	1	-----------	16.0	-----	-----
	F	--	-----------	17.0	-----	-----
Length of ear	M	1	-----------	8.0	-----	-----
	F	1	-----------	12.0	-----	-----
Condylobasal length	M	-	-----------	-----	-----	-----
	F	2	18.2-19.0	18.6	.40	.57
Zygomatic breadth	M	1	-----------	11.9	-----	-----
	F	2	11.2-12.0	11.6	.40	.57
Depth of braincase	M	1	-----------	8.6	-----	-----
	F	2	8.6-8.9	8.7	.15	.21
Length of rostrum	M		-----------	-----	-----	-----
	F	1	-----------	7.6	-----	-----
Alveolar length of upper molar row	M	1	-----------	3.7	-----	-----
	F	2	3.0-3.5	3.3	.25	.35
Post-palatal length	M	1	-----------	8.1	-----	-----
	F	2	7.0-7.3	7.2	.15	.21
Length of mandibular molar row	M		-----------	-----	-----	-----
	F	1	-----------	3.3	-----	-----
Least interorbital breadth	M	1	-----------	4.20	-----	-----
	F	2	3.2-4.3	3.75	.55	.78
	Age 2					
Total length	M	15	130-154	142.3	1.6	6.1
	F	12	135-167	146.4	2.3	8.1
Length of body	M	15	70-103	81.1	1.8	6.9
	F	12	70-97	79.5	2.0	7.0
Length of tail	M	15	52-73	63.1	1.3	5.1
	F	12	62-77	66.9	1.2	4.3
Length of hind foot	M	15	13-19	17.1	.4	1.7
	F	12	15-19	17.5	.3	1.1
Length of ear	M	15	10-17	14.9	.4	1.8
	F	12	10-18	14.6	.6	2.2
Condylobasal length	M	14	19.9-21.9	21.1	.2	.6
	F	9	21.0-22.4	21.8	.2	.5
Zygomatic breadth	M	15	11.5-13.0	12.4	.1	.4
	F	10	12.0-13.4	12.6	.1	.4
Depth of braincase	M	14	8.4-9.8	9.1	.1	.3
	F	9	9.1-9.5	9.3	.04	.1

TABLE 1.—CONTINUED.

Variant	Sex	N	Range	Mean	SE	SD
Length of rostrum	M	15	7.5-10.0	8.9	.2	.7
	F	10	8.5-10.0	9.3	.1	.5
Alveolar length of upper molar row	M	14	3.4-3.9	3.7	.03	.1
	F	9	3.6-3.9	3.7	.02	.1
Post-palatal length	M	14	7.5-8.9	8.4	.1	.4
	F	7	8.4-9.0	8.8	.1	.2
Length of mandibular molar row	M	..	----------	-----	-----	-----
	F	..	----------	-----	-----	-----
Least interorbital breadth	M	15	3.5-4.5	4.2	.1	.3
	F	10	4.1-4.5	4.4	.03	.1
	Age 3					
Total length	M	11	146-160	153.9	1.5	5.0
	F	12	139-174	158.1	3.0	10.5
Length of body	M	11	74-90	83.8	1.6	5.2
	F	12	76-106	88.6	2.3	8.1
Length of tail	M	11	62-77	70.1	1.2	3.9
	F	12	55-80	69.5	2.2	7.8
Length of hind foot	M	11	15-21	17.1	.5	1.5
	F	12	16-20	17.8	.4	1.3
Length of ear	M	10	11-16	13.4	.5	1.6
	F	12	13-17	15.5	.3	1.1
Condylobasal length	M	11	21.5-23.2	22.4	.1	.5
	F	8	21.4-23.2	22.3	.2	.7
Zygomatic breadth	M	11	12.3-13.3	12.9	.1	.3
	F	8	12.3-13.6	12.9	.2	.4
Depth of braincase	M	11	8.6-9.7	9.3	.1	.3
	F	8	9.0-9.7	9.3	.1	.3
Length of rostrum	M	11	8.7-10.1	9.4	.1	.4
	F	8	9.1-10.1	9.6	.1	.4
Alveolar length of upper molar row	M	11	3.5-3.8	3.7	.02	.1
	F	8	3.4-3.9	3.7	.1	.1
Post-palatal length	M	11	8.0-9.6	8.9	.1	.4
	F	8	8.6-9.8	9.2	.2	.4
Length of mandibular molar row	M	1	----------	3.6	-----	-----
	F	..	----------	-----	-----	-----
Least interorbital breadth	M	11	3.8-4.8	4.4	.1	.2
	F	8	3.7-4.6	4.3	.1	.3
	Age 4					
Total length	M	10	153-171	160.9	1.8	5.9
	F	10	140-170	159.7	3.3	10.6
Length of body	M	10	80-96	87.6	1.6	5.0
	F	10	80-103	89.5	2.5	7.9
Length of tail	M	10	68-79	73.1	1.1	3.4
	F	10	63-85	73.2	2.4	7.5

TABLE 1.—CONTINUED.

Variant	Sex	N	Range	Mean	SE	SD
Length of hind foot	M	10	17-19	17.6	.2	.7
	F	10	17-19	17.9	.2	.7
Length of ear	M	10	11-17	15.6	.6	1.8
	F	10	13-17	16.1	.5	1.4
Condylobasal length	M	10	22.5-23.4	22.9	.1	.3
	F	9	22.3-24.0	23.1	.2	.6
Zygomatic breadth	M	10	12.8-13.6	13.3	.1	.3
	F	9	13.4-13.9	13.6	.1	.2
Depth of braincase	M	10	9.3-9.7	9.5	.03	.1
	F	9	8.7-9.7	9.3	.1	.3
Length of rostrum	M	9	9.6-10.8	9.9	.1	.4
	F	9	9.5-10.5	9.9	.1	.3
Alveolar length of upper molar row	M	10	3.6-3.9	3.8	.03	.1
	F	9	3.5-3.8	3.6	.04	.1
Post-palatal length	M	10	9.1-9.7	9.4	.1	.2
	F	8	8.2-9.7	9.3	.2	.5
Length of mandibular molar row	M	--	----------	------	------	------
	F	2	3.3-3.4	3.4	.1	.1
Least interorbital breadth	M	10	4.2-4.6	4.4	.04	.1
	F	9	3.6-4.6	4.3	.1	.4
	Age 5					
Total length	M	5	167-174	170.0	1.1	2.5
	F	1	----------	131.0	------	------
Length of body	M	5	84-100	93.2	2.7	6.1
	F	1	----------	68.0	------	------
Length of tail	M	5	70-85	76.9	2.8	6.3
	F	1	----------	63.0	------	------
Length of hind foot	M	5	18-19	18.2	.2	.4
	F	1	----------	19.0	------	------
Length of ear	M	5	16-17	16.6	.2	.5
	F	1	----------	11.0	------	------
Condylobasal length	M	5	23.0-23.8	23.4	.1	.3
	F	--	----------	------	------	------
Zygomatic breadth	M	5	13.5-13.8	13.7	.1	.1
	F	--	----------	------	------	------
Depth of braincase	M	5	9.3-9.7	9.5	.1	.1
	F	--	----------	------	------	------
Length of rostrum	M	5	9.4-10.4	10.1	.2	.4
	F		----------	------	------	------
Alveolar length of upper molar row	M	5	3.7-3.8	3.8	.02	.1
	F	--	----------	------	------	------
Post-palatal length	M	5	9.5-9.9	9.7	.1	.2
	F	--	----------	------	------	------
Length of mandibular molar row	M	--	----------	------	------	------
	F	-	----------	------	------	------
Least interorbital breadth	M	5	4.2-4.6	4.4	.1	.2
	F	-	----------	------	------	------

epiphyses of all long bones distinct from diaphyses; under fur of pelage grayish-black, guard hairs dusky-blackish, remaining hair on dorsum golden-brown (agouti tips short) and near 7.5YR 5/6 (Munsell, 1954); hairs on belly white at tip and gray at base, giving dusky white appearance; tail bicolored, ears golden, upper parts of hind feet white (see Table 1).

Age 2.—Mice with M3 and m3 erupted; small degree of wear evident on cusps, styles, and lophs of all molars; basisphenoid-basioccipital and basisphenoid-presphenoid sutures evident; tympanic bullae and dentary bone smooth (also in all older age groups); epiphyseal-diaphyseal sutures not distinct in long bones save the tibia; guard hairs with brownish tones (less blackish than in age one), agouti band broader, resulting in a more golden brown color on dorsum than in age one, but still near 7.5YR 5/6 on Munsell scheme; belly with slight suffusion of yellow with individual hairs pale yellow-gray at base, whitish near tips; tail slightly bicolored, more fully haired than in age one; hair on hind feet white; ears golden brown (see Table 1).

Age 3.—Wear on enamel of major cusps sufficient to reveal dentine bands; lophs and styles evident (see Fig. 2), but with wear (particularly on M3 and m3); sutures in cranium not evident; distal diaphyseal-epiphyseal suture of femur and proximal diaphyseal-epiphyseal suture of tibia faintly visible; guard hairs on dorsum brownish-black (less profuse than in age two); golden-reddish agouti band broadened at expense of grayish base, resulting in overall golden-red tone (color 5YR 5/8 middorsally); belly whitish with yellow-orange overtones, basal parts of hair gray; tail indistinctly bicolored; hind feet whitish above; ears orange-red (see Table 1).

Age 4.—All teeth show considerable wear with dentine lake in center of M3 and m3; mesolophs and mesolophids of first and second molars well worn, resulting in confluence of dentine with mure between paracone (protoconid) externally and hypocone (entoconid) internally; distal suture between epiphysis and diaphysis of tibia faintly visible; little change in color of pelage from age three except overall tones of upper parts more golden brown than in age three (see Table 1).

Age 5.—All teeth well worn, essentially without pattern of cusps, lophs, and styles, and with only a thin peripheral band of enamel surrounding lake of dentine; sutures on long bones ankylosed; pelage somewhat ragged, but not differing appreciably from pelage of ages three and four, color near 5YR 5/8 middorsally (see Table 1).

SECONDARY SEXUAL VARIATION

Variation resulting from differences between sexes in each of the age classes was studied following the method of Hubbs and Hubbs (1953). Females of adult age groups tended to have slightly longer and broader skulls and may be somewhat more variable than males, but the differences were not significant (see Fig. 3).

Because no significant secondary sexual variation was revealed in this study, the sexes have been considered together in the analysis of geographic variation. All specimens used in analysis of secondary sexual variation were collected in a period from January

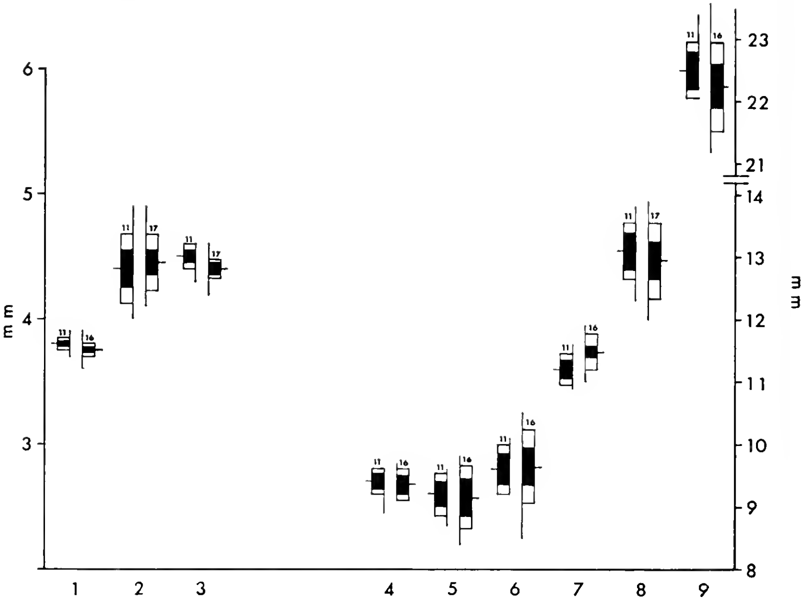

Fig. 3. Analyses of secondary sexual variation. Numbers at base of abscissa refer to variants analyzed as follows: (1) alveolar length of maxillary toothrow; (2) depth of cranium; (3) breadth of braincase; (4) length of rostrum; (5) length of incisive foramina; (6) least interorbital breadth; (7) postpalatal length; (8) condylobasal length; (9) zygomatic breadth. Vertical lines represent range, solid black bar equals one standard error of the mean, open bar equals one standard deviation; numerals directly above each diagram represent size of sample; in each matching set of diagrams, samples of males are on the left and females on the right.

to May from the Stephen F. Austin Experimental Forest (a part of the Angelina National Forest), located about 10 mi. SW Nacogdoches, Texas.

Individual Variation

Golden mice from the same population, when grouped into comparable age and sex categories, vary little from each other. Hooper (1957) reported little variation in the dental patterns of these mice. External measurements were more variable than those of the cranium but this may reflect the technique of measuring by the different collectors. Linzey and Linzey (1967a) found some variation in detail of the pattern of molt, but the basic pattern varied little. My study of molt patterns are essentially in agreement with theirs. A series of 54 bacula of golden mice were measured and studied and only minor variations were recorded. Measurements and ratios of basal width to total length and bacular length to body length do not differ appreciably from those reported by Blair (1942). The hyoid apparatus of 38 golden mice from the Nacogdoches County, Texas, sample did not vary from the pattern reported by Sprague (1941). Illustrations of the phallus by Hooper (1958) and Hooper and Musser (1964) suggest little variation present in that organ. Rinker (1960) and Manville (1961) reported the absence of the entepicondylar foramen in the humerus of *Ochrotomys* (Blair, *in* Blair *et al.*, 1968:518, erroneously reports its presence). Rinker had four specimens and Manville five. I examined 92 golden mice humeri from various parts of the geographic range and found no entepicondylar foramen. Patton and Hsu (1967) reported a diploid number of 52 chromosomes in the golden mouse. No variation from this number was recorded although sample size (four) was exceedingly small. Peterson (1968) reported a stable densito-metric curve, on the basis of two specimens, in the blood serum pattern of *nuttalli*. Rinker (1963) reported a consistent myological plan on the basis of three specimens dissected. Examination and dissection of 11 additional specimens in this study (particularly the M. *pronator quadratus* and M. *pronator teres*) suggests little variation.

The most impressive aspect of the study of individual variation of *O. nuttalli* is the small degree of it when compared to other cricetines. The relative lack of much individual variation in golden mice suggests the species to be extremely genetically homogenous.

Genus **Ochrotomys** Osgood

1909. *Ochrotomys* Osgood, N. Amer. Fauna, 28:222, April 17. Type, *Arvicola nuttalli* Harlan.

Diagnosis.—Size medium (total length in adults from 140-190); tail longer, or about equal to, head and body; hind foot in adults 15-21; ears medium (10-18) and rounded; color of pelage of young slightly duskier than of adults, varying on dorsum from 7.5YR 5/6 (young) to 5YR 5/8 (adults) on the Munsell (1942) system; color of adults tawny ochraceous on upper parts and ears, creamy with ochraceous wash on underparts; tail faintly bicolored; feet similar to underparts in color; plantar tubercles six with rudimentary seventh adjacent to large tubercle at base of fifth digit; mammae 6 (inguinal 2/2, pectoral 1/1); posterior palatine foramina nearer interpterygoid fossa than to posterior terminus of anterior palatine foramen; mental foramen of mandible situated laterally and in medial plane of ramus; molariform teeth with tendency to brachyodonty; enamel folds compressed and thick, those of two sides of a molar touching when worn and resulting in five subtriangular islands of dentine in M1 and m1, four in M2 and m2; prominent accessory lophs and styles on all molars, full mesoloph (-id), mesostyle (-id), ectoloph, and ecotostylid, mesoloph (-id) joined with prominent mesostyle (-id) apically; loph extends lateral from mure;

glans penis with unusually large spines, protractile tip and adjoining portions of glans without spines, bilobed urethral flap protecting meatus urinarius, distal margin of glans body scalloped; baculum capped with long cartilaginous cone, broad at base, shaft short; electrophoretic pattern with one T band, one po. A band; chromosome diploid number, 52; dental formula, 1/1, 0/0, 0/0, 3/3 = 16.

GEOGRAPHIC VARIATION

The same cranial and external measurements were used for the analysis of geographic variation as were used for determining the degree of variation within a population. Therefore, 13 characteristics were analyzed in each of the 10 major geographic groupings (previously described). In certain instances, where relatively large samples permitted, specimens from Georgia, North Carolina, and Virginia were divided each into coastal plain, piedmont, and mountain divisions for analysis. Only adult specimens (age classes 3-5) were used in this study (measurements are summarized in Table 2).

Total length.—Specimens from the coastal plains of Virginia, North Carolina, and Georgia average larger in this measurement than those from the Piedmont Region of the same states. Populations from Illinois, Missouri, Texas, and the Gulf Coastal plains of Louisiana, Mississippi, and northern Florida are smallest in this character save for the sample from Amelia Court House, Virginia (which merits special consideration, see summary of geographical variation and systematic account of subspecies). There is considerable overlap in samples but clinal variation from Atlantic Coastal to Piedmont populations seems evident. There is a rather sharp break in this cline of decreasing size in that populations from the Appalachian Mountains average larger than those on the Piedmont.

Degree of variation in each sample, expressed by coefficient of variation, is considerably greater in external characters than in cranial features (see Table 2), and conclusions concerning trends in variations may be less meaningful than those revealed by cranial measurements.

Length of body.—Trends in variation in this characteristic are similar to those for total length, but several departures of note exist. Body length of specimens from Arkansas (Ozark Mountains) is as large as in those from the Atlantic Coastal Plains. Specimens from the peninsula of Florida and the Gulf Coast region of Louisiana, Mississippi, and Florida are smallest in body length.

Length of tail.—Pattern of variation in this characteristic resembles that in total length. A notable exception is the Arkansas sample wherein length of tail does not coincide with the pattern of variation in length of body. Thus, mice from Arkansas have large bodies with proportionately shorter tails. Samples from the mountainous regions of Georgia, North Carolina, Virginia, western Virginia, Tennessee, and Kentucky reveal considerable concordance in having longer tails than do samples from the Piedmont.

Length of hind foot.—This measurement varies in much the same way as do the foregoing features. Specimens from Texas, Illinois, Missouri, and the Gulf Coastal region have the smallest hind feet, whereas specimens from

Arkansas average longer in hind foot length (being similar to average size of samples from the Appalachian Mountains). Specimens from Amelia Court House, Virginia, average as long in this character as do specimens from the mountains to the west, and the total range of variation overlaps considerably that of the coastal plains populations.

