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Bats From Guatemala

BY

J. KNOX JONES, JR.

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INTRODUCTION

The chiropteran fauna of Middle America is rich in number of species owing to the presence there of elements associated primarily with the South American tropics, elements having temperate affinities, and a noteworthy array of authochthonous species. This faunal diversity has commanded the attention of mammalogists for more than a century. In the past decade or so, increasingly intensive efforts have been made to study systematically the bats of various natural and political areas in the North American tropics. The results of these studies have been manifested in a steadily increasing number of publications—descriptions of new kinds, lists of faunal elements, and notes on ecology, distribution, and taxonomy. Nevertheless, much still remains to be done.

From December 15, 1954, until April 6, 1955, James W. Bee collected mammals in Guatemala for the Museum of Natural History. Unfortunately, Bee's carefully kept field notes were stolen, save for his catalogue, just before he left the country, but his specimens, few of which have been reported previously, provided a nucleus for further work there. Additional collections were made in Guatemala by representatives of this institution in several years from 1956 to 1961 as follows: in 1956, J. R. Alcorn and his family collected at several localities along the Pan-American Highway; in 1960, W. E. Duellman and I collected in February and March at camps of the Ohio Oil Company of Guatemala at Chinajá, on the border between Alta Verapaz and El Petén, and at Toocog, at the southern edge of the savannas of the central Petén, while at the same time E. S. Booth, accompanied by J. H. Bodley and J. L. Fish, worked in the central part of the country; and finally, Duellman and associates collected a few bats in each of the summers of 1960 and 1961, principally in the vicinities of Chinajá and Cobán, and in the Motagua Valley.

The present report is based primarily on specimens housed in the Museum of Natural History, although some material from other collections also has been examined. Additionally, records of Guatemalan bats that have appeared in the published literature are included. In the accounts that follow I have stressed distributional data, but information on systematics and ecology also is recorded. It should be noted that little precise information is available concerning the natural history of many of the species of bats that occur in Guatemala, and the relationships and zoogeographic affinities of some species remain to be clarified.

Fifty-six species of bats are treated in this report but as many as 100 species may eventually be found to occur in Guatemala. Unless noted otherwise, specimens listed as examined (a total of 888) are in the Museum of Natural History at The University of Kansas. All measurements given are in millimeters.

ACCOUNTS OF SPECIES

Family EMBALLONURIDAE

Rhynchonycteris naso (Wied-Neuwied, 1820)

Brazilian Long-nosed Bat

Specimens examined (5).—EL PETEN: Río San Román, 16 km. NW Chinajá, 1; Sayaxché, 4.

Additional records.—IZABAL: Izabal (Dobson, 1878:368). SAN MARCOS: Ocos (Sanborn, 1937:327).

Goodwin (1934:7) reported this species as common along the Río Naranjo at Ocos where individuals were found in daytime "clinging to the bark of the mangroves overhanging the water." A specimen from Izabal was "one of a flock disturbed from the wooded shore of the Lake of Yzabal" (Alston, 1879-1882:27). The specimen from along the Río San Román was shot as it rested on a tree trunk in early afternoon.

Each of three females taken in mid-March in southern El Petén carried a single embryo on the left side. The embryos measured 4, 15, and 23 in crown-rump length; the largest was near term.

Saccopteryx bilineata (Temminck, 1838-39)

Greater White-lined Bat

Specimens examined (10).—ALTA VERAPAZ: Chinajá, 550 ft., 1. EL PETEN: El Remate, 2 (USNM); Tikal, about 935 ft., 2. JUTIAPA: 1 mi. SE Mongoy, 3. SANTA ROSA: 5 mi. S Chiquimulilla, 200 ft., 2.

Additional records (Sanborn, 1937:331, unless otherwise noted).—ALTA VERAPAZ: Rosario, 50 m. (Ryan, 1960:7). EL PETEN: Uaxactún. ESCUINTLA: Santa Lucía (Dobson, 1878:373). IZABAL: Bobós. JUTIAPA: 5 km. N Lago Atescatempa [= 8 km. SSE Asunción Mita] (Ryan, 1960:8). SAN MARCOS: Hda. California. SUCHITEPEQUEZ: Mocá. Precise locality unknown: "Vera Paz" (Dobson, 1878:373).

The white-lined bat evidently is distributed widely in lowlands and at moderate elevations in Guatemala. The species has been found to roost in buildings, "well-lighted rooms" in Mayan ruins (in El Petén), in hollows in trees, on the shaded trunks of trees, and in at least one instance along shaded ledges of a rocky escarpment (Ryan, 1960:8). This bat characteristically appears in flight earlier in the evening than most other species. Ryan (*loc. cit.*) even observed individuals in flight at all hours of the day in a forested canyon in Jutiapa.

According to Murie (1935:18), five of six females from El Petén that were taken on March 28 and two more obtained on May 8 were pregnant; each carried a single embryo. Among the females in my material, one taken on February 10 and another captured on April 4 each contained a single embryo that measured 5 (crown-rump), whereas two females obtained on July 31 evidenced no reproductive activity.