Length of ear.—A cline of decrease in length of ear from coastal plain to Piedmont in Georgia, then a reverse to larger ear size in the mountains, is discernible. This is similar to the pattern noted in total length. However, the coastal plains populations of North Carolina are nearly identical to those of the Piedmont and both have ears that average longer than do those of populations from the mountains. Longest ear length is in the sample from the Virginia Piedmont, averaging considerably longer than in specimens from the Virginia coastal plains and western mountainous regions. Seemingly there is considerably discordance in trends of this character when compared to other external measurements.

Condylobasal length.—There is little detectable pattern of variation in this feature. Eastern coastal plain and Piedmont samples are nearly identical, and average somewhat larger than do specimens from the mountains of North Carolina, but are similar in size to those from the western Appalachians (Kentucky, Tennessee, and Virginia). Specimens from Arkansas average somewhat longer than do those from surrounding areas of Texas, Illinois, and Missouri, and approach the size of the sample from the western Appalachian Mountains.

Zygomatic breadth.—Two patterns of variation in this character are evident: (1) specimens from the eastern coastal plains average broader with size decreasing westward toward the mountains (this is particularly evident in North Carolina); (2) Arkansas mice average larger than those from eastern Texas, Missouri, and Illinois.

Depth of braincase.—The trends in variation of this character differ little from variation of total length. Samples from the Appalachian Mountains average larger than those from the Atlantic Piedmont and coastal plains. A clinal pattern is evident between Piedmont and the coastal plain populations, with the latter averaging larger. Populations from eastern Texas and Arkansas average smaller than eastern samples and overlap the range of variation observed in the Gulf Coast specimens from Louisiana, Mississippi and Florida.

Length of rostrum.—This character varies in much the same way as condylobasal length. Specimens from Amelia Court House, Virginia, are significantly smaller in rostral length than all eastern coastal specimens examined. Specimens from eastern Texas, Arkansas, Illinois, and Missouri are similar in this character.

Alveolar length of maxillary toothrow.—Variation in length of upper molar row is essentially non-clinal and little agreement exists between the patterns of variation of this character and others. Variation in length of maxillary toothrow of specimens from Amelia Court House is within the range of variation of the specimens from the coastal plain and Piedmont of Virginia.

Post-palatal length.—This feature shows no marked patterns of variation. There is considerable overlap among all populations studied. Specimens from the coastal plains of North Carolina and Georgia are nearly identical to those from the Piedmont of those states, whereas coastal plains specimens from Vir-

TABLE 2.—ANALYSIS OF GEOGRAPHIC VARIATION IN EXTERNAL AND CRANIAL MEASUREMENTS OF ADULT GOLDEN MICE. PARENTHETICAL ABBREVIATIONS FOLLOWING SOME LOCALITIES ARE: CP (COASTAL PLAIN); P (PIEDMONT); M (MOUNTAINS).

Locality	N	Mean ± 1 SD	Range	SE	CV
Total Length					
North Carolina (CP)	6	174.16±4.79	180-167	1.95	2.75
North Carolina (P)	46	166.89±8.54	183-146	1.25	5.12
North Carolina (M)	24	170.00±12.82	191-151	2.61	7.54
Virginia (CP)	26	176.80±8.52	200-165	1.67	4.82
Virginia (P)	18	163.94±9.63	180-149	2.27	5.87
Virginia-Tennessee-Kentucky (M)	11	168.00±10.61	183-154	3.19	6.32
Amelia, Virginia	11	149.63±10.55	170-134	3.18	7.06
Georgia (CP)	13	164.92±10.05	183-150	2.78	6.10
Georgia (P)	32	155.00±10.50	172-127	1.85	6.78
Georgia (M)	10	164.50±8.05	175-150	2.54	4.90
South Carolina	11	164.36±7.07	175-152	2.13	4.30
Illinois-Missouri	28	156.28±9.66	174-138	1.82	6.18
Arkansas	18	164.66±8.60	181-146	2.02	5.22
Texas	79	159.11±9.68	178-139	1.08	6.09
Gulf Coast	51	155.78±15.88	200-106	2.22	10.20
Florida	28	157.60±10.65	178-135	2.01	6.75
Length of Head and Body					
North Carolina (CP)	6	91.50±3.27	96-88	1.33	3.57
North Carolina (P)	46	91.69±6.13	104-79	.90	6.69
North Carolina (M)	24	90.37±9.04	105-77	1.84	10.01
Virginia (CP)	26	93.46±4.76	103-83	.93	5.09
Virginia (P)	19	88.05±5.95	98-75	1.36	6.77
Virginia-Tennessee-Kentucky (M)	11	88.72±6.70	98-80	2.02	7.56
Amelia, Virginia	11	83.72±6.58	94-75	1.98	7.87
Georgia (CP)	13	89.69±5.42	99-81	1.50	6.05
Georgia (P)	32	85.34±8.20	103-68	1.45	9.62
Georgia (M)	10	87.00±4.89	95-75	1.54	5.60
South Carolina	11	86.72±3.16	93-82	.95	3.65
Illinois-Missouri	28	86.42±6.99	100-71	1.32	8.09
Arkansas	18	92.44±7.89	102-73	1.86	8.54
Texas	49	86.96±7.08	115-74	.79	6.09
Gulf Coast	51	82.82±9.87	115-51	1.38	11.92
Florida	28	85.00±7.77	100-64	1.46	9.15
Length of Tail					
North Carolina (CP)	6	82.16±5.81	91-75	2.37	7.08

TABLE 2.—CONTINUED.

Locality	N	Mean ± 1 SD	Range	SE	CV
North Carolina (P)	46	75.17±5.44	89-61	.80	7.24
North Carolina (M)	24	79.62±6.34	94-70	1.29	7.97
Virginia (CP)	26	83.34±5.42	97-73	1.06	6.51
Virginia (P)	18	75.94±5.09	89-69	1.20	6.71
Virginia (M)	11	79.27±6.16	90-71	1.85	7.78
Amelia, Virginia	11	65.90±7.27	77-55	2.19	11.03
Georgia (CP)	13	75.23±6.28	86-65	1.74	8.36
Georgia (P)	32	69.65±8.10	85-51	1.43	11.64
Georgia (M)	10	76.50±5.03	83-68	1.59	6.59
South Carolina	11	77.63±5.85	87-68	1.76	7.54
Illinois-Missouri	29	69.89±4.32	81-62	.80	6.19
Arkansas	18	72.22±7.08	81-59	1.66	9.81
Texas	49	72.12±5.48	85-60	.61	7.60
Gulf Coast	52	72.90±8.15	95-50	1.13	11.18
Florida	28	72.32±5.80	85-60	1.09	8.03
Length of Hind Foot					
North Carolina (CP)	6	18.66±.51	19-18	.21	2.77
North Carolina (P)	46	17.95±1.11	20-16	.16	6.21
North Carolina (M)	24	18.25±.84	20-17	.17	4.64
Virginia (CP)	25	19.60±.57	21-19	.11	2.95
Virginia (P)	19	19.05±.62	20-18	.14	3.26
Virginia (M)	9	18.88±.60	20-18	.20	3.18
Amelia, Virginia	6	18.50±1.40	20-17	.42	5.67
Georgia (CP)	13	18.07±.95	20-17	.26	5.23
Georgia (P)	32	17.53±.94	19-16	.16	5.42
Georgia (M)	10	18.20±.91	20-17	.29	5.05
South Carolina	11	19.00±.77	20-18	.23	4.08
Illinois-Missouri	29	17.72±1.70	20-12	.31	9.64
Arkansas	18	18.44±1.29	20-14	.30	7.01
Texas	49	17.83±1.20	21-15	.13	6.74
Gulf Coast	50	18.26±2.22	29-13	.31	12.21
Florida	28	17.78±1.34	19-13	.25	7.55
Length of Ear					
North Carolina (CP)	6	16.50±1.04	18-15	.42	6.36
North Carolina (P)	38	16.31±1.11	20-14	.18	6.85
North Carolina (M)	12	15.00±1.47	17-13	.42	9.85
Virginia (CP)	2	17.50±2.12	19-16	1.50	12.12
Virginia (P)	10	18.60±.96	20-17	.30	5.19

TABLE 2.—CONTINUED.

Locality	N	Mean ± 1 SD	Range	SE	CV
Virginia (M)	8	17.37±1.40	20-16	.49	8.10
Amelia, Virginia	----	-------------------	--------	------	------
Georgia (CP)	6	16.00±.89	17-15	.36	5.59
Georgia (P)	11	14.45±2.25	18-12	.67	15.58
Georgia (M)	3	15.33±.57	16-15	.33	3.77
South Carolina	4	15.50±1.29	17-14	.64	8.33
Illinois-Missouri	29	15.41±1.57	17-10	.29	10.19
Arkansas	11	16.45±.68	18-16	.20	4.18
Texas	46	15.72±1.53	18-11	.17	9.78
Gulf Coast	41	16.26±2.51	26-12	.39	13.22
Florida	27	15.88±1.36	21-14	.26	8.61
		Condylobasal Length			
North Carolina (CP)	4	23.22±1.22	24.2-21.5	.61	5.29
North Carolina (P)	32	23.32±.68	24.6-22.3	.12	2.92
North Carolina (M)	26	22.74±.95	24.7-21.0	.18	4.18
Virginia (CP)	24	23.94±.62	25.1-22.8	.12	2.61
Virginia (P)	15	22.68±.67	23.7-21.8	.17	2.95
Virginia (M)	11	23.58±.87	24.6-21.6	.26	3.71
Amelia, Virginia	5	22.40±.75	23.7-21.9	.33	4.70
Georgia (CP)	9	23.26±.83	24.6-22.3	.27	3.61
Georgia (P)	17	22.41±1.72	25.0-17.0	.41	7.69
Georgia (M)	8	22.90±.71	24.1-22.1	.25	3.13
South Carolina	6	23.46±.55	24.1-22.7	.22	2.36
Illinois-Missouri	25	22.70±.51	23.8-21.9	.10	2.27
Arkansas	23	23.30±.45	24.3-22.4	.09	1.96
Texas	43	22.66±.61	23.8-21.4	.07	2.70
Gulf Coast	42	22.43±1.48	25.0-18.6	.22	6.63
Florida	22	22.70±.97	24.3-20.8	.20	4.28
		Zygomatic Breadth			
North Carolina (CP)	4	13.80±.14	14.0-13.7	.07	1.02
North Carolina (P)	33	13.37±.37	14.3-12.7	.06	2.78
North Carolina (M)	26	13.18±.54	14.3-12.2	.10	4.16
Virginia (CP)	26	13.85±.36	14.5-13.0	.07	2.62
Virginia (P)	15	13.19±.38	13.9-12.6	.10	2.94
Virginia (M)	11	13.56±.41	14.2-12.7	.12	3.06
Amelia, Virginia	5	13.10±.27	13.5-12.8	.12	2.09
Georgia (CP)	9	13.56±.50	14.4-12.7	.16	3.69

TABLE 2.—CONTINUED.

Locality	N	Mean ± 1 SD	Range	SE	CV
Georgia (P)	21	12.90±.75	13.8-10.6	.16	5.87
Georgia (M)	8	13.25±.45	13.9-12.6	.16	3.45
South Carolina	8	13.56±.46	14.3-13.0	.16	3.46
Illinois-Missouri	26	12.99±.42	13.8-11.8	.08	3.27
Arkansas	22	13.45±.37	14.2-12.7	.08	2.79
Texas	43	13.18±.42	13.9-12.3	.04	3.20
Gulf Coast	46	13.10±.72	14.7-11.3	.10	5.56
Florida	24	13.17±.44	14.1-12.1	.09	3.37
Depth of Braincase					
North Carolina (CP)	4	9.90±.86	10.9-9.0	.43	8.69
North Carolina (P)	25	9.52±.28	10.2-9.0	.05	2.99
North Carolina (M)	13	9.55±.26	10.0-9.2	.07	2.82
Virginia (CP)	20	9.55±.22	10.1-9.2	.05	2.39
Virginia (P)	15	9.52±.42	10.3-8.4	.11	4.44
Virginia (M)	11	9.87±.18	10.1-9.6	.05	1.87
Amelia, Virginia	4	9.00±.40	9.2-8.4	.20	4.44
Georgia (CP)	5	9.64±.38	10.3-9.3	.17	3.99
Georgia (P)	14	9.35±.55	10.7-8.3	.15	5.99
Georgia (M)	4	9.43±.28	9.7-9.1	.14	2.92
South Carolina	4	9.80±.41	10.1-9.2	.20	4.17
Illinois-Missouri	25	9.29±.34	9.9-8.7	.07	3.69
Arkansas	1	9.30	----------	------	------
Texas	43	9.37±.19	9.7-9.0	.02	2.10
Gulf Coast	33	9.28±.44	10.0-8.0	.08	4.71
Florida	21	9.67±.28	9.8-8.5	.06	2.97
Length of Rostrum					
North Carolina (CP)	4	9.65±.37	10.2-9.4	.18	3.83
North Carolina (P)	30	9.72±.51	10.6-8.6	.09	5.33
North Carolina (M)	17	9.34±.42	10.2-8.7	.10	4.54
Virginia (CP)	23	9.61±.37	10.2-9.0	.08	3.80
Virginia (P)	16	9.25±.35	9.8-8.8	.09	3.79
Virginia (M)	11	9.73±.71	10.5-8.3	.21	7.30
Amelia, Virginia	11	8.53±.48	9.6-7.8	.14	5.63
Georgia (CP)	5	8.90±.82	9.8-7.8	.37	9.27
Georgia (P)	20	8.98±.92	10.1-5.9	.21	10.23
Georgia (M)	6	9.12±.13	9.3-9.0	.05	1.46
South Carolina	5	9.62±.55	10.3-8.8	.24	5.67

TABLE 2.—CONTINUED.

Locality	N	Mean ± 1 SD	Range	SE	CV
Illinois-Missouri	26	9.67±.55	10.7-8.8	.11	5.70
Arkansas	1	10.00	----------	------	- ----
Texas	42	9.75±.49	10.8-8.0	.06	5.12
Gulf Coast	38	9.14±.70	10.3-7.4	.11	7.72
Florida	19	9.24±.53	10.1-8.1	.12	5.79
Length of Upper Molar Toothrow					
North Carolina (CP)	4	3.80±.14	3.9-3.6	.07	3.72
North Carolina (P)	37	3.66±.15	3.9-3.1	.02	4.09
North Carolina (M)	18	3.80±.13	4.0-3.5	.03	3.43
Virginia (CP)	23	3.56±.12	3.8-3.4	.03	3.45
Virginia (P)	16	3.72±.13	3.9-3.5	.03	3.43
Virginia (M)	11	3.90±.54	4.0-3.8	.02	1.38
Amelia, Virginia	11	3.65±.14	3.9-3.4	.04	3.76
Georgia (CP)	5	3.60±.16	3.8-3.4	.07	4.39
Georgia (P)	19	3.67±.18	3.9-3.1	.04	4.81
Georgia (M)	7	3.54±.23	3.9-3.3	------	------
South Carolina	5	3.82±.25	4.2-3.6	.11	6.52
Illinois-Missouri	26	3.76±.13	4.0-3.5	.03	3.52
Arkansas	1	3.70	----------	------	------
Texas	43	3.73±.10	3.9-3.5	.01	2.71
Gulf Coast	39	3.77±.10	3.9-3.7	.01	2.08
Florida	22	3.67±.10	3.9-3.5	.02	2.81
Post-palatal Length					
North Carolina (CP)	4	8.98±.67	9.5-8.1	.33	7.47
North Carolina (P)	25	8.99±.48	9.8-8.0	.09	5.28
North Carolina (M)	13	9.14±.64	10.4-8.2	.18	7.06
Virginia (CP)	19	9.02±.41	9.7-8.3	.09	4.55
Virginia (P)	14	8.76±.36	9.4-8.1	.09	4.09
Virginia (M)	3	8.80±.60	9.4-8.2	.35	6.82
Amelia, Virginia	5	8.46±.39	9.1-8.1	.17	4.62
Georgia (CP)	5	8.66±.15	9.2-8.3	.15	3.88
Georgia (P)	15	8.72±.86	9.7-6.2	.22	9.88
Georgia (M)	5	9.10±.45	9.6-8.5	.20	4.98
South Carolina	3	9.60±.79	10.5-9.0	.46	8.27
Illinois-Missouri	25	8.67±.38	9.8-8.3	.08	4.29
Arkansas	1	9.20	----------	-- ---	------
Texas	42	9.27±.39	9.9-8.5	.05	4.21

TABLE 2.—CONCLUDED.

Locality	N	Mean ± 1 SD	Range	SE	CV
Gulf Coast	33	8.70±.77	10.1-7.1	.13	8.89
Florida	21	8.81±.44	9.5-8.0	.09	4.95
Length of Lower Molar Toothrow					
North Carolina (CP)	4	4.00±.16	4.2-3.8	.08	4.08
North Carolina (P)	30	3.69±.21	4.0-3.2	.04	5.08
North Carolina (M)	16	3.90±.17	4.1-3.4	.04	4.23
Virginia (CP)	23	3.59±.12	3.9-3.4	.03	3.40
Virginia (P)	16	3.84±.14	4.0-3.5	.04	3.67
Virginia (M)	3	4.00±.20	4.2-3.8	.12	5.00
Amelia, Virginia	11	3.69±.15	4.0-3.5	.05	4.10
Georgia (CP)	5	3.60±.32	3.9-3.2	.14	9.00
Georgia (P)	20	4.11±.17	4.3-3.7	.04	4.07
Georgia (M)	6	3.48±.30	3.9-3.2	.12	8.79
South Carolina	4	4.35±.24	4.5-4.0	.12	5.47
Illinois-Missouri	26	3.84±.19	4.1-3.2	.04	4.95
Arkansas	1	3.70	----------	------	------
Texas	19	3.77±.09	4.0-3.6	.02	2.48
Gulf Coast	26	3.86±.08	4.0-3.7	.02	2.08
Florida	22	3.80±.12	4.5-3.7	.04	4.13
Least Interorbital Breadth					
North Carolina (CP)	4	4.50±.14	4.6-4.3	.07	3.14
North Carolina (P)	37	4.24±.15	4.5-3.9	.02	3.53
North Carolina (M)	18	4.31±.09	4.5-4.2	.02	2.09
Virginia (CP)	22	4.12±.19	4.4-3.7	.04	4.49
Virginia (P)	16	4.29±.16	4.5-3.9	.04	3.80
Virginia (M)	11	4.47±.15	4.7-4.3	.04	3.33
Amelia, Virginia	11	4.00±.13	4.2-3.8	.04	3.24
Georgia (CP)	5	4.08±.24	4.4-3.8	.11	5.85
Georgia (P)	20	4.11±.17	4.3-3.6	.04	4.07
Georgia (M)	6	3.91±.21	4.2-3.6	.09	5.46
South Carolina	5	4.36±.11	4.5-4.2	.05	2.61
Illinois-Missouri	26	4.10±.20	4.6-3.8	.04	4.86
Arkansas	1	4.00	----------	------	------
Texas	43	4.38±.17	4.8-4.0	.02	3.99
Gulf Coast	40	4.18±.14	4.0-3.9	.02	3.88
Florida	22	4.22±.17	4.5-3.7	.04	4.13

ginia average shorter than mice from the Piedmont and mountains in that state. Specimens from the mountains of Georgia average somewhat longer than those from the Georgia coastal plains and Piedmont. Mice from eastern Texas average longer than samples from Illinois and Missouri. Mice from South Carolina, mostly from the Piedmont, average longest of all specimens examined but overlap considerably coastal and Piedmont samples from Georgia and North Carolina.

Length of mandibular toothrow.—Mice from South Carolina have a significantly longer lower molar row than all other samples studied; slight overlap occurs with the coastal plains population from North Carolina and mice from the mountains of Tennessee, western Virginia, and Kentucky. In North Carolina, mice possessing longer molar rows are on the coastal plains with decreasing length on the Piedmont and increasing length in mountain samples. There is concordance between all Piedmont samples. Specimens from the mountains of Georgia have shortest lower molar rows. There is a cline of decreasing size from northernmost populations progressing southward into the mountains of Georgia. Specimens from Texas, Illinois, Missouri, and Gulf Coast areas of Louisiana, Mississippi, and Florida are nearly identical in this feature. Mice from peninsular Florida are considerably longer in this measurement than are adjoining populations from the coastal plains of Georgia.

Least interorbital breadth.—A cline of decreasing size from the northern Appalachians of western Virginia south to Georgia is evident. A cline involving decrease in size is also evident from the coastal plains of the Carolinas to the Piedmont, but this trend is not evident in Georgia. There the mountain populations are smaller than Piedmont and coastal plains samples which resemble each other closely. Samples from the mountains of North Carolina and Virginia are larger in this feature than Piedmont populations. Eastern Texas populations, average considerably larger than specimens from Illinois and Missouri, and those from the Gulf Coast.

Color of pelage.—Specimens from the Atlantic Coastal Plain of Virginia, the Carolinas, and Georgia are somewhat brighter (more reddish yellow) than those from the Piedmont and mountainous areas to the west, which are more brownish as a result of blacker overtones (greater suffusion of black guard hairs). Mice from Texas, northern Louisiana, Missouri, and Illinois tend to a brighter color with yellowish overtones, whereas those from the Florida Peninsula are rich yellowish brown.

Summary of Patterns of Geographic Variation

Several trends of variation seem well-defined as follows: (1) a cline of decreasing size from north to south exists in the Appalachian Mountains in all external features studied and in certain cranial features (condylobasal length, depth of braincase, length of rostrum, length of maxillary toothrow, length of mandibular toothrow), yet these populations show more concordance with each other than they do with those of the eastern Piedmont or coastal plains; (2) a cline of decreasing size in breadth of cranium, interorbital breadth, post-palatal length, and depth of braincase occurs from the Atlantic

Coastal Plain to the Piedmont; (3) a decreasing cline in external size (total length, length of body, length of tail, and length of hind foot) exists between Atlantic Coastal Plains and Piedmont populations; samples from the Appalachian Mountains mostly average large in these characters; (4) specimens from Arkansas have longer hind feet, larger crania, but shorter tails than surrounding populations from Missouri, Illinois, and eastern Texas; (5) specimens from Amelia Court House, Virginia, are smaller in nearly all characters that would be expected to be small in a subadult sample, whereas in characters such as length of toothrows that approach maximal size in subadults (class two mice), they are not significantly different from surrounding populations; (6) Gulf Coast populations from Louisiana, Mississippi, and northwestern Florida are highly variable (see coefficients of variation of measurements) suggesting a secondary zone of intergradation; (7) South Carolina (mostly Piedmont) mice have a significantly long lower molar toothrow; (8) specimens from peninsular Florida (Ocala Ridge) have the brightest orange-yellow color of pelage (specimens to the north have a reddish brown overtone, and those to the west more yellowish red), with little variation in color of pelage throughout other parts of the geographic range; (9) specimens from Amelia Court House, Virginia, are a dull yellow with blackish overtones similar to age two mice (subadults).

Seemingly there are five groups of golden mice that are distinct enough from each other to warrant subspecific recognition as follows: (1) Atlantic Coastal plains and Piedmont populations (clinal variation exists between these populations and the overlap in characters studied is of such magnitude that they should be considered as one subspecies); (2) Appalachian Mountains populations with specimens from the mountains in Georgia smaller in most features studied than those to the north in North Carolina and Virginia; (3) specimens from peninsular Florida, with much brighter orange-colored pelage and longer molar rows than in other races; (4) populations from eastern Texas, northern Louisiana and Mississippi, western Tennessee, Missouri, and Illinois; (5) the mountainous region of Arkansas and southern Missouri.

NATURAL HISTORY

Populations and habitat.—McCarley's (1958) study in eastern Texas revealed a population density, in a lowland flood plain with hardwoods and considerable underbrush, varying from as few as .3 per acre in summer to as many as 2.2 per acre in early spring.

Home range in the same area was 1.46 ± .17 acres for males and 1.40 ± .22 acres for females. Sex ratios in the study in eastern Texas did not depart significantly from the expected 1:1. McCarley (1959a) found that irradiation of 500 R on male testes reduced the population density in similar habitat.

The habitat of golden mice varies from flood plain, principally hardwood forests with underbrush, to upland pine-oak and pine stands. Specific notes on habitat are: Virginia, Handley and Patton (1947) and Handley (1948), woods and thickets usually associated with honeysuckle and occasionally in cane brakes; South Carolina, Golley (1966), in wooded and brushy areas particularly in thickets of honeysuckle and greenbrier; Georgia, Golley (1962), lowland swamp forest to open drier upland forest; Tennessee, Kellogg (1939), in hemlock among moss-covered boulders, swampy woodlands, along borders of broomsedge fields, and in brier patches; Kentucky, Barbour (1942) and Goodpaster and Hoffmeister (1954), in brushy valleys with beech, dogwood, greenbrier, and honeysuckle; Illinois, Hoffmeister and Mohr (1957), in thick timber bordering cypress swamps; Missouri, Schwartz and Schwartz (1959) and Easterla (1968), in moist thickets, forests, borders of broomsedge fields, and rocky-oak hillsides; Arkansas, Sealander (1956), in oak-pine uplands; Louisiana, Lowery (1936, 1943), in habitat similar to that reported for eastern Texas; Texas, McCarley (1959b), Davis (1960), Packard and Garner (1964), upland pine-oak woodland, heavily forested hardwood flood plain, and on hillsides with considerable lianas such as grapevine and honeysuckle. Packard (1968), while studying fulvous harvest mice, found the distribution of golden mice on the same area of intensive study (where eight habitat types were present) to be significantly correlated with that of the pine-oak habitat.

Behavior.—Golden mice are quite docile in comparison with other peromyscoid mice, and are much less aggressive than pygmy mice *(Baiomys)*, which are about half their size. Golden mice seem quite social (see McCarley, 1958, and Dunaway, 1955). Both arboreal globular nests and ground nests are utilized for feeding (Goodpaster and Hoffmeister, 1954) and rearing litters (Packard and Garner, 1964). Layne (1960) reported in detail the behavior of young and parental care. He also suggested that golden mice become increasingly wild after long periods of captivity. The tail is frequently used prehensily in climbing and in moving through vines (see Packard and Garner, 1964, and Rippy and Harvey, 1963).

McCarley (1959b) reported these mice as having a rather distinct odor different from that of other peromyscoids. My studies of golden mice, both in the field and laboratory, suggest a crepuscular and nocturnal activity cycle.

Reproduction.—Golden mice may be polyestrous (see Goodpaster and Hoffmeister, 1954) in certain parts of their geographic range and monestrous in other parts (see McCarley, 1958). Breeding occurs chiefly in the winter to late winter period followed by a gestation period of 25 to 30 days (average of 15 litters, 27 days); two to four young are born per litter (average 2.65 in 85 litters—see Linzey and Linzey, 1967b).

ACCOUNTS OF SUBSPECIES

Ochrotomys nuttalli aureolus (Audubon and Bachman)

Mus (Calomys) aureolus Audubon and Bachman, Proc. Acad. Nat. Sci. Philadelphia, 1:98, 1841.

[*Peromyscus nuttalli*] *aureolus*, Elliot, Field Columb. Mus., Zool. Ser., 2:140, 1901 (part).

Ochrotomys nuttali [*sic*] *aureolus*, Rippy and Harvey, Trans. Kentucky Acad. Sci., 24:5, 1963.

Holotype.—Not known to exist. Because no holotype, syntypes, nor lectotype are known to be extant, I designate as a neotype an adult female. skin and skull, no. 104075 University of Michigan, Museum of Zoology; from Marshall, Madison Co., North Carolina (a place approximately 45 miles northwest of the South Carolina state line).

Range.—Appalachian Mountains, from Clark County Virginia south through North and South Carolina into northwestern Georgia, thence northward into eastern one-half of Tennessee and Kentucky (see Fig. 1).

Diagnosis.—Size medium to large for the species; external and cranial characters of populations in north average larger than those to the south in the mountains; middorsal region reddish brown 5YR 4/4, ears of same color; belly dusky cinnamon, sides dusky tawn. A dark reddish brown colored subspecies resulting from a profusion of black guard hairs from the nape posterior to the base of the tail (see Table 2 for measurements of samples from North Carolina mountainous area).

Comparisons.—For comparisons with *O. n. lisae, O. n. nuttalli, O. n. floridanus,* see accounts of those subspecies. From *O. n. flammeus*, to the west *O. n. aureolus* differs in: ears and dorsal color of body darker reddish brown; belly duskier, tail darker above; total length and length of tail averaging longer; ears average smaller.

Remarks.—In most internal and cranial characters studied, *O. n. aureolus* shows decrease in size from Virginia southward into Georgia. Mice from central Kentucky and Tennessee show intergradation in color and size from *O. n. lisae* to the west, but seem best referred to *aureolus*. Golden mice in the Appalachian Mountains average larger than Piedmont samples to the east in most external and certain cranial features (depth of braincase, post-palatal length, length of mandibular toothrow). Mice from the mountains are duskier reddish-brown than those from the Piedmont and coastal plains. This results from a greater profusion of black guard hairs on the dorsum in the samples from the mountains. Because of the sharp break in the clines detected from the coastal plain to the Piedmont, mice from the mountains comprise a distinct subspecies to which I restrict the name *O. n. aureolus.*

The original type locality for *aureolus*, "oak forests of South Carolina," is of little use, because oak forests are found in both upland and lowland areas there. I have chosen to restrict the type locality to the mountains (pine and oak), and also select a place as close to the original generally defined area as the availability of a suitable specimen would permit. The result of selecting a new type locality also has the advantage of more accurately correlating the patterns of variation detected in this species.

Specimens examined (169).—GEORGIA. *Rabien Co.:* unspecified locality, 1 (UG). *Stephens Co.:* Toccoa, 1 (USNM). *Union Co.:* Margret, 2 (UG), 3 (USNM). *Walker Co.:* Pinetucky, 5 (AMNH). KENTUCKY. *Barrew Co.:* .45 mi. ENE Little Hope Church, 1 (UI). *Carter Co.:* 10 mi. E Olive Hill, 1 (UI). *Christian Co.:* 1 mi. NNE Parklodge, 1 (UI). *Edmondson Co.:* Mammoth Nat'l Park, 1 (KU). *Flemming Co.:* Crancreek, 2 (UI); 8 mi. S Flemmingsburg, 11 (UG); Wallingford, 1 (KU). *Hopkins Co.:* 1.37 mi. NW junction of Ky. 109 and US 62, 1 (UI). *Lewis Co.:* Salt Lick Creek, 2½ mi. W Charters, 1 (UI); 6½ mi. W Vanceburg, 2 (UI); 6 mi. E Vanceburg, 14 (UI); 2 mi. S Vanceburg, 1 (KU); 1 mi. W Vanceburg, 1 (UI). *Madison Co.:* 2 mi. S Big Hill, 3 (UI). *McCrealy Co.:* 4½ mi. NE Greenwood, 2 (UI). *Pulaski Co.:* Eubanks, 7 (USNM). *Rowan Co.:* Morehead, 1 (USNM); 2 mi. S Rodburn, 1 (UI); Rodburn, 21 (UI), 2 (USNM). *Trigg Co.:* 8 mi. NNE Golden Pond, 1 (MZ). NORTH CAROLINA. *Buncombe Co.:* Asheville, 3 (MZ), 1 (NCS); Weaverville, 25 (AMNH), 4 (FM). *Cherokee Co.:* Murphy, 3 (UG). *Macon Co.:* Highlands, 9 (UG). *Madison Co.:* Marshall, 10 (MZ). *Transylvania Co.:* White Water River, 1 (NCS). TENNESSEE. *Carter Co.:* 3 mi. SSW Roan Mt., 3 (MZ); Roan Mt., 1 (USNM). *Jefferson Co.:* unspecified locality, 2 (USNM). *Johnson Co.:* 3 mi. NE Holston Mt., 4 (USNM). *Knox Co.:* Knoxville, 1 (USNM). *Union Co.:* Maynardville, 6 (MZ). VIRGINIA. *Montgomery Co.:* vic. Blacksburg, 6 (VPI), 1 (AMNH). *Scott Co.:* 6 mi. SE Norton, 1 (MZ).

Ochrotomys nuttalli flammeus (Goldman)

Peromyscus nuttalli flammeus Goldman, Proc. Biol. Soc. Washington, 54:190, December 8, 1941.

Holotype.—Adult female, skin and skull, no. 170591 U.S. National Museum (Biological Surveys Collection); from Delight, Pike Co., Arkansas; obtained on November 16, 1910, by Walter G. Savage, original number 8221.

Range.—Ouachita Mountains of easternmost central Oklahoma and west-central Arkansas; also in Arkansas from the type locality eastward to the vicinity Pine Bluff, Jefferson County, north to the vicinity of Beebe, White County, thence northwest into the Boston Mountains in the vicinity of Fayetteville (see Fig. 1).

Diagnosis.—Size medium to large for the species; length of body larger and tail proportionately shorter than in specimens from Texas, northern Louisiana, southern Missouri, and Illinois; middorsal region an ochraceous-tawny, black guard hair more profuse on head; sides cinnamon-buff, underparts creamy to pale cinnamon-buff; tail faintly bicolored, ochraceous above, cream-colored below (see Table 2 of measurements for external and cranial variants).

Comparisons.—*O. n. flammeus* intergrades with *O. n. lisae* to the southwest in Texas and toward the Mississippi River Valley to the east of the Ouachita and Ozark uplifts; to the north, *flammeus* intergrades with *lisae* northeastward across the Ozark Plateau. Because of this, *flammeus* is compared only with *lisae*.

Young adults of both subspecies in unworn pelage show best the colors that differentiate the two subspecies. *O. n. flammeus* dorsally has orange-red overtones, whereas *lisae* is yellowish red (this difference results mostly from a greater profusion of black guard hairs on *O. n. flammeus*). Crania of *flammeus* are larger (averages of condylobasal length and zygomatic breadth) than those of *lisae*, and *flammeus* possesses somewhat longer ears, averages larger in body length, but has a proportionately shorter tail.

Remarks.—When Goldman (1941) described *O. n. flammeus* (on the basis of 15 specimens), he noted that ". . . additional specimens are needed for the more exact delimitation of the ranges of the subspecies . . . ," suggesting that the degree of variation within western populations of the species merited further analysis to better interpret patterns of variation. Patterns of variation revealed in my studies suggest that a combination of characteristics (length of tail proportionate to body length, larger ears and crania, and somewhat different color patterns) do delimit the populations from the Ouachita and Boston mountains and southwestern part of the Ozark Plateau from those to the southwest, south, east, and northeast with which they intergrade. The habitat occupied by *flammeus* in the uplands is also slightly different (rocky with pine) from those populations on the alluvial regions to the north, east, and south.

Specimens examined (46).—ARKANSAS. *Garland Co.:* 3 mi. N Buckville, 1 (UA); Sulphur Gorge, Hot Springs, 2 (UI). *Jefferson Co.:* 10 mi. N Pine Bluff, 5 (UA); Pine Bluff, 2 (UA). *Pike Co.:* type locality, 7 (USNM), 4 (MCZ). *Polk Co.:* 6.3 mi. NW Rich Mountain, 2 (UA); 6 mi. N, 3 mi. E Mena, 1 (KU); Cave, 1 (KU); Shady Lake area, 1 (UA). *Scott Co.:* Fourch La Fave River, 1 (FM). *Washington Co.:* Fayetteville, 1 (UA), 1½ mi. W Farmington, 1 (UA); 7 mi. NE Winslow, 4 (KU); Winslow golf course, 3 (KU); 1 mi. N Winslow, 1 (KU); Winslow, 5 (KU). *White Co.:* Beebe, 1 (USNM), Big Spring, 1 (USNM). OKLAHOMA. Redland (in eastern Oklahoma originally located in "Indian Territory"), 2 (USNM).

Ochrotomys nuttalli floridanus, new subspecies

Holotype.—Adult male, skin and skull, no. 119422 Museum of Natural History, The University of Kansas; from Welaka, Putnam Co., Florida; obtained on February 18, 1948, by G. H. Pournelle, original number 268.

Range.—Peninsular Florida; northern limits in area of Wakulla and Leon counties in the northwest, east to the Atlantic Coast (vicinity of Jacksonville); south to approximately 27° latitude.

Diagnosis.—Size medium to small for the species (for measurements, see Table 2); tail short relative to body length; hind foot short; braincase shallow; middorsal region yellowish brown (10 YR 5/8), belly cream buff with yellowish overtone extending onto region of upper and lower jaws; ventralmost vibrissae white; tail bicolored, pale cinnamon above, cream-colored below; ears uniformly orange; general appearance, burnished orange.

Comparisons.—From *O. n. nuttalli, O. n. floridanus* differs in: dorsal coloration brighter orange; upper parts of hind feet white rather than gray; tail cinnamon-orange above rather than blackish brown; ears orange rather than brownish red; belly with yellowish-white wash rather than dusky white; averaging smaller in most external and cranial measurements (see Table 2).

From *O. n. aureolus, O. n. floridanus* differs in: dorsal color orange-red rather than brownish red; tail cinnamon-orange above rather than blackish brown; ears orange rather than blackish red to brown; belly yellowish white rather than dusky white with cinnamon overtones; averaging smaller in total length.

From *O. n. lisae, O. n. floridanus* differs in: dorsal color brighter orange rather than yellowish; tail cinnamon-orange rather than brown above, yellowish rather than dusky white below; ears orange rather yellowish brown; belly yellowish white rather than whitish with tones of cinnamon; rostal length and post-palatal length averaging shorter.