A specimen from Chinajá was parasitized in and about the ears by several hundred chiggers, *Trombicula saccopteryx*.

Peropteryx macrotis macrotis (Wagner, 1821)

Lesser Doglike Bat

Specimens examined (18).—ALTA VERAPAZ: ½ mi. W Lanquín Cave, 1330 ft., 5. EL PETEN: 12 km. NNW Chinajá, 13.

Additional records (Sanborn, 1937:340, unless otherwise noted).—ALTA VERAPAZ: Cobán (Alston, 1879-1882:29). EL PETEN: Uaxactún. IZABAL: Escobas. SACATEPEQUEZ: Dueñas (Alston, *loc. cit.*). SUCHITEPEQUEZ: Patulul.

The specimens from 12 km. NNW Chinajá were collected in two adjacent limestone caverns. *P. macrotis* was the only species found in one cave, but shared the other with a small number of *Myotis nigricans*. Bats were shot from daytime roosts high (15 to 25 feet) on ceilings and walls, where they hung singly, or as they flew along passages of the small caves after being disturbed. Neither cave, one of which had several entrances, harbored more than a dozen or so individuals of *Peropteryx*. One of two females obtained on February 28 carried a single embryo as did two of five females captured on March 12. The embryos measured 5, 6, and 10, respectively. None of three January-taken females from Alta Verapaz was pregnant.

Murie (1935:18) reported pregnant females (and one female accompanied by a juvenile) taken in March and April at Uaxactún, where he obtained specimens in a room in Mayan ruins.

Peropteryx kappleri kappleri Peters, 1867

Greater Doglike Bat

The only report of this species from Guatemala appears to be the specimens mentioned by Sanborn (1936:94 and 1937:344) from Escobas, Izabal, which were found on November 30, 1933, "in a small cave, caused by the piling up of large limestone boulders, at the foot of a cliff."

Centronycteris maximiliani centralis Thomas, 1912

Maximilian's Bat

A single specimen of this bat, shot in flight over a creek at Escobas on November 30, 1933 (Sanborn, 1936:94), is on record from Guatemala.

Balantiopteryx plicata plicata Peters, 1867

Peters' Sac-winged Bat

Specimens examined (5).—EL PROGRESO: El Rancho, 2 (USNM). JUTIAPA: 1 mi. SE Mongoy, 3.

Peters' bat may be rare in Guatemala. On June 31, 1956, Albert A. Alcorn collected a male and two non-pregnant females in Jutiapa from a small group in a crevice in a cliff.

Balantiopteryx io Thomas, 1904

Thomas' Sac-winged Bat

Specimens examined (36).—ALTA VERAPAZ: Lanquín Cave, 1022 ft., 35. IZABAL: Escobas, 1 (USNM).

Additional records.—ALTA VERAPAZ: Chimoxán (Goodwin, 1934:8); Río Dolores, near Cobán (type locality).

This small bat is known in Guatemala only from the Caribbean lowlands of Alta Verapaz and Izabal. None of 26 females collected at Lanquín Cave by James W. Bee in the period January 11-16, 1955, was pregnant; the testes of nine males from there averaged 1.4 (1-2) in length. The 35 specimens from Languín Cave weighed an average of 4.2 (4-6) grams.

Previously reported specimens of *B. io* were taken in a small cave (at Chimoxán) and from a crevice in a limestone cliff (at Escobas).

Diclidurus virgo Thomas, 1903

White Bat

Specimens examined (6).—ALTA VERAPAZ: 4 km. S Chinajá, 1950 ft., 5. RETALHULEU: Champerico, 1 (USNM).

Additional record.—Precise locality unknown: "Probably from the neighbourhood of Coban" (Alston, 1879-1882:30).

In February of 1960 when William E. Duellman and I were at Chinajá as guests of the Ohio Oil Company of Guatemala, we learned that employees of the company often saw bats at night in the lights at a nearby drilling rig. On February 27 we visited the rig, which was 4 km. S Chinajá in a saddle on the ridge of the Serrania de Chinajá at an elevation of 1950 feet. Almost all vegetation within 40 yards of the rig had been cleared away. Dense forest surrounded the clearing.

Upon our arrival, at approximately eight o'clock (well after dark), we noted dozens of bats, perhaps as many as 100, foraging around the derrick. Many were so high that they were difficult to see in the poor light; others foraged lower, less than 50 feet above the ground, and individuals occasionally swooped within 10 feet of us. The flight was erratic and fairly swift. In order to see the bats better, we adjusted two of the flood lights that illuminated the working areas at the rig so that the beams were cast almost directly upward. As if to avoid these lights, some bats left the immediate area and those that remained flew even higher than before; few came within range of our specially loaded shells. Thereupon, Richard Raines, one of the workers at the rig, climbed to a 98-foot-high platform on the derrick from where he shot five bats in about half an hour. According to Raines, some bats were flying at about the level of the platform but others flew as high as, or higher than, the 142-foot tower of the rig. Insofar as all of us could determine, all bats seen were *D. virgo*.