Remarks.—The most striking differences of *floridanus* are the lack of a profusion of black dorsal guard hairs on the posterior half of the back and upper parts of the tail, resulting in an orange or golden-red pelage. This distinctive color differentiates *floridanus* from the other subspecies. *O. n. floridanus* intergrades with *lisae* and *nuttalli* in western Florida, southern Alabama, and Mississippi. Specimens from southern Georgia and northern Florida are intergrades between *floridanus* and *nuttalli.* Specimens from the Ocala Ridge in Florida show best those features that differentiate this subspecies.

Specimens examined (53).—FLORIDA. *Alachua Co.:* 10 mi. NW Gainesville, 1 (UF); 8 mi. NW Gainesville, 2 (MZ), 1 (UF); 7 mi. NW Gainesville, 1 (UF); San Felasco Hammock, Gainesville, 4 (UI); Gainesville, 2 (AMNH); Gracie's Crossing, 1 (MZ), 2 (UF); ½ mi. N Paradise, 1 (UF). *Citrus Co.:* Homosassa Springs, 3 (AMNH). *Clay Co.:* 3 mi. SW Middleburg, 1 (UF). *Duval Co.:* New Berlin, 1 (AMNH). *Columbia Co.:* Winfield, 1 (UF). *Gadson Co.:* Chattahoochee, 6 (AMNH). *Highlands Co.:* Hicoria (Archbold Biological Station), 3 (UF). *Leon Co.:* 10 mi. SE Tallahassee, 3 (AMNH). *Levy Co.:* Gulf Hammock, 7 (UF). *Putnam Co.:* type locality, 8 (UF), 1 (UK). *St. John's Co.:* 2 mi. W Crescent Beach, 1 (UF). *Taylor Co.:* 4 mi. SW Perry, 1 (UF). *Wakulla Co.:* Spring Creek, 1 (UF). *Volusia Co.:* Enterprise, 1 (AMNH).

Ochrotomys nuttalli lisae, new subspecies

Holotype.—Young adult male, skin, skull, and body skeleton, no. 119421 Museum of Natural History, The University of Kansas; from La Nana Creek bottoms, 1 mi. E Stephen F. Austin State College campus, Nacogdoches, Nacogdoches Co., Texas; obtained on January 18, 1961, by Robert L. Packard, original number 829.

Range.—Eastern Texas, central and northern Louisiana, northward into extreme eastern Arkansas (in the Mississippi Valley), Missouri, and southern Illinois, thence to western parts of Kentucky, Tennessee, and Mississippi.

Diagnosis.—Size medium to small for the species (for measurements see Table 2); total length small, with tail averaging short for the species and body size small; hind foot averaging shorter than most populations from other areas examined; ear of average size for the species; cranial breadth average for the species, but condylobasal length averaging shorter and braincase shallower; length of toothrows (upper and lower) of average length for the species; dorsal ground color near 7.5 YR 5/6 (strong brown), some specimens with more yellowish wash (particularly in western Louisiana and eastern Texas); belly cream colored with some overtones of cinnamon; tail bicolored, cinnamon above, cream below.

Comparisons.—For comparisons with *O. n. flammeus*, see account of that subspecies. From *O. n. aureolus*, with which *O. n. lisae* intergrades to the east, *lisae* differs in: dorsal color paler, having yellowish overtones than being reddish brown with dusky overtones; belly somewhat paler, more whitish rather than yellowish to cream-colored (particularly true of freshly taken specimens); tail more distinctly bicolored rather than tending to unicolor; toothrows averaging shorter except for populations from northwestern Georgia; smaller in most cranial dimensions except rostral length; total length and length of tail averaging less.

Remarks.—*O. n. lisae* is typically a yellowish-washed, small subspecies of the alluvial bottomlands and low rolling hills of the Austroriparian part of eastern Texas, central and northern Louisiana, and northward into the Mississippi River Valley. Osgood (1909) assigned the few specimens available to him from west of the Mississippi River to *O. n. aureolus* or to *O. n. nuttalli*. Goldman (1941) considered all specimens (15) that he examined from west of the Mississippi River to be *O. n. flammeus*. Studies of much larger series of specimens than were available to either of the aforementioned workers reveal two distinct subspecies in the Trans-Mississippi region. Populations in the mountainous areas in Arkansas and eastern Oklahoma seem typical of *flammeus* and are different from those in the alluvium and low rolling hills of neighboring regions. It seems best to restrict the range of *flammeus* to the mountains of Arkansas and Oklahoma in order to accord with Goldman's original description.

Lowery (1943) recognized (based on communication with Goldman) the possible presence of an undescribed population(s) of pale golden mice in Louisiana. Examination of specimens from that state leads me to conclude these pale (yellowish-colored) mice are typical of *lisae* as they compare favorably with specimens from eastern Texas. In northern Louisiana, there is evidence of intergradation in color with *flammeus* to the north, but specimens from this area are best referred to *lisae*.

Specimens from southern Missouri and southern Arkansas intergrade with *flammeus*, but seem to have more concordance with *lisae* in characters studied and are assigned to it. Eastwardly, *lisae* intergrades broadly with *O. n. aureolus*, and specimens from eastern Louisiana and Mississippi are difficult to assign to either *lisae* or *aureolus*, or in some cases *floridanus*. I assign these to *lisae* mostly because there is concordance in color of pelage. Interestingly, these specimens from the Gulf Coast Region are quite variable (see Table 2), suggesting a secondary zone of intergradation. Perhaps the western populations (west of the general area of the Mississippi River Valley) were separated for a period of time from those to the east, although there is nothing in the fossil record to substantiate this.

This subspecies is named in memory of my daughter, Lisa Ann.

Specimens examined (289).—Arkansas. *Chicot Co.:* Island 80, 1 (UA); vic. El Dorado, 1 (UA). Illinois. *Alexander Co.:* Olive Branch, 20 (FM), 1 (SIU). *Johnson Co.:* 1 mi. S Forman, 1 (UI). *Pope Co.:* sec. 28, T. 12 S, R. 5 E, 6 (UI). *Union Co.:* Pine Hills, 3 (UI); Wolf Lake, 1 (SIU); 3 mi. SW Ware, 1 (SIU); 2 mi. SE Ware, 2 (SIU). Louisiana. *Bienville Parish:* 2 mi. SW Bienville, 2 (SFA). *Bossier Parish:* ½ mi. W Webster, ¼ mi. S Arkansas line, 1 (LSU). *Caddo Parish:* 2 mi. E Zylkes, 1 (LSU); ¾ mi. E Zylkes, 1 (LSU); ½ mi. E Zylkes, 1 (LSU). *Caldwell Parish:* 6¾ mi. N Columbia, 1 (LSU); Columbia, 8 (FM); Hackley, 3 (FM). *Claiborne Parish:* ½ mi. S Marsalis, 1 (LSU). *Desoto Parish:* Mansfield, 1 (USNM). *East Baton Rouge Parish:* 7 mi. SE Baton Rouge, 2 (LSU); Baton Rouge, 1 (LSU); 4 mi. S Lindsay, 1 (LSU); 3 mi. S Lindsay, 1 (LSU); 2 mi. S Lindsay, 3 (LSU); Lindsay, 2 (USNM); Plains, 5 (MZ); ½ mi. E, 2 6/10 mi. S Union, 1 (LSU); 11-12 mi. S University, 2 (LSU); 6⅔ mi. SE University, 2 (LSU); 4-5 mi. S University, 2 (LSU); 3 mi. S University, 3 (LSU), 1 (USNM); 2 mi. S University, 1 (LSU). *East Feliciana Parish:* E. Jackson, 1 (LSU). *Lincoln Parish:* Ruston, 1 (USNM); 2 mi. N Tremont, 3 (LSU). *Livingston Parish:* 2 mi. S Watson River, 1 (LSU). *Morehouse Parish:* 4 mi. SE Bastrop, 2 (LSU); Cheminahaut State Park, 2 (LUS). *Ouachita Parish:* 12 mi. W Monroe, 19 (TU); 4 mi. W Monroe, 2 (TU). *Rapides Parish:* 5 mi. E Lind, 1 (LSU). *Union Parish:* 3½ mi. N, ½ mi. E Bernice, 4 (UI); 7 mi. NE Farmerville, 1 (LSU); 4 mi. NE Farmerville, 1 (LSU); 3 mi. NE Farmerville, 2 (LSU). *Washington Parish:* 8 mi. SE Angie, 1 (TT); 7 mi. S, 5 mi. W Angie, 3 (TT); 6 mi. S Angie, 1 (TT); ½ mi. N Angie, 3 (TT). Mississippi. *Adams Co.:* unspecified locality, 1 (MGF). *Bolivar Co.:* Bogue Phalia, 1 (MGF). *Clark Co.:* Linton area, 1 (MGF). *Coahoma Co.:* Palmer Lake area, 1 (MGF). *Copiah Co.:* Crystal Springs, 1 (MGF). *Forest Co.:* Burkett Creek, 1 (MGF); McKinnon Springs, 2 (MGF); Shelby State Park, 3 (TT). *Jones Co.:* unspecified locality, 1 (MGF). *Lamar Co.:* Lumberton area, 1 (MGF). *Lauderdale Co.:* Okatibbee area, 1 (MGF). *Pearl River Co.:* Poplarville, 1 (MGF). *Pike Co.:* Percy Quinn State Park, 1 (TT). *Prentiss Co.:* 20-mile Bottom area, 2 (MGF). *Rankin Co.:* Spear Farm, 1 (MGF). *Tippah Co.:* Gillard Farm, 1 (MGF). *Tishomingo Co.:* 2½ mi. E, 2½ mi. S Tishomingo, 2 (KU). *Wayne Co.:* Trigg Area, 1 (MGF). *Wilkinson Co.:* Percis Creek, 1 (MGF). *Winston Co.:* Sulphur Springs, 1 (MGF). *Yazoo Co.:* 2 mi. SE Yazoo City, 1 (LSU). Missouri. *Bollinger Co.:* Duck Creek Refuge, 4 (UM); Puxico, 2 (UM). *Camden Co.:* Hahatonka, 1 (MZ). *Dent Co.:* Salem, 3 (UM). *Franklin Co.:* Meramec State Park, 3 (UM). *Gasconde Co.:* Owensville, 1 (UM). *Girardeau Co.:* Cape Girardeau, 3 (UM). *Howell Co.:* Willowspring, 3 (UM). *Iran Co.:* 2 mi. SW Grantsville, 1 (UI). *Jefferson Co.:* St. Louis, 1 (USNM). *Pulaski Co.:* Richland, 2 (UM). *Reynolds Co.:* West Fork, 1 (UM). *Ripley Co.:* Pratt, 1 (UM). *Texas Co.:* unspecified locality, 1 (UM). *Wayne Co.:* Williamsville, 1 (UM). Tennessee. *Lake Co.:* Real Foot Lake, 4 (UI); Tiptonville, 1 (UI). *Lauderdale Co.:* 1.9 mi. E Open Lake, 1 (UI). *Shelby Co.:* 2 mi. S Germantown, 1 (LSU). Texas. *Angelina Co.:* Lufkin, 1 (TU). *Anderson Co.:* 20 mi. NW Palestine, 6 (TU), 1 (SFA). *Cherokee Co.:* 5 mi. E Rusk, 1 (SFA); 3 mi. SE Rusk, 2 (SFA); 2 mi. N Rusk, 1 (SFA). *Harrison Co.:* 15 mi. NE Marshall, 1 (SFA). *Nacogdoches Co.:* type locality, 20 (SFA), 3 (TT), 1 (UK); 12 mi.

N Lufkin, 1 (TAM); 20 mi. SW Nacogdoches, 4 (SFA), 2 (KU); 14 mi. SW Nacogdoches, 1 (SFA); Stephen F. Austin Experimental Forest (9½ mi. SW Nacogdoches), 36 (SFA), 2 (MZ), 4 (TU), 5 (TT); 6 mi. SW Nacogdoches, 1 (SFA). *Panola Co.:* 4 mi. SE Long Branch, 1 (SFA). *Rusk Co.:* 2 mi. E Old London, 2 (SFA).

Ochrotomys nuttalli nuttalli (Harlan)

Arvicola nuttalli Harlan, Monthly Amer. Jour. Geol. Nat. Sci., Philadelphia, p. 446, April, 1832.

Ochrotomys nuttalli, Hooper, Misc. Publ. Mus. Zool., Univ. Michigan, 105:23, December 29, 1958.

Peromyscus nuttalli lewisi A. H. Howell, Jour. Mamm., 20:498, November 14, 1939 (type locality, Amelia Court House, Amelia Co., Virginia).

Holotype.—Not known to exist. Because no holotype, syntypes, nor lectotype are known to be extant, I designate as a neotype an adult female, skin and skull, no. 95889 U.S. National Museum (U.S. Biological Surveys); from Lake Drummond, Dismal Swamp, Nansemond Co., Virginia (30 miles southwest of the original type locality at Norfolk, Virginia).

Range.—Coastal plains and Piedmont of central and southern Virginia, south on the coastal plains and Piedmont of North and South Carolina, and Georgia, to central Alabama and northwestern Florida.

Diagnosis.—Size large for the species; total length, body length, and tail length in northern populations average larger than other populations studied; skull broad, particularly on coastal plains, braincase deeper on coastal plain, becoming shallower on Piedmont; middorsal region strong brown (7.5 YR 5/8), ears of same color; hind feet dusky white above; belly white with pale yellowish tint.

Comparisons.—For comparisons with *O. n. floridanus,* see account of that subspecies. From *O. n. aureolus, O. n. nuttalli* differs in: dorsum brownish red rather than with black overtones (resulting from fewer black guard hairs); upper part of tail brown rather than black-brown; facial area paler, washed with a slight yellowish tone; belly paler, having less cinnamon wash; tail averaging longer (particularly in coastal plain samples); ear and hind foot averaging longer; overall cranial size somewhat larger.

From *O. n. lisae, O. n. nuttalli* differs in: dorsum darker, red-brown rather than yellow-brown; upper parts of hind feet dusky white rather than white, ventral side of tail duskier and less fully haired; averaging larger in most external and cranial characteristics examined (see Table 2 for comparisons).

Remarks.—There are two trends in variation in *O. n. nuttalli* as follows: (1) Virginian specimens from both coastal plain and Piedmont are larger in most external and cranial characters than are samples from the south (Georgia), and the pattern in variation is clinal; (2) specimens on the coastal plain are larger in total length, length of tail, length of hind foot, depth of braincase, and post-palatal length than samples from the adjacent Piedmont—thus, a cline of decreasing size occurs from east to west. Although populations on the Piedmont differ to varying degrees from those on the coastal plains, the mice from these two areas share enough features in common to consider them as the same subspecies. The break in clinal variation occurs chiefly between the mice inhabiting the Appalachian Mountains and those of the Piedmont Region.

Osgood (1909:225) noted that specimens from Virginia were larger than those from more southerly localities, but because of the small sample sizes available to him (particularly to the west), the trends in variation were obscured. It seems best to consider the mice of the Atlantic coastal plains and Piedmont as *O. n. nuttalli*, and specimens from the mountains as *O. n. aureolus*.

O. n. lewisi is regarded as representative of a subadult population of age two (see age categories) and is considered as synonymous with *O. n. nuttalli*.

Specimens examined (244).—ALABAMA. *Escumbria Co.:* Brewton, 1 (USNM). *Houston Co.:* Dothan, 1 (USNM). *Lee Co.:* Auburn, 9 (AU), 2 (MZ); Beauregard, 1 (AU). *Mobile Co.:* Mobile, 2 (USNM). *Russell Co.:* Seale, 1 (USNM). GEORGIA. *Ben Hill Co.:* Fitzgerald, 1 (UG). *Bibb Co.:* 5 mi. NE Macon, 1 (LSU). *Camden Co.:* St. Marys, 1 (UG). *Charlton Co.:* Okefinokee, 2 (KU). *Clark Co.:* Athens, 25 (UG); Sandy Creek, 3 (UG); White Hall, 2 (UG). *Cobb Co.:* Marietta, 2 (MZ); Rozwell, 2 (KU), 4 (MZ); Vinings, 1 (UG). *Columbia Co.:* Dickey's Branch, 1 (UG). *DeKalb Co.:* Decatur, 1 (MZ); 2 mi. N Emory, 1 (UI). *Grady Co.:* 4 mi. S Beachton, 1 (UI); Sherwood Plantation, 3 (UI). *Emanuel Co.:* Adrian, 1 (UG). *Lincoln Co.:* unspecified locality, 1 (UG). *Lloyd Co.:* 8 mi. W Rhome, 1 (UI). *Lowndes Co.:* Naylor, 1 (UG). *Merriwether Co.:* Singer's Hill, 1 (UG). *Mitchell Co.:* W Side Camilla, 1 (UI). *Richmond Co.:* unspecified locality, 2 (USNM). *Sumpter Co.:* unspecified locality, 3 (UG). *Thomas Co.:* Thomasville, 3 (AMNH). *Ware Co.:* 2 mi. W Camp Cornelia, 1 (KU). *White Co.:* unspecified locality, 1 (UG). *Wilkes Co.:* unspecified locality, 1 (UG). FLORIDA. *Okaloosa Co.:* Ft. Walton, 1 (KU); 5 mi. SW Laurel Hill, 1 (UF). NORTH CAROLINA. *Beaufort Co.:* Core Point, 1 (NCS). *Currituck Co.:* NW River Marsh, 1 (NCS). *Durham Co.:* 4 mi. W Duke, 5 (DU); Duke Forest, 4 (KU); Duke University, 4 (DU); 3½ mi. E Durham, 5 (DU). *Mecklenburg Co.:* Charlotte, 6 (NCS), 1 (UI); Davidson, 3 (MZ). *North Hampton Co.:* Roanoke Rapids, 1 (FM). *New Hanover Co.:* Carolina Beach, 1 (NCS). *Orange Co.:* unspecified locality, 1 (NCS). *Stanley Co.:* unspecified locality, 1 (NCS). *Wake Co.:* Apex, 2 (FM); Green Laurel, 1 (NCS); Raleigh, 11 (AMNH), 5 (NCS), 3 (MZ), 2 (FM), 1 (IU), 1 (KU). SOUTH CAROLINA. *Abbeville Co.:* Abbeville, 2 (KU); Calhoun Falls, 9 (FM). *Aiken Co.:* unspecified locality, 2 (UG); Aiken State Park, 1 (UI). *Barnwell Co.:* unspecified locality, 2 (UG). *Dorchester Co.:* St. George, 1 (USNM). *Greenville Co.:* Cliff Ridge Road, 1 (KU); Jones Gap, 1 (KU). *Richland Co.:* Columbia, 1 (USNM). VIRGINIA. *Amelia Co.:* Amelia, 14 (USNM), 1 (MZ), 1 (VPI). *Brunswick Co.:* Seward Forest, 5 (USNM), 5 (MZ). *Campbell Co.:* Lynchburg, 9 (MZ). *Charlotte Co.:* Brookneal, 1 (MZ); 5 mi. E Charlotte, 1 (MZ); 1 mi. W Charlotte, 1 (MZ). *Halifax Co.:* 5 mi. N Clover, 1 (MZ). *Nansemond Co.:* Lake Drummond (Dismal Swamp), 4 (AMNH); Dismal Swamp, 34 (USNM).

SUMMARY

There is little fossil evidence that would account for the origin and relationship of the golden mouse. A single Pleistocene record exists from Missouri (see Olson, 1940) in an area where these mice are found today. Hibbard (1968) suggested that the neotomyine-peromyscine group had an origin in the Oligocene or early Miocene.

In degree of specialization, *Ochrotomys* possesses features suggesting that as much time has been involved in their evolution as in the case of *Onychomys*, and possibly *Baiomys* and *Scotinomys.* If so, then golden mice may have evolved in the Pliocene, though no record documents this. The relationship of *Ochrotomys* to other cricetine genera as proposed by Hooper and Musser (1964) seems most cogent. The work of Arata (1964) lends strength to the proposal that *Ochrotomys* is one of the more primitive members of the neotomyine-peromyscine line. Additional data bearing on the degree of gastric specialization in *Ochrotomys* and other genera has been reported recently by M. D. Carleton (personal communication). In 1964, one of my students, William Grabowski, made a brief survey of the gastric anatomy of representatives of the subgenera (Osgood, 1909) of *Peromyscus.* Relative to *Ochrotomys,* he found an internal fold delimiting the pyloric region from the rest of the stomach (a similar fold was detected in *Baiomys*). In addition, in all representatives studied except *Ochrotomys* and *Baiomys,* he found a region located on the ventral floor of the stomach that appeared, externally, paler in color in comparison to surrounding areas. Internally, this region was found to be thicker in comparison with the rest of the epithelium of the stomach and was always delimited by a fold (*incisura angularis* of Vorontsov, 1957).

Golden mice seem to have undergone little differentiation if *Ochrotomys* is as old as other seemingly closely related genera. I judge that the semi-arboreal habits and rather uniform habitat occupied may account for this. The genus is limited to the pine-oak forests of the United States and may have been there for some considerable time. Blair (1958) pointed to changes in the Pleistocene in the area now occupied by golden mice. Perhaps the species was divided into two separate entities in Pleistocene times, one in Florida and the other westward in Texas and northern Mexico. Sufficient time elapsed for the differentiation of several subspecies but not for species differentiation. This may account for the high degree of variation in the Gulf Coast area detected in this study. A second possibility is suggested. Golden mice may have differentiated south and west (in Mexico) of the area now occupied. These mice then could have moved northeastward through the subhumid pine-oak corridor that once existed in the Gulf Coast area (vestiges of which are the lost pines near San Marcos, Texas). Upon arrival in the southeastern United States, their geographic range may have been constricted in periods of glacial advance to the Florida Peninsula as were the ranges of certain other species of mammals. After glacial retreat, populations then dispersed northeastward and northwestward to occupy the current geographic range. I am certain this is an oversimplification, but it is all I can propose in the absence of a fossil record.

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ALGUNOS MURCIELAGOS DEL NORTE DE ARGENTINA

POR

BERNARDO VILLA-R. Y MARTHA VILLA CORNEJO

La rabia es una zoonosis que a pesar de su antiguedad, sigue siendo un problema actual que atrae la atención de muchos investigadores, así como de instituciones nacionales e internacionales. En América el padecimiento adquiere un mayor relieve, a causa de que ha demostrado su presencia entre los mamíferos del orden Chiroptera que actúan como portadores, destacándose entre ellos los vampiros o murciélagos chupadores de la familia Desmodontidae, peculiares solamente del Nuevo Mundo, que por sus hábitos alimenticios pueden ser vectores eficientes para infectar a otros mamíferos (Villa-R., 1966:469-471; Bernstein, 1952:82-87, 92-93).

Durante los meses de junio, julio, y agosto de 1965, bajo el patrocinio de la Oficina Sanitaria Panamericana, Organización Mundial de la Salud (a promoción del Servicio de Luchas Sanitarias (SELSA), Dirección General de Sanidad Animal, Secretaría de Estado de Agricultura y Ganadería de la Nación, República Argentina), uno de nosotros (Villa-R.), en calidad de consultor a corto plazo, de la Organización Mundial de la Salud, llevó a cabo trabajos de Campo, con el objeto de colectar ejemplares de murciélagos y otros mamíferos del norte de la República Argentina para estudiar la distribución geográfica, la ecología, la etología de los murciélagos y sus relaciones con el virus de la rabia.

AGRADECIMIENTOS

Nos es placentero manifestar nuestra gratitud a las personas siguientes, por las innumerables muestras de fraternal camaradería que, en una o en otra forma, hicieron agradable nuestra estancia en aquel país o que, con su compañía y cooperación facilitaron nuestros trabajos: Dr. Boris Szyfres, Director del Centro Panamericano de Zoonosis: Dr. Cézar A. Mayer, Director Técnico del Servicio de Luchas Sanitarias; Dr. Guillermo Forrest; Dr. Abel Retamozo Yepes, del mismo servicio (SELSA), y al entusiasta y generoso Dr. Guztavo A. González Blanco, Segundo Jefe de la Campaña contra la rabia paresiante en el norte de Argentina, quien no escatimó ningún esfuerzo para el logro de nuestros propósitos.

Al personal a sus órdenes patentizamos también nuestra profunda gratitud. Roberto L. Menini, del personal del Centro Panamericano de Zoonosis (CEPANZO), nos acompañó durante los tres meses, llevando al cabo con entusiasmo y devoción las tareas que se le encomendaron. Su esposa nos

acompañó durante el último mes de nuestra estancia; por su grata compañía, conservamos imborrables recuerdos y les expresamos, igualmente, nuestra gratitud. El Dr. Jorge A. Crespo nos permitió examinar los ejemplares a su cargo, en el Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; William López-Forment, nos ayudó a elaborar, estadísticamente, las medidas de los ejemplares estudiados. El Biólogo José Ramírez Pulido preparó la mayoría de los mapas que figuran en el texto.

Sería interminable la lista de todas las personas que nos colmaron de solícita atención, pero no podemos terminar esta parte del presente trabajo, sin hacer mención de la hospitalidad ejemplar de las maestras de la Escuela Provincial Número 138 de Palma Sola, Departamento de Santa Bárbara, al oriente de la Provincia de Jujuy, profesoras María Mercedes del Valle Castro, María Brígida Irades, Amanda Dávalos, Martha Matche, Ana María Quibal, y la familia del enfermero, señor S. Roberto Jiménez. La Señorita Herminia Martínez González escribió el manuscrito en su forma final.

Material y Metodos

Nuestras observaciones se basan en más de un millar de ejemplares colectados en diferentes localidades de las provincias de Jujuy, Salta, Formosa, Chaco, Catamarca, Tucumán, Córdoba, Santa Fé, Corrientes y Misiones. De todo este material se prepararon ejemplares convencionales para estudio científico (piel y cráneo), tratando de tener representadas, en esta forma, a las especies capturadas durante nuestra visita. La mayoría de los murciélagos obtenidos correspondió a *Desmodus rotundus rotundus* y a *Tadarida brasiliensis brasiliensis*. De estas especies, los animales no preparados para estudio científico se repartieron en partes iguales entre el Centro Panamericano de Zoonosis y SELSA, para investigaciones virológicas. Algunos ejemplares se transportaron vivos hasta la Ciudad de Buenos Aires, al Centro Panamericano de Zoonosis, en Azul, o se exhibieron en las exposiciones ganaderas de Perico del Carmen, Jujuy y Palermo, un barrio de la Ciudad Capital de la Argentina. En las colecciones del Instituto de Biología, de la Universidad Nacional Autónoma de México, están depositados, por tanto, 100 ejemplares para estudio, (piel y cráneo). Además, se examinó el material existente en el Museo Argentino de Historia Natural (Bernardino Rivadavia) y en los casos pertinentes, se hicieron comparaciones con material proveniente de México, Costa Rica, Panamá, Colombia, Perú, Brasil, y Chile.

Más del cincuenta por ciento del total de los ejemplares a que se ha hecho referencia se capturó usando el método de envenenamiento con gas Cyanamid, un procedimiento que se había puesto en uso por el personal de SELSA para el combate de los murciélagos por las razones que en el lugar apropiado se explicarán.

Además, se colectó haciendo uso de redes entomológicas para la captura de murciélagos y, sobre todo, se usaron redes japonesas de seda, "mist nets," de diferente tamaño.

Para el tratamiento sistemático seguimos el procedimiento clásico basado en los caracteres morfológicos externos y craneales, apoyándolos en características numéricas. Como no fué posible, en todos los casos, someter los ejemplares a tratamientos estadísticos, para obtener la media aritmética y las medidas de variabilidad, se consignan los promedios y se registran la mínima y la máxima de las características mensurables; el número de ejemplares promediados o sometidos a tratamientos estadísticos se dá entre paréntesis, después de las cifras relativas a los otros datos.

Las medidas se dan en milímetros. De entre éstas, la longitud total del cuerpo que generalmente se toma desde la punta de la nariz, hasta la punta de la cola vertebral, sin tomar en cuenta los pelos cuando los hay, en *D. r. rotundus* se eliminó, considerando que arroja cifras muy variables y, fundamentalmente, porque carece de cola, lo mismo que *Artibeus.* Las medidas craneales se tomaron con un "metric dial calipers," hasta décimas de milímetro.

Los nombres de los colores del pelaje escritos con mayúscula están de acuerdo con Ridgway (1912). Los especimenes que forman la base de este estudio se encuentran catalogados en el Instituto de Biología, Universidad Nacional Autónoma de México.

En el estudio de las sombras del mismo pelaje, sobre todo de *Desmodus rotundus*, buscando las diferencias entre las dos subespecies hasta ahora reconocidas, se usó la técnica colorimétrica utilizando un fotómetro. Weston Master, que coincide con el procedimiento descrito por Desha (1965: 233-236).

LAS ZONAS FITOGEOGRAFICAS DEL NORTE ARGENTINO

Como la presencia de los mamíferos está determinada fundamentalmente por la presencia o ausencia de "habitats" adecuados, de los que las plantas son parte importante y, puesto que las observaciones se hicieron en un lapso corto y durante una sola estación del año (el invierno), para dar una mejor idea de la ecología del norte Argentino, seguimos aquí el trabajo de Cabrera (1953). Veanse, además, Castellanes y Pérez Moreau (1944) y Hauman (1917). Por otra parte, se verá en su oportunidad, que los vampiros de esta parte de las Américas, tienen, como refugios diurnos, principalmente la oquedad de los árboles, en mayor proporción; en tanto que, en México, se les encuentra más frecuentemente en cuevas, minas abandonadas, fisuras de rocas, casas deshabitadas y, en último lugar, en el hueco de los árboles.

Según Cabrera (1953), la parte norte de Argentina corresponde a la región Neotropical con las siguientes subdiviciones (véase Fig. 1).

Dominio de la America Subtropical

El Dominio de la América Subtropical ocupa una superficie muy reducida en el norte Argentino y está tipificado por la Provincia Subtropical Occidental y la Provincia Oriental. El clima es cálido y húmedo con lluvias principalmente en el Verano y heladas durante el invierno. La vegetación predominante es pedemontaña.

La Provincia Subtropical Occidental presenta los siguientes distritos, Oranense, Tucumanense, y Montano. El Distrito Tucumanense se extiende por los contrafuertes de la cordillera, a través del sur de Salta y por el centro de Tucumán, penentrando ligeramente en el este de Catamarca. La composi-

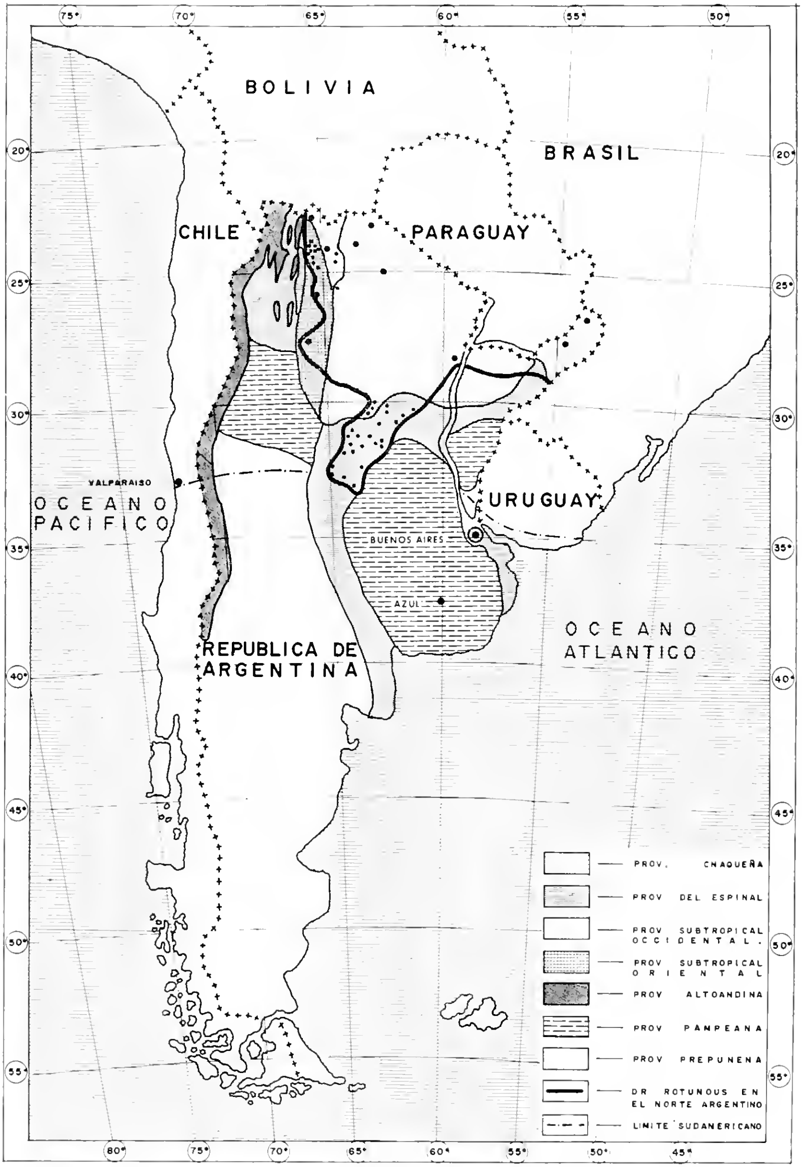

FIG. 1. Las zonas fitogeográficas del Norte de Argentina, donde se efectuaron los trabajos de campo a que se hace referencia en el texto, señalandose con una línea gruesa el límite más sureño de la distribución del vampíro de patas pelonas *Desmodus rotundus*. A pesar de las diferencias de la flora, de la topografía, de las condiciones naturales ambientales, en todas se registra la presencia de estos murciélagos hematófagos.

ción es parecida a la del Distrito Oranense, pero con menor número de especies. Los bosques ribereños son de la misma composición que en el Distrito Oranense.

El Distrito Montano ocupa las laderas orientadas al este de las montañas del noroeste de la Argentina, por arriba de los distritos Oranense y Tucumanense entre los 1500 y los 2500 metros de altura. El clima es más fresco que en los anteriores. La vegetación dominante está constituída por bosque en las laderas empinadas y en las quebradas y por praderas en las laderas suaves.

La Provincia Subtropical Oriental se extiende por el extremo noroeste de la República, ocupando todo el Territorio de Misiones y el noroeste de Corrientes. Además, se prolonga en forma de galería, a lo largo de los ríos Paraná y Uruguay, hasta El Plata. También asciende por los afluentes de estos grandes ríos. Al sur y al oeste limita con el dominio Chaqueño, al norte y al este penetra en el Paraguay y en el Brasil donde alcanza su mayor extensión. Estos corredores destacan claramente en vista aérea volando desde Iguazú a Posadas y a Resistencia.

El Clima de esta provincia es cálido y húmedo, con precipitaciones durante todo el año, torrenciales en el verano. La precipitación puede alcanzar los 2000 mm. anuales en el norte de Misiones, descendiendo a 1400 mm. en Corrientes. En esta Provincia ecológica, el suelo es laterítico, rojo. La vegetación predominante es de selvas y sabanas. Al tiempo de nuestras observaciones un extenso desmonte modificaba el estado de la vegetación característica.

Esta provincia ecológica está cercanamente relacionada con la subtropical occidental, pero son notables o exclusivos los géneros *Araucaria, Balfourodendron, Holocalyx, Cabralea,* y *Mabbaerium.* Es rica en bambusaseas y en helechos arborescentes.

Según el autor que hemos venido siguiendo, en esta región se pueden distinguir tres distritos: Distrito de los Pinares, por la presencia y generalmente abundancia de *Araucaria angustifolia*; Distrito de las Selvas Mixtas, fundamentalmente con los mismo elementos del distrito anterior, pero sin *Araucaria*; y Distrito de los Campos, caracterizado por la predominancia de las sabanas.

Dominio Chaqueño

El Dominio Chaqueño es el que ocupa la mayor parte del territorio del norte Argentino a que se refiere el presente trabajo. Se extiende prácticamente desde el Atlántico hasta la Cordillera de los Andes y desde el límite con el Paraguay hasta el norte de Chubut. La fisonomía de su vegetación es polimorfa—bosques xerófilos, caducifolios, estepas arbustivas, estepas herbáceas, sabanas, praderas, palmares, pajonales y otras.

Su clima es continental, con lluvias escasas (con excepción de la Provincia Bonaerense), estivales en la parte Norte del Dominio, primaverales y otoñales en el Sur. La temperatura es elevada en el verano y templada en el invierno. En ciertas zonas la oscilación diaria es muy amplia con diferencia hasta de 39° C.

El Dominio Chaqueño se divide en cinco provincias que se pueden reconocer por los siguientes caracteres: Provincia Chaqueña o del Chaco, con predominancia de *Shinopsis* y *Aspidosperma*; Provincia del Espinal, muy semejante a la anterior, pero sin *Schinopsia* y con predominancia del género *Prosopis*; Provincia Prepuneña, con especies escasas y predominancia de

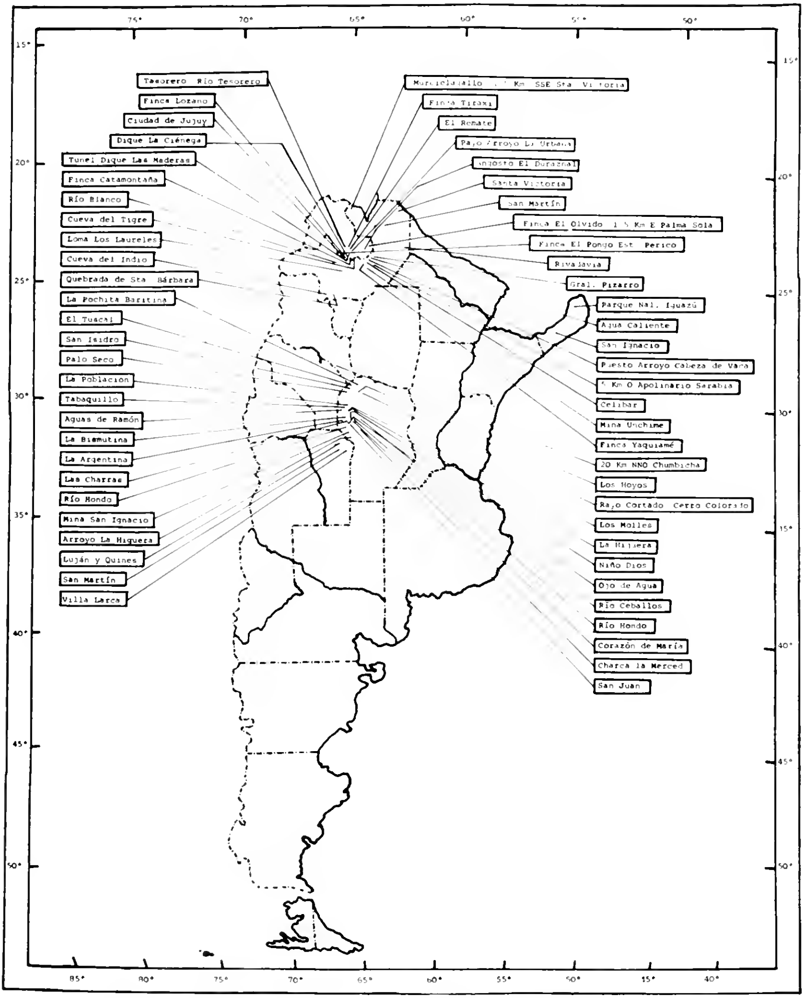

Fig. 2. Localidades de donde procede el material examinado.

cactáceas careiformes y cigofiláceas, leguminosas y compuestas arbustivas; Provincia del Monte, sin árboles o con especies arbóreas enanas y predominancia de cigofiláceas arbustivas del género *Larrea* y Provincia Pampeana, sin árboles, con predominancia de gramineas xerófitas de los géneros *Stipa, Piptochaetrum, Andropogon, Elionurus* y otros.

El Distrito Chaqueño oriental ocupa la mitad oriental del territorio de Formosa, del de la Provincia (política) del Chaco, del norte de Santa Fé y al oeste de Corrientes. Entre los árboles que le caracterizan, entre otros muchos, haremos especial mención del "guayacán," *Caesalpinia paraguayensis.* En general, es el área de los quebrachales, algarrobales y palmares.

El Distrito Chaqueño occidental se extiende por la mitad occidental de Formosa y el Chaco, todo el oriente de Salta, todo el extremo oriental de Jujuy y Tucumán. Este distrito es más seco que el oriental, con vegetación formada por bosques xerófilos, casi sin interrupción, algunos palmares, estepas halófitas y sabanas originadas por incendios y desmontes. Entre la variada composición de árboles que se encuentran en este distrito, también haremos especial mención del "yuchán" o "palo borracho," *Chorisia insignis.*

El Distrito Chaqueño Serrano se extiende de norte a sur, a lo largo de las montañas bajas que forman los primeros contrafuertes de la Cordillera Andina y en el este de la Provincia de Jujuy, en el centro de Salta y Tucumán; en el extremo oriental de Catamarca, prolongándose hasta las sierras de Córdoba, San Luis, y la Rioja. Llega aproximadamente hasta los 33 grados de latitud Sur; suele ocupar las laderas bajas de los cerros y quebradas, formando un complicado engranaje con la provincia Subtropical Occidental constituída por bosques serranos y estepas serranas. Esta es la región mejor conocida por nosotros, porque en ella nos movimos constantemente; sobre todo, es la parte de la Argentina en donde colectamos con más intensidad. En la Figura 1, se indican las zonas fitogeográficas arriba mencionadas, en las que se extiende, precísamente; la distribución de los vampiros *Desmodus rotundus rotundus,* señalada con una linea muy negra y continua en su parte más sureña.

NOMENCLATOR GEOGRAFICO

Las siguientes localidades en donde se obtuvieron los ejemplares de murciélagos estudiados (véase Fig. 2) fueron registradas siguiendo el mapa general de la República Argentina (la escala 1: 3,750,000) las localidades correspondientes a otros países se han anotado de acuerdo con el "Hammond's Map of Latin América" (a la escala de 1: 10,000). También se hizo uso de la Carta Aeronautica Mundial, OACI (a la escala de 1: 1,000,000), particularmente en el caso de las localidades de la República del Uruguay.

TRATAMIENTO SISTEMATICO

Familia NOCTILIONIDAE

Noctilio leporinus rufipes D'Orbigny

Murciélago ictiófago

Ejemplares examinados (3).—PROVINCIA DE SALTA, Hickman, Chaco Salteño, 1. PROVINCIA DE JUJUY, Embarcación, Finca Tres Pozos, Departamento San Martín, 247 km. NE San Salvador de Jujuy, 2.

Medidas.—Ejemplares nos. 9495, 9497, 9498 consignadas en el mismo orden: longitud total del cuerpo, 128.0, 11.0, 115.0; cola vertebral, 16.4, 20.0, 20.0; oreja desde la escotadura 32.3, 26.0, 30.2; pata trasera, 25.4, 29.0, 27.0; antebrazo, 87.5, 86.4, 87.1; tibia, 33.8, 32.2, 39.9; tercer dedo metacarpiano, 79.1, 78.6, 77.8; primera falange, 20.7, 20.2, 20.6; segunda falange, 9.4, 7.4, 8.9; longitud mayor del cráneo, 25.8, 26.0, 27.3; longitud condilobasal, 21.5, 21.5, 21.6; longitud palatal, 13.1, 12.9, 13.5; anchura bicigomática, 19.9, 19.1, 19.5; anchura interorbitaria, 7.3, 7.1, 7.1; anchura del rostro, 12.0, 12.0, 12.1;

anchura de la caja craneal, 15.4, 13.8, 13.8; hilera superior de dientes, 10.2, 10.3, 10.7; anchura a través de los caninos, 8.9, 8.9, 8.5; anchura a través de M3-M3, 12.5, 12.4, 12.5.

Observaciones.—El nombre de la subespecie se usa aqui siguiendo las concluciones de Cabrera (1935:13). Este autor deja explicadas claramente las razones por las que adoptó el nombre *Noctilio leporinus rufipes.* Evidentemente, son animales de tamaño mayor que *N. l. mexicanus.* Se han hecho comparaciones directas con el material de *N. l. mexicanus* existente en las colecciones del Instituto de Biología (UNAM) y no hay duda en cuanto a la diferencia de tamaño. En los tres ejemplares examinados, el color dorsal varía de Ochraceous-Tawny a Buckthorn Brown, con el cuello ligeramente más claro, así como la línea media dorsal; el vientre es Orange-Buff; por tanto no es tan rojizo como se infiere de la descripción de Cabrera. En los ejemplares que tenemos a nuestra disposición, todas hembras, no hay diferencias marcadas a este respecto, Villa-R. (1966:164-165) refiriéndose a *N. l. mexicanus* explica que en esta especie hay una gran variación en el color que va desde el Brussels Brown hasta el Zinc Orange, pasando por el Buckthorn Brown; este color, como se ve, lo encontramos en los ejemplares argentinos, pero no estamos en condiciones de aclarar si es un fenómeno generalizado, a causa del exiguo material examinado.

Aunque no es la primera vez que se cita a *N. l. rufipes* del extremo norte de Argentina, porque ya fue mencionado por Burmeister que, según Cabrera (*op. cit.*: 6), más bien se refería a *"Dirias albiventer,"* en esta ocasión está representado de modo inequívoco, de la Provincia Subtropical de Salta y de Jujuy en los ejemplares estudiados, muy dentro del territorio continental, cerca de ríos y depósitos dulceacuicolas.

Familia PHYLLOSTOMATIDAE

Tonatia silvicola silvicola (D'Orbigny)

Murciélago de orejas redondas

Ejemplares examinados (1).—PROVINCIA DE MISIONES: Cataratas del Iguazú, 125 m.

Medidas.—Longitud total del cuerpo, 29.0; cola vertebral, 20.0; pata trasera, 16.0; oreja desde la escotadura, 29.0; antebrazo, 53.7; tibia, 22.4.

Observaciones.—El ejemplar fue colectado junto con otros del género *Sturnira,* en las cercanías de la caída de agua "Dos Hermanas" donde colocamos varias redes, en las inmediaciones de un restaurante en cuyo interior se encontraban varios racimos de plátanos suspendidos de las vigas de madera del techo. Esta especies tiene una distribución extensa desde Brazil Central y el norte de Bolivia hasta México. Aparentemente, con este ejemplar la distribución debe agregarse el noreste de Argentina.

Fue el primer ejemplar que atrapamos a las siete horas de la tarde. En este lugar la temperatura, durante el día, era de 27° C. a las tres horas de la tarde con gran humedad debido a la cercanía de las imponentes Cataratas del Iguazú que marcan la frontera entre Brasil y la República Argentina. La vegetación es característicamente tropical. Debemos aclarar que el cráneo de este murciélago fué examinado con cuidado, inmediatamente después que fue preparada la piel, pero por desgracia, lo perdimos en el trayecto. El tratamiento sistemático que se da aquí está basado en los caracteres externos, principalmente. Según parece, es este el primer registro de la especie en territorio Argentino. En septiembre de 1967. Fornes *et al.* (1967:149-152) describen otro ejemplar de Palma Sola, Provincia de Jujuy.

Chrotopterus auritus australis Thomas

Gran murciélago carnívoro

Ejemplares examinados (3).—PROVINCIA DE SALTA: Mina Pablo, Unchimé, 25 km. E General Guemes, 1100 m., 2; Río Mojo Toro, 5 km. N Salta, 1. Véase tambien explicacíon bajo observaciones.

Medidas.—Ejemplares nos. 9496 (hembra), 9678 (hembra), y 9579 (macho) siguiendo este mismo orden son como sigue: longitud total del cuerpo, 110.0, 110.0, 110.0; oreja desde la escotadura, 26.0, 29.0, 23.0; pata trasera, 43.0, 50.5, 52.1; antebrazo, 80.0, 85.0, 78.9; tibia, 36.8, 39.1, 36.7; longitud mayor del cráneo, 36.5, 37.0, 36.8; longitud cóndilobasal, 32.1, 32.8, 32.7; longitud palatal, 17.3, 17.7, 16.9; anchura bicigomática, 19.5, 19.2, 19.7; anchura interorbitaria, 6.3, 6.3, 6.2; anchura del rostro, 8.7, 8.4, 9.3; anchura mastoidea, 15.2, 15.3, 15.4; anchura de la caja craneal, 14.0, 14.0, 14.1; hilera superior de dientes, 13.5, 13.4, 13.9; anchura a tráves de los caninos, 7.4, 7.3, 7.0; anchura a través de M3-M3, 12.0, 11.0, 11.0.

Observaciones.—Los ejemplares registrados en el presente trabajo amplían su distribución hasta la Provincia de Salta. Cinco ejemplares vivos fueron obtenidos el 31 de julio de 1965, en el interior de la Mina Pablo, a 40 metros de profundidad medidos desde la entrada. La captura se hizo con una red de mano, a las cinco horas de la tarde, la temperatura era de 20° C. con una humedad relativa de 80 por ciento. Los murciélagos formaban un grupo compacto, suspendidos del techo con las patas y con la cabeza hacia abajo. Puede decirse de ellos, según la clasificación de Villa-R. (1966:224-226) que son murciélagos litófagos internos libres.

Directamente abajo del grupo, sobre el piso de la mina fueron encontrados fragmentos de esqueletos, piel y pelos de pequeños mamiferos, probablemente del género *Ctenomys*, indudables residuos de la dieta de los murciélagos en cuestión. Los cinco animales fueron transportados vivos para exhibirse en una exposición ganadera local en Perico del Carmen, Jujuy; se les alimentó en la misma noche del día de su captura, con carne de una ave conocida localmente con el nombre de "Chuña pata colorada" *(Carioma cristata).* En los días siguientes se les alimentó con carne de vaca. Posteriormente, en marzo y abril de 1967, en una pequeña oquedad conocida con el nombre de Furna de Zafreire, en las cercanías de la Universidad Rural do Brasil, Río de Janeiro, Brasil, uno de nosotros (Villa-R.) colectó otro ejemplar, ocupando el mismo refugio con *Desmodus rotundus rotundus.* En cautiverio se observó otro ejemplar en el Instituto Biológico de Sao Paulo, devorando ejemplares de *Desmodus* y ratones blancos de laboratorio. De los cinco murciélagos obtenidos, preparamos como ejemplares para estudio científico, un macho y una hembra; el macho tenía los testículos escrotados y la hembra un embrión en los primeros estados del desarrollo. El otro ejemplar fue capturado en las fisuras de una roca de los bancos del Río Mojo Toro, en las cercanías de la Ciudad de Salta.

Esta especies es notable por su cuerpo robusto y las grandes orejas redondeadas, con la base y el borde inferior interno cubierto de pelos sedosos de color Light Ochraceous-Buff. Casi las tres cuartas partes del antebrazo están cubiertas de pelo, dorsal y ventralmente. La membrana interfemoral es ancha y la membrana alar se desprende de la base de las falanges, comprendiendo todo el borde externo del tarso. La coloración general del dorso es Mummy Brown, con el cuello ligeramente más claro, los pelos de esta parte del cuerpo son francamente blancos. El pelaje es largo, denso y sedoso. La región cercana a los órganos genitales es ligeramente Russet.

Sturnira lilium lilium (É. Geoffroy St.-Hilaire)

Murciélago de Charreteras

Ejemplares examinados (15).—PROVINCIA DE JUJUY: Finca El Remate, 24 km. SE San Salvador de Jujuy, 740 m., 3; Arroyo de la Urbana, 45 km. E y 5.4 km. N San Salvador de Jujuy, 620 m., 1; Palma Sola, 550 m., 2. PROVINCIA DE MISIONES, Cataratas del Iguazú, 125 m., 9.

Medidas.—El promedio, mínima y máxima entre paréntesis, de las medidas somáticas son como sigue: longitud total del cuerpo, 64.0 (55.7-72.8); pata trasera, 13.0 (10.0-19.9); oreja desde la escotadura, 15.0 (16.3). Las medidas craneales fueron tratadas de ocho ejemplares: longitud mayor del cráneo, 26.4 (22.7-22.9); longitud condilobasal, 20.9 (20.5-21.5); longitud palatal, 9.9 (10.3); anchura bicigomática, 13.0 (13.0-13.6); anchura interorbitaria, 5.8 (5.4-6.2); anchura del rostro, 6.3 (6.1-7.1); anchura mastoidea, 12.2 (10.7-13.5); hilera superior de dientes, 6.5 (6.1-6.9); anchura a través de los caninos, 6.5 (6.0-6.6), 7 ejemplares; anchura a través de M3-M3, 8.1 (7.9-8.4).

Observaciones.—Los murciélagos de esta especies fueron los que con más frecuencia atrapamos en las redes. En las cercanías de las Cataratas del Iguazú, constituyeron el mayor número del total de animales atrapados a las primeras horas del crepúsculo vespertino. En esta localidad, la temperatura alcanzaba, en el tiempo de nuestra visita, hasta 27° C., con una gran humedad relativa.

Como se ha dicho al tratar de *Tonatia,* la vegetación es exuberante, como corresponde a la Provincia Subtropical Oriental.

En general, las medidas de S. *l. lilium* son difinitivamente mayores que las de la especies de México, pero por sus caracteres externos no se pueden diferenciar claramente. Entre el material que existe en la colección, se observan dos fases de coloración, una marcadamente rojiza y la otra café, con tonalidades intermedias que van desde el Ochraceous-Tawny, pasando por el Tawny hasta el Mars Brown. La mancha amarilla de los hombros sólo aparece bien notable en dos ejemplares machos y es Raw Sienna. La membrana interfemoral está profusamente cubierta de pelos que se proyectan más allá de su borde. Según las observaciones en el lugar de su colecta, toman los frutos de la palma datilífera y en las cercanías de las Cataratas del Iguazú eran atraídos por los racimos de platanos (*Musa* sp.) suspendidos de las vigas de madera del techo del restaurante en cuyas cercanías colocamos las redes.

La hembra (no. 9533) se encontraba lactando; los machos tenían los testículos no escrotados.

Artibeus lituratus lituratus (Olfers)

Gran murciélago frutero

Ejemplares examinados (7).—PROVINCIA DE JUJUY: Finca El Remate, 24 km. SE San Salvador de Jujuy, 740 m., 2; Finca La Carolina, Los Perales, San Salvador de Jujuy, 1310 m., 5.

Medidas.—Los promedios de los siete ejemplares con las mínimas y máximas correspondientes entre paréntesis son como sigue: longitud total del cuerpo, 88.0 (75.0-98.0); pata trasera, 17.0 (12.4-23.0); oreja desde la escotadura, 17.0 (18.0-23.0); antebrazo, 65.1 (64.4-65.0); tibia, 21.9 (21.3-22.5); longitud mayor del cráneo, 30.6 (30.2-31.4); longitud cóndilobasal, 27.6 (27.1-28.2); longitud palatal, 15.1 (14.3-15.6); anchura bicigomática, 19.2 (18.8-20.0); anchura interorbitaria, 74.0 (73.0-77.0); anchura del rostro, 11.4 (11.0-12.0); anchura mastoidea, 16.2 (15.8-16.8); anchura de la caja craneal, 13.6 (13.0-13.8); hilera superior de dientes, 11.3 (11.0-11.9); anchura a través de los caninos, 7.8 (7.5-8.1); anchura a través de M3-M3, 13.7 (13.1-14.9).

Observaciones.—Este gran murciélago se distingue facilmente de *A. jamaicensis jamaicensis* por su gran tamaño; el antebrazo alcanza y sobrepasa los 65 mm.; en la Finca El Remate, donde se cultiva principalmente algodón, encontramos una pequeña fracción de terreno cercana a la casa principal, con un buen número de palmas en plena fructificación y algunos naranjales, también en floración; las redes fueron colocadas entre las palmeras. Durante las primeras horas del crepúsculo capturamos algunos ejemplares de *Sturnira lilium lilium* y entrada la noche observamos gran número de *Artibeus lituratus lituratus* en torno de las frondas de las palmeras apoderándose de los frutos maduros o tomando el polen de las flores. Como acontece con los higos silvestres en México (véase Villa-R., 1966:298), algunos frutos de las palmeras se desprendían cayendo al suelo, produciendo un ruido que era fácilmente perceptible por quienes atendíamos las redes. A las siete horas de la tarde atrapamos los ejemplares. Posteriormente las capturas disminuyeron. Lo mismo aconteció en la Finca La Carolina, completamente abandonada.

En todos los cráneos examinados se encuentra el tercer molar diminuto, excepto en uno. Los ejemplares registrados en este trabajo demuestran la presencia de este murciélago en la Provincia de Jujuy.

Familia DESMODONTIDAE

Desmodus rotundus rotundus (É. Geoffroy St.-Hilaire)

Vampiro de patas pelonas, chupador o mordedor de Azara

Ejemplares examinados (37).—PROVINCIA DE SALTA: Cueva de Murcielagallo, 15 km. SSO Santa Victoria, 2000 m., 5; 30 km. SSO General M. M. de Güemes, 6; Toma de los Laureles, 6 km. SSO Chicoana, 1400 m., 4; Cueva del Indio, 4 km. O Cafayate, 1800 m., 1. PROVINCIA DE JUJUY: Angosto El Duraznal, 15 km. S Palma Sola, 1225 m., 4; Cueva del Tigre, 74 km. N Pampa Blanca (por carretera), 700 m., 3; Finca Catamontaña, 33 km. SSE San Salvador de Jujuy, 925 m., 2; Arroyo la Urbana, 45 km. E y 5.4 km. N San Salvador de Jujuy, 620 m., 1. PROVINCIA DEL CHACO: Colonia Benítez, 20 km. N Resistencia, 30 m., 3. PROVINCIA DE MISIONES: Colonia Mártires, Chacra Ferreira, 125 m., 6. PROVINCIA DE CÓRDOBA: Tabaquillo, 15 km. E (por carretera) Cruz del Eje, Departamento Cruz del Eje, 1; Córdoba, 1.

Además, en el Museo de Historia Natural "Bernardino Rivadavia" existen ejemplares de la Provincia de Córdoba y de la Provincia de San Luis. House (1953:13) hace saber que es común en la Provincia de Coquimbo y que se ha esparcido hasta el paralelo 34, al norte de Rancagua, y Mann (1951:3) colectó ejemplares en la Caleta de Cuya, Provincia de Tarapacá.

Observaciones.—Osgood (1912:63) encontró marcadas diferencias en el tamaño, comparando ejemplares típicos de *Desmodus rotundus* de Paraguay y ejemplares de México y Centro América. Esto ha servido de base para usar el nombre *Desmodus rotundus murinus*, para los murciélagos vampiros de la América Central y de México, y el de *Desmodus rotundus rotundus* para los de toda la América del Sur, según las conclusiones de Cabrera (1958:93).

Los límites de separación entre estas dos razas no están, sin embargo, delimitados. Es casi seguro que la zona de integración se halle en el norte de Sudamérica, tal vez a lo largo del flanco noroeste de la Cordillera Occidental de Colombia y Ecuador. Es interesante notar, como expresa Villa-R. (1966:327), que estas subespecies no difieren en sus caracteres externos marcadamente.

Haciéndo uso de un exposímetro Weston Photronic Exposure Meter (Modelo 650) y tomando como fuente de luz la del sol en el cenit de la Ciudad de México, a las 12 horas del día, los resultados fueron iguales así en los ejemplares mexicanos, como en los argentinos. La cifra obtenida fue invariablemente de 25, de manera que no encontramos diferencias en la luz reflejada por el pelaje del dorso, ni en los machos ni en las hembras de los dos grupos comparados. Con excepción de la fuente de luz, el procedimiento para esta operación fue el mismo que explica Desha (1965:233-236). La usamos con el propósito de encontrar diferencias en las tonalidades de la coloración. Por otra parte, las medidas de pata, antebrazo y tibia, en los ejemplares mexicanos, son francamente menores que las de los ejemplares de Argentina. Esto ya había sido observado por Goldman (1920:209), quien explica que en tanto que los individuos son prácticamente indistinguibles, la raza del sur, en promedio, es considerablemente mayor, siendo más notable la diferencia en las medidas del cráneo.

Se pudo observar en las medidas craneales, que excepto la longitud basal, la anchura interorbitaria, y la anchura del rostro, todas son más grandes en los ejemplares sudamericanos, tomando en cuenta la media aritmética, la máxima y la mínima. En los ejemplares de otros países de Sudamérica, aparte de Argentina, que existen en las colecciones del Instituto de Biología, Universidad Nacional Autónoma de México, se observa la misma tendencia.

En el norte de Argentina, el refugio diurno de los vampiros es el hueco de los árboles, con frecuencia en el tronco de los "yuchanes," *Chorisia insignis* y en el de los "guayacanes" *Caesalpinia paraguayensis* donde encuentran temperatura y humedad relativa constantes. Los brocales de los pozos, donde la vegetación ha sido severamente perturbada, son también lugares de abrigo, contaminando el agua con sus deyecciones e inutilizandola para uso humano.

Familia VESPERTILIONIDAE

Myotis chiloensis atacamensis (Lataste)

Murciélago insectívoro

Ejemplares examinados (2).—PROVINCIA DE SALTA: Finca La Rosa, Cafayate, 1; Río Blanco, 35 km. SO Salta, 1600 m., 1.

Medidas.—Las medidas somáticas de los ejemplares nos. 9594 y 9592 (hembra y macho) son las siguientes: longitud total del cuerpo, 85.3, 83.4; cola vertebral, 40.2, 41.6; oreja desde la escotadura, 6.8, 7.7; pata trasera, 12.2, 11.0; antebrazo, 37.4, 37.2; tibia, 14.3, 14.3.

Las medidas craneales del cráneo no. 9592 son las siguientes: longitud mayor del cráneo, 14.9; longitud cóndilobasal, 14.2; longitud palatal, 7.3;

anchura bicigomática, 8.2; anchura interorbitaria, 3.1; anchura del rostro, 4.5; anchura mastoidea, 7.2; anchura caja craneal, 6.4; anchura a través de los caninos, 3.4; anchura a través de M3-M3, 5.5.

Observaciones.—Se nos informó que los murciélagos de esta especie son abundantes en las casas abandonadas. El que lleva el número 9594 fue capturado en el techo de la Finca La Rosa, alguna vez señorial, pero en el momento de la captura, una ruina, donde si es cierto que observamos gran número de excrementos, los murciélagos habian desaparecido. Sólo estaba el que se menciona en este trabajo y no tenía embrión. El número 9592 (macho) tenía los testículos no escrotados y también se le observó aislado.

Myotis albescens (É. Geoffroy St.-Hilaire)

Murciélago insectívoro

Ejemplares examinados (1).—PROVINCIA DE SALTA: Casa habitada, Salta.

Medidas.—Las medidas del ejemplar (no. 9523, macho) son las siguientes: longitud total del cuerpo, 82.0; cola vertebral, 35.0; oreja desde la escotadura, 8.0; pata trasera, 12.0; antebrazo, 35.3; tibia, 14.1; longitud mayor del cráneo, 14.1; longitud cóndilobasal, 13.2; longitud palatal, 6.4; anchura del rostro, 4.3; anchura mastoidea, 7.3; anchura caja craneal, 7.8; hilera superior de dientes, 4.8; anchura a través de los caninos, 3.6; anchura a través de M3-M3, 5.4.

Observaciones.—Nuestro único ejemplar es de coloración dorsal pardo obscuro, con el extremo del pelo amarillento pálido, de modo que el dorso, en general, es Rood's Brown, lustroso. No encontramos la zona desprovista de pelo en la nuca a que se refieren Miller y Allen (1928:203) ni recordamos haberle visto en el animal recientemente capturado.

El pelaje de la región ventral, concuerda con la descripción de Miller y Allen (*op. cit.:* 202), esto es, la base de los pelos es de color chocolate claro, con la porción terminal blanquecina, produciendo una superficie más pálida que la del dorso. Posteriormente la extensión blanquecina de la punta de los pelos aumenta en longitud y el borde del abdómen resulta blanquecino. La región perianal es definitivamente blanca, presentando el mismo efecto descrito por Acosta y Lara (1950:7). De acuerdo con este autor (*op. cit.:* 6), la localidad tipica correspondería a la estancia de San Solano, junto al estero de Iberá (Sur del Río Paraná), en la República Argentina y no al Paraguay.

Myotis nigricans nigricans (Schinz)

Murciélago insectívoro

Ejemplares examinados (1).—PROVINCIA DE JUJUY: Arroyo la Urbana, 45 km. E y 5.4 km. N San Salvador de Jujuy, 620 m.

Medidas.—Las medidas del ejemplar (no. 9520, macho) son las siguientes: longitud total del cuerpo, 72.7; cola vertebral, 35.0; oreja desde la escotadura, 12.5; pata trasera, 6.8; antebrazo, 34.2; tibia, 13.3; longitud mayor del cráneo, 13.5; longitud cóndilobasal, 12.3; longitud palatal, 7.9; anchura bicigomática, 8.2; anchura interorbitaria, 31.1; anchura del rostro, 4.0; anchura mastoidea, 6.6; anchura caja craneal, 6.1; hilera superior de dientes, 4.9; anchura a través de los caninos, 3.2; anchura a través de M3-M3, 5.1.

Observaciones.—Esta pequeña especie de murciélagos insectívoros fue atrapada en una red de seda, junto con *Lasiurus* y *Desmodus.* Durante el tiempo en que vigilamos la red, extendida a través de un pequeño remanso del arroyo, observamos que un buen número esquivaba con maestría la trampa. El ejemplar macho que se registra aquí, se atrapó al tiempo en que un ejemplar de *Lasiurus borealis* pugnaba por escaparse de las mallas inferiores de la red sumergida en el agua, dando muestra de una gran habilidad para nadar. Los frecuentes chillidos de *Lasiurus* parecen haber atraído a *M. n. nigricans.*

No lo encontramos formando colonias, en ningún refugio de los que pudimos explorar; es posible que sea abundante, pero durante nuestra visita al norte de Argentina nos dejó la impresión de que no lo era mucho. Por el contrario, en las cercanías de Río de Janeiro, Brasil, en el mes de abril, es de tal manera abundante que penetra a las habitaciones y fácilmente se les captura, según explica Villa-R. quien los derribaba en el interior de la habitación que ocupaba en la Universidad Rural de Brasil solamente con la mano, o con una toalla.

Eptesicus innoxius (Gervais)

Murciélago insectívoro

Ejemplares examinados (2).—PROVINCIA DE JUJUY: Palma Sola, 550 m.

Medidas.—Las medidas somáticas de los ejemplares (9532, macho, y 9534, macho) son las siguientes: longitud total del cuerpo, 90.0, 91.0; cola vertebral, 36.0, 38.0; oreja desde la escotadura, 13.0, 10.0; pata trasera, 9.0, 8.0; antebrazo, 38.9, 39.1; tibia, 14.7, 14.8; longitud mayor del cráneo, 15.6, 15.5; longitud cóndilobasal, 14.9, 15.1; longitud palatal, 7.2, 7.1; anchura bicigomática, 9.5; anchura interorbitaria, 3.7, 3.6; anchura caja craneal, 7.2, 6.9; hilera superior de dientes, 5.6, 5.5; anchura a través de los caninos, 4.5, 4.3; anchura a través de M3-M3, 6.2, 6.3.

Observaciones.—El tratamiento sistemático que se da aquí a este murciélago insectívoro, está de acuerdo con las conclusiones de Davis (1965:229-240) en su revisión del complejo *Eptesicus brasiliensis,* quien explica que los miembros del complejo examinado por él, se apartan en dos grupos basándose en el tamaño de los dientes molariformes.

E. innoxius, forma parte del grupo de los dientes molariformes pequeños, con *E. punicus* Thomas, *E. furinalis* (D'Orbigny), *E. chiralensis* Anthony, *E. melanopterus* (Jentink), *E. fidelis* Thomas, y según la propia expresión de Davis, "probably *E. diminutus* Osgood, and the two forms in Middle America." Entre el material que se obtuvo en el norte de Argentina, sólo capturamos los dos ejemplares a que nos venimos refiriendo y a no ser porque el antebrazo de uno de ellos es de 39.1, la hilera superior de dientes queda dentro de las medidas que registra Davis en la clave sinóptica correspondiente (*op. cit.:* 239). Es, pues, evidente, que el área de distribución de la especie alcanza esta parte de la República Argentina.

Nuestros ejemplares los atrapamos en las redes japonesas de seda, cuando había desaparecido el crepúsculo vespertino, a las 8 de la noche. Las redes se colocaron a través de un estancamiento somero de una pequeña corriente de agua. El bosque mixto dejaba espacios descubiertos y nuestro sitio de trabajo no estaba distante de un camino que eventualmente servía para el paso de vehículos de motor cargados con trozos de madera.

La distribución de esta especies, fue limitado al oeste de Ecuador y Perú, incluyendo la isla de Puná, por Cabrera (1958:107). Según nuestro registro, a la distribución conocida debe agregarse el norte de Argentina.

Histiotus montanus montanus (Phillipi y Landbeck)

Murciélago orejon

Ejemplares examinados (6).—PROVINCIA DE JUJUY: Casa Club Náutico, Dique la Ciénega, 30 km. SSO San Salvador de Jujuy, 1000 m., 2; Finca La Toma, 25 km. SO San Salvador de Jujuy, 1. PROVINCIA DE SALTA: Toma de Los Laureles, 6 km. SSO Chicoana, 1400 m., Depto. Chicoana, Salta, 3.

Medidas.—Las medidas de los ejemplares 9503 (hembra), 9504 (hembra), 9536 (macho), 9584 (macho), 9586 (macho), y 9585 (macho) son las siguientes: longitud total del cuerpo, 150.0, 100.2, 109.4, 104.0, 112.3, ——; cola vertebral, 40.0, 40.2, 50.5, 47.0, 53.7, 56.0; pata trasera, 31.7, 30.3, 34.6, 36.5, 32.7, 37.5; antebrazo, 46.4, 46.9, 46.4, 45.8, 48.1, 45.5; tibia, 17.5, 17.5, 17.0, 17.3, 17.1, ——; longitud mayor del cráneo, 18.6, 17.9, 18.4, 18.5, 18.5, ——; longitud cóndilobasal, 17.4, 17.0, 17.1, 17.5, 17.5, 17.4; longitud palatal, 8.4, 8.0, 7.2, 7.5, 9.1, 8.9; anchura bicigomática, 10.7, 10.3, 10.0, 10.8, 10.5, 10.6; anchura interorbitaria, 3.8, 3.5, 3.8, 3.9, 3.7, 3.7; anchura rostro, 6.1, 5.9, 5.6, 5.9, 6.4, 6.0; anchura mastoidea, 9.6, 9.2, 9.3, 9.8, 9.3, 9.3; anchura caja craneal, 8.5, 7.8, 7.9, 8.3, 8.1, 8.2; hilera superior de dientes, 6.1, 5.7, 5.7, 5.9, 5.8, 5.8; anchura a través de los caninos, 4.8, 4.6, 4.5, 4.9, 4.7, 4.7.

Observaciones.—Tres de los ejemplares examinados aquí se les capturó en el techo de la casa del Club Náutico de las cercanías de Perico del Carmen, en redes de seda, colocadas sobre el techo de lámina, paralelas a un alero de otro techo bajo cuyas láminas se refugiaban estos animales en gran número, en convivencia con *Tadarida* y otros molósidos. Desde las siete horas de la tarde en que emergieron los primeros individuos, la actividad de todos los que participamos, fué constante, desprendiendo de las redes a los ejemplares capturados. La temperatura era de 5° C. con una humedad relativa de 80 por ciento, lo que causaba una incómoda situación de frío. No obstante, los murciélagos se lanzaban a la persecución de sus víctimas.

Los ejemplares restantes, también se obtuvieron del techo de casas habitadas, formando grupos numerosos.

Lasiurus borealis varius (Poeppig)

Murciélago rojizo

Ejemplares examinados (1).—PROVINCIA DE SALTA: Finca La Florida, Rosario de Lerma, 25 km. SSO Salta.

Medidas.—Las medidas del ejemplar (9519, macho) son las siguientes: longitud total del cuerpo, 101.5; cola vertebral, 45.8; oreja desde la escotuadura, 10.0; pata trasera, 9.5; antebrazo, 39.7; tibia, 15.9; longitud mayor del cráneo, 116.0; longitud cóndilobasal, 113.0; longitud palatal, 5.5; anchura bicigomática, 8.9; anchura rostro, 5.3; anchura mastoidea, 7.6; anchura caja craneal, 7.3; hilera superior de dientes, 3.9; anchura a través de los caninos, 4.6; anchura a través de M3-M3, 5.6.

Observaciones.—El pelaje de la membrana interfemoral es denso en las cercanías del cuerpo, largo y sedoso. En el borde es ligeramente más corto y ralo; el color, en general, es Hazel y aparece como fondo, con rayas grisaseas o Deep Mouse Gray; en los hombros este color es predominante en la superficie y, en la parte superior de la región cervical, aparece salpicando el fondo de la coloración superficial; es el resultado del color individual del pelo que en su base es obscuro, seguido de una amplia banda de Ochraceous-Buff, terminando en Hazel y la punta de coloración Deep Mouse Gray. Ventralmente el antebrazo está recubierto de pelos Ochraceous-Buff, en toda su longitud; en la porción distal de cada fémur, el pelo es muy abundante. La parte de la membrana alar, entre los costados y el brazo, también presentan abundante pelo como una prolongación del pelaje ventral; este es de color Ochraceous-Buff. El ejemplar fue capturado en una red de seda.

Lasiurus cinereus villosissimus (É. Geoffroy St.-Hilaire)

Murciélago canoso

Ejemplares examinados (1).—PROVINCIA DE SALTA: Finca Belgrano, Cerrillos, 30 km. SO Salta.

Medidas.—Las medidas somáticas del ejemplar (9528, macho) son las siguientes: longitud total del cuerpo, 150.0; cola vertebral, 54.5; oreja desde la escotadura, 11.4; pata trasera, 12.6; antebrazo, 52.1; tibia, 20.0.

Observaciones.—El color de este ejemplar es moreno amarillento variando de moreno caoba salpicado con color plateado, dando la apariencia de canoso o escarchado. Como expresa Villa-R. (1966:409-411), en la base del pelo presenta un color Mummy Brown, en la porción media, un color moreno amarillento y en la punta un color blanco plateado. El plagiopatagio está cubierto por un pelaje denso, desde el nivel del codo, hasta cerca de la articulación húmero-carpal, cubriendo la base del quinto y cuarto dedos. El color es cercanamente Antimony Yellow. La parte ventral es semejante a la dorsal. La membrana interfemoral es de color Cinnamon Brown; el pelo es denso, largo y sedoso.

La adscripción de este material, a la especie *L. c. villosissimus* se establece aquí sobre la base de precedentes o de costumbre, por las siguientes razones: En la misma red que se capturó este ejemplar, fué atrapado otro de la misma apariencia externa que, al tratar de desprenderlo, se escapó de las manos de uno de nosotros (Villa-R.); llevaba una banda de aluminio, muy desgastada, en el antebrazo. Por tratar de examinar con menticulosidad la borrosa inscripción de esta banda, el animal se escabulló y no hubo ocasión de obtener la información pertinente. Lo anterior nos planteó la interesante cuestión de saber si se trataba de la misma especie neártica *L. c. cinereus* emigrado hasta aquella parte de Sudamérica, tomando en cuenta que carecemos de información acerca de que alguna persona recientemente haya estado anillando con propósitos de investigación, en aquella parte del Continente. Por otro lado, no tenemos suficiente material para hacer comparaciones detenidas. Con los ejemplares obtenidos en México y almacenados en las colecciones del laboratorio de Mastozoología del Instituto de Biología, no vemos diferencias fundamentales.

Lasiurus ega argentinus (Thomas)

Murciélago amarillo

Ejemplares examinados (1).—PROVINCIA DE JUJUY: Arroyo La Urbana, 45 km. E y 5.4 km. N (por carretera), 620 m., San Salvador de Jujuy.

Medidas.—Las medidas del ejemplar (9521, hembra) son las siguientes: longitud total del cuerpo, 121.3; cola vertebral, 42.0; oreja desde la escotadura, 10.3; pata trasera, 17.7; antebrazo, 48.2; tibia, 18.1; longitud mayor del cráneo, 16.1; longitud cóndilobasal, 6.5; longitud palatal, 7.7; anchura bicigomática, 11.7; anchura interorbitaria, 4.2; anchura mastoidea, 9.4; anchura de la caja craneal, 8.4; hilera superior de dientes, 5.7; anchura a través de los caninos, 6.6; anchura a través de M3-M3, 7.6.

Observaciones.—El color dorsal es amarillento, llegando al Warm Buff, también se extiende en la parte ventral, pero en la punta de la membrana interfemoral, el pelo se vuelve más amarillento, llegando al Yellow Ocher. Este ejemplar lo atrapamos en una red; fue de los primeros en caer.

El nombre genérico adaptado aquí es el que sigue Dalquest (1953:61) y Handley (1960:473) por las mismas razones explicadas por Villa-R. (1966: 405). Al parecer, estos murciélagos se acomodan durante el día entre las hojas secas de las frondas de las palmeras. Se les ha encontrado en el techo de paja o de hojas de palma de las casas de los campesinos. La hembra que forma parte de nuestra colección, carecía de signos de reproducción.

Familia MOLOSSIDAE

Molossops temminckii temminckii (Burmeister)

Murciélago moloso

Ejemplares examinados (2).—PROVINCIA DE JUJUY: Palma Sola, 550 m.

Medidas.—Las medidas de los ejemplares 9592 (hembra) y 9530 (hembra) son las siguientes: longitud total del cuerpo, 70.0, 69.0; cola vertebral, 22.0, 27.0; pata trasera, 5.7, 6.7, oreja desde la escotadura, 11.7, 12.0; antebrazo, 30.3, 30.5; tibia, 9.4, 10.0; longitud mayor del cráneo, 12.8, 12.9; longitud cóndilobasal, 11.0, 10.9; longitud palatal, 5.8, 5.6; anchura interorbitaria, 5.4, 5.5; anchura del rostro, 3.3, 3.2; anchura mastoidea, 8.0, 8.3; anchura caja craneal, 6.6, 6.7; hilera superior de dientes, 4.9, 5.9; anchura a través de los caninos, 4.9, 5.9; anchura a través de M3-M3, 5.8, 6.9.

Observaciones.—Aunque esta especie es sumamente de pequeña talla, en todos los otros respectos superficiales es un murciélago típico de la familia Molossidae. El examen del cráneo reveló, sin embargo, su verdadera posición sistemática. Los incisivos superiores aparecen en cercano contacto uno con otro, pero separados de los caninos por un estrecho espacio; las coronas son delgadas, fuertemente encorvadas hacia adelante, con la cara anterior suavemente convexa; la posterior, ligeramente cóncava. Los ejemplares examinados, solo presentan incisivos inferiores más bajo que el cíngulo del canino y el borde cortante profundamente bífido; los dos dientes emergen de alvéolos colocados enfrente de la base de los dos caninos. El premaxilar está completo y no presenta espacio libre como en los otros géneros de la familia.

El 25 de junio de 1965, estos dos ejemplares fueron los primeros que cayeron en la parte superior de nuestra red. Otros animales de la misma especie aparecían con frecuencia volando en torno, pero esquivaban con maestría las mallas. Ninguno mostraba signos de reproducción al momento de su captura. La temperatura era fría en el sitio en que capturamos a estos pequeños murciélagos.

Tadarida brasiliensis brasiliensis (I. Geoffroy St.-Hilaire)

Murciélago guanero o de cola libre

Ejemplares examinados (6).—PROVINCIA DE SALTA: Finca La Cruz, 28 km. SSE (por carretera) Salta, 4; Casa Club Náutico, Dique La Ciénega, 30 km. SSO San Salvador de Jujuy, 1000 m., 2.

Medidas.—Las medidas de los ejemplares (machos), 9577, 9583, 9582, y 9507, son las siguientes: longitud total del cuerpo, 95.0, 92.0, 96.0, 90.0; cola vertebral, 31.0, 32.0, 32.0, 32.0; oreja desde la escotadura, 19.0, 19.5, 18.0, 19.0; antebrazo, 42.4, 44.7, 48.3, 42.5; tibia, 13.3, 12.4, 11.7, 10.9; longitud mayor del cráneo, 16.7, 17.1, 16.6, 16.6; longitud cóndilobasal, 15.8, 16.5, 15.8, 16.6; longitud palatal, 7.0, 6.9, 6.9, 7.0; anchura interorbitaria, 3.8, 3.9, 4.0, 4.1; anchura rostro, 5.8, 5.0, 5.6, 5.7; anchura mastoidea, 9.4, 9.0, 8.3, 9.3; anchura caja craneal, 8.1, 8.6, 8.1, 8.5; hilera superior de dientes, 5.9, 6.2, 5.8, 5.9; anchura a través de los caninos, 6.8, 7.1, 6.7, 6.9.

Observaciones.—*Tadarida brasiliensis brasiliensis* es, sin duda, una especie muy abundante en Sudamérica, tanto como en el Sur de los Estados Unidos y el Norte de México. En este trabajo, con finalidades puramente taxonómicas, solo hemos considerado la observación de los ejemplares que preparamos en piel, pero una gran cantidad se entregó a los laboratorios de SELSA, INTA, y CEPANZO, para estudios virológicos, tomando en cuenta que en los Estados Unidos de Norteamérica y en México son los que con mayor frecuencia y en alto porcentaje se han hallado infectados con virus rábico, en condiciones naturales. Nuestro propósito era que se estudiaran en estas tres instituciones.

Es muy posible que en la Ciudad de Buenos Aires, su población sea extraordinariamente abundante durante el verano. Se nos informó que en esta estación del año constituyen un gran problema en las casas con techo de teja y en multitud de edificios de la Capital Federal.

En Iguazú, cerca de las Cataratas de este nombre, también nos dieron informes interesantes al respecto. Se nos explicó que, durante el verano, aparece una extraordinaria cantidad de estos murciélagos, acomodándose entre los tejados de las casas. Debido a su abundancia, se les ve hasta en las paredes del interior de las habitaciones. Como consecuencia, los gatos domésticos los devoran y, después, se observa que enferman mostrando dificultad en mover el tren posterior; algunas veces atacan a las personas. No se nos explicó que se hayan presentando casos de rabia en humanos, pero sí se nos informó que posteriormente, cuando han desaparecido los murciélagos, aparecen perros rabiosos. Las personas que nos proporcionaron esta información, nos hicieron patente su extrañeza por la aparición en masa de los murciélagos en época de calor y luego su desaparición en época de otoño; lo curioso, nos dijeron, es que no se mueren muchos. Solo desaparecen. Esto puede explicarse por el hecho bien conocido en Norteamérica de las emigraciones de la subespecie *T. b. mexicana*. Aunque no tenemos información de que se hayan efectuado investigaciones acerca de los movimientos migratorios de *T. b. brasiliensis* en la América del Sur, es posible que presenten igual comportamiento biológico. Para corroborar esta suposición, nos parece pertinente citar aquí, que en el diario "La Nación" del día 3 de abril de 1968, se dió la información que en la Ciudad de Neuquen, un establecimiento escolar fue clausurado debido al extraordinario número de murciélagos que se alojaban en "los mil y un recovecos del vetusto edificio inagurado en el año de 1910" según la información. "Se trata de la Escuela Nacional No. 2—sigue diciendo el diario-ubicado en el corazón de la Ciudad." Para lograr la eliminación de los murciélagos, se trabajó durante un día; después de tres de asueto por ese motivo, los escolares retornaron a la aulas, estimándose que la escuela había quedado libre de estos animales. El diario no identifica a los murciélagos, pero Villa-R. observó a muchos de éstos, volando en las cercanías del Hotel Llao-Llao, en los últimos días de marzo. Este Hotel se encuentra a 25 kilómetros al sur de San Carlos de Bariloche, en el Parque Nacional Nahual Huapai; es posible, por tanto, que se trate de la misma especie.

Acosta y Lara (1950:42), por su parte, refiere que "*Tadarida brasiliensis* habita tanto en las viejas y aisladas construcciones de nuestro campo—Uruguay—como en lo más céntrico de las ciudades donde se puede localizar sus guaridas en las torres y campanarios de varias iglesias bien conocidas."

Es significativo que este mismo autor refiere que la "despoblación de los nidos puede ser motivada por el desarrollo de epizootias, como sucede con otros animales cuya procreación es grande y no está contraloreada por la existencia de enemigos naturales proporcionalmente fuertes y numerosos." Es bien conocido el hecho de que en *Tadarida brasiliensis mexicana* se ha comprobado la presencia de rabia.

Eumops perotis perotis (Schinz)

Gran murciélago mastín

Ejemplares examinados (3).—PROVINCIA DE SALTA: Escuela 149, 30 km. NE Salta, 1; Dragones, Chaco Salteño, 1. PROVINCIA DE JUJUY: Casa Club de Pesca, Dique La Ciénega, 30 km. SSO San Salvador de Jujuy, 1000 m., 1.

Medidas.—Las medidas de los ejemplares no. 9499 (macho), no. 9580 (hembra), y no. 9505 (macho) son las siguientes: longitud total del cuerpo, 170.7, 180.0, 185.0; cola vertebral, 51.8, 50.8, 62.3; pata trasera, 16.3, 15.0, 19.5; oreja desde la escotadura, 36.8, 42.3, 40.0; antebrazo, 78.6, 77.5, 79.2; tibia, 20.4, 20.6, 16.4; longitud mayor del cráneo, 33.5, 33.4, 32.3; longitud cóndilobasal, 32.7, 31.6, 31.1; longitud palatal, 14.9, 14.2, 13.9; anchura bicigomática, 19.1, 19.3, 18.9; anchura interorbitaria, 5.7, 6.1, 5.6; anchura rostro, 8.9, 8.4, 7.3; anchura mastoidea, 15.8, 16.4, 15.5; anchura caja craneal, 13.5, 13.2, 13.1; hilera superior de dientes, 12.7, 12.2, 13.0; anchura a través de los caninos, 8.4, 8.1, 8.1; anchura a través de M3-M3, 12.9, 13.4, 12.6; anchura del rostro entre los procesos lacrimales, 10.2, 11.1, 10.4.

Observaciones.—El examen de los ejemplares mencionados nos hace llegar a la conclusión de que la subespecie *Eumops perotis perotis* corresponde propiamente a Sudamérica. Por consiguiente, y de acuerdo con Cockrum (1960:79), los murciélagos mastines de Norteamérica, representan solo una sola subespecie, *Eumops perotis californicus.* Para comparación solo tenemos un ejemplar, colectado en el techo de una casa habitada de la Universidad Rural de Brasil (km. 47), Río de Janeiro, y a no ser por la coloración del pelaje, que en éste es ligeramente más obscuro, la anchura del rostro entre los procesos lacrimales, varía de 10.0 a 11.4 mm., como lo señala Sanborn (1932: 351).

Molossus ater nigricans Miller

Murciélago moloso

Ejemplares examinados (4).—PROVINCIA DE JUJUY: Casa Club Náutico, Dique la Ciénega, 30 km. SSO San Salvador de Jujuy, 1000 m., 2. PROVINCIA DE SALTA: Ciudad de Salta, 2.

Medidas.—Las medidas de los ejemplares no. 9509 (hembra), no. 95081 (macho), no. 95381 (hembra), y no. 9537 (hembra) son las siguientes: longitud total del cuerpo, 121.0, 125.0, 135.0, 121.0; cola vertebral, 46.0, 40.5, 42.0, 43.4; pata trasera, 15.0, 11.8, 10.0, 13.5; oreja desde la escotadura, 15.0, 11.4, 14.5, 14.1; antebrazo, 48.7, 46.6, 48.4, 48.2; tibia, 15.5, 15.8, 14.9, 15.1; longitud mayor del cráneo, 20.8, 21.6, 21.6, 20.4; longitud cóndilobasal, 19.3, 19.9, 19.6, 19.1; longitud palatal, 7.9, 8.1, 7.8, 8.0; anchura bicigomática, 12.7, ——, ——, ——; anchura interorbitaria, 4.4, 4.7, 4.5, 4.2; anchura rostro, 5.0, 6.4, 6.4, 5.8; anchura mastoidea, 12.4, 13.3, 13.4, 11.8; anchura caja craneal, 10.4, 10.9, 10.6, 10.7; hilera superior de dientes, 7.8, 7.9, 8.2, 7.7; anchura a través de M3-M3, 9.6, 10.1, 10.1, 9.9.

Observaciones.—Los dos ejemplares capturados en el techo de la casa del Club Náutico, Jujuy, adultos, son parte de un número mayor que fué atrapado en una red de seda, junto con murciélagos de las especies *Histiotus montanus, Eumops perotis* y *Tadarida brasiliensis,* acomodados debajo de las láminas de zinc del techo. La captura se llevó al cabo a las 6:30 horas de la tarde, a una temperatura de 14.4° C. y con 100 por ciento de humedad relativa, produciendo una sensación de gran incomodidad por el frío invernal en aquellas latitudes. Los otros dos, también adultos, fueron llevados al laboratorio de virus de SELSA, por personas que los consideraban vampiros, a causa de su gran talla.

En el tratamiento específico sigo las concluciones de Goodwin (1960:6). Al llevar al cabo las comparaciones con el material de México registrado por Villa-R. (1966:454-455) y que se conserva en las Colecciones del Instituto de Biología de la Universidad Nacional Autónoma de México, no he hallado diferencias, ni en los caracteres taxonómicos externos, ni en los craneales. Fué examinado, además, un ejemplar, el no. 9817 (macho), colectado en la Gruta de Limoiero, 200 m. O Limoiero, Estado de Espíritu Santo, Brasil. Este ejemplar formaba parte de más de 20 animales que fueron obligados a dejar su refugio en un agujero de la roca calcárea de la Gruta, usando una antorcha.

Comparaciones.—En el material de México, el dicromatismo es bien definido; por lo tanto, encontré ejemplares de coloración dorsal Bister y Slate-Black predominantemente, con algunos de pelambre color Hazel y Auburn. El material de Jujuy y Salta es, sin excepción, de coloración Bister; el ejemplar de la Gruta de Limoiero, Brasil, es Slate-Black; otros murciélagos de esta especie que formaban el grupo eran de color Hazel.

Los promedios de las medidas somaticas y craneales, la mínima y la máxima entre paréntesis, con el número de ejemplares tratados a continuación de los datos anteriores, del material mexicano, formado por ejemplares adultos son como sigue: Cola vertebral, 48.0 (43.0-56), 17; antebrazo, 50.6 (48.5-53.5), 20; tibia, 15.0 (14.2-17.7), 20; longitud mayor del cráneo, 21.8 (21.0-23.5), 20; longitud cóndilobasal, 20.3 (19.6-21.5), 10; longitud palatal, 8.0 (7.7-8.8), 20; anchura bicigomática, 14.0 (13.4-15.2), 18; anchura interorbitaria, 4.2 (4.1-4.8), 20; anchura del rostro, 7.3 (6.5-8.3), 20; anchura mastoidea, 13.2 (12.2-12.4), 20; anchura de caja craneal, 106.6 (10.0-11.8), 20; hilera superior de dientes, 8.2 (7.8-8.6), 20; anchura a través de los caninos, 5.9 (5.7-6.4), 20; anchura a través de M3-M3, 10.0 (9.7-10.1), 21. La longitud de la cabeza y la del cuerpo nos parecen inadecuadas para propósitos de tratamiento estadístico, porque el error personal y la naturaleza misma de las partes medidas, les hace muy variables.

El ejemplar no. 9847 obtenido en Brasil mide: cola vertebral, 55.5; antebrazo, 50.1; tibia, 16.9; longitud mayor del cráneo, 22.8; longitud cóndilobasal, 21.1; longitud palatal, 8.1; anchura bicigomática, 13.9; anchura interorbitaria, 4.8; anchura del rostro, 7.9; anchura mastoidea, 14.1; anchura de la caja craneal, 11.2; hilera superior de dientes, 8.3; anchura a través de los caninos, 6.2; anchura a través de M3-M3, 10.0.

Las comparaciones de estas medidas y los caracteres externos, hacen evidente que el material del norte de Argentina que colectamos y que hemos estudiado, corresponde, sin duda, a la subespecie *Molossus ater nigricans* Miller, 1902.

SUMMARY

In June, July, and August of 1965, the senior author collected bats in northern Argentina in conjunction with a survey of rabies in that region. Of the 18 species obtained, two *(Tonatia silvicola* and *Eptesicus innoxius)* are here recorded for the first time from Argentina; the distributions of several other species are extended geographically within the country. The generalized vegetational zones of northern Argentina are outlined and briefly discussed in an introductory section.

Measurements and notes on natural history are recorded for each of the 18 kinds of bats, and comments on systematics and incidence of rabies are incorporated into several accounts. Specimens of *Molossus ater* are referred to the Mexican subspecies *(M. a. nigricans),* because we found no fundamental differences between Mexican and Argentinean specimens.

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