We were not again permitted to shoot near the oil rig and efforts to net the bats proved futile because we were unable to raise nets high enough above the ground in the clearing. On two or three occasions during our visit a foul-smelling gas escaped from the hole being drilled on the Serrania de Chinajá and workers reported to us that they saw no bats on nights when this gas permeated the air in the vicinity of the rig. Neither did they observe bats on nights when rain fell. The number of white bats seen on February 27 and subsequent nights suggested to us the possibility that this species is colonial, but a search of the general area, including several small limestone caves, failed to reveal a daytime retreat.

After the specimens had been prepared, they were shown to many of the Guatemalan workers at Chinajá, a number of whom came from Alta Verapaz and El Petén; none previously had seen a white bat.

External and cranial measurements of the five bats collected, three females (non-pregnant) and two males, all adults, are given in Table 1. The two males are nearly pure white over-all (individual hairs are white terminally and pale grayish basally) whereas the females are grayish white to (in one case) pale buffy gray. Judging from the accompanying measurements, males are smaller than females in some dimensions. In preparing the specimens, I was impressed with the thinness and tenderness of the skin and the ease with which patches of pelage sloughed from the skin.

Table 1.—External and Cranial Measurements of Five Specimens of Diclidurus virgo.

Measurement	81988 KU, ♀	81989 KU, ♀	81990 KU, ♂	81991 KU, ♀	81992 KU, ♂
Total length	103	102	94	102	91
Length of tail	21	22	20	21	21
Length of hind foot	11	11	12	11	11
Length of ear	17	17	17	16	16
Length of forearm*	66.6	69.2	62.5	67.3	64.3
Greatest length of skull**	19.5	19.1	18.9	19.2	19.4
Zygomatic breadth	12.7	....	12.5	12.3	12.5
Breadth of braincase	9.2	9.2	9.4	9.2	9.3
Mastoid breadth	10.2	10.1	9.8	10.0	10.0
Interorbital constriction	5.6	5.7	5.5	5.6	5.6
Length of maxillary tooth-row	7.7	8.0	7.8	7.8	7.8
Length of mandibular tooth-row	9.9	9.8	9.8	9.9	9.8
Breadth across M3	8.9	9.0	8.9	9.0	8.9

* Average of both forearms.

** Includes incisors.

Family PHYLLOSTOMATIDAE

Pteronotus davyi fulvus (Thomas, 1892)

Davy's Naked-backed Bat

Specimens examined (52).—Alta Verapaz: Lanquín Cave, 1022 ft., 50. Chiquimula: Jocotán, 1350 ft., 2.

This bat seems not to have been reported previously from Guatemala. None of 27 females collected at Lanquín Cave in mid-January by J. W. Bee was pregnant; the testes of 13 males from there averaged 3.1 (2-5) in length. A female from Jocotán, obtained on March 7, 1960, carried a single embryo (11 crown-rump).

The two specimens from Jocotán were netted over a small stream by E. S. Booth and J. H. Bodley. Other species of bats taken in the same net (numbers in parentheses) were *Carollia subrufa* (1), *Glossophaga soricina* (2), *Mormoops megalophylla* (1), *Phyllostomus discolor* (2), *Pteronotus parnellii* (1), *Pteronotus psilotus* (1), and *Sturnira lilium* (3). All were taken prior to 10 in the evening.

The membrane was removed from the back of one specimen, revealing long (8-9), dense, fluffy pelage that is pale brownish gray in over-all appearance (the individual hairs are whitish terminally and dark brownish gray basally). In contrast, the pelage of the anterior part of the dorsum is shorter and dark brownish.

Pteronotus parnellii fuscus (J. A. Allen, 1911)

Parnell's Mustached Bat

Specimens examined (100).—Alta Verapaz: Lanquín Cave, 1022 ft., 4. Chimaltenango: Acatenango, 1 (USNM); Yepocapa, 1 (USNM); Río Queleya, ½ mi. E Yepocapa, 4300 ft., 4; ¾ mi. E, 1 mi. S Yepocapa, 4280 ft., 41. Chiquimula: Jocotán, 1350 ft., 1. El Peten: 15 km. NW Chinajá, about 120 m., 6; 12 km. NNW Chinajá, 36; Toocog, 15 km. SE La Libertad, 540 ft., 3. El Progreso: Puente Punta Gordo, 2050 ft., 3.

Additional records.—El Peten: 2 mi. S Flores (Goodwin, 1955:1). Sacatepequez (Dobson, 1878:453): Ciudad Vieja; Dueñas.

All specimens of *P. parnellii* examined from El Petén were taken in limestone caves. In a small cave 12 km. NNW Chinajá, described in the account of *Trachops cirrhosus*, this mustached bat was found along with *T. cirrhosus*, *Carollia perspicillata*, and *Myotis nigricans*, whereas the species was the only inhabitant of a cave 15 km. NW Chinajá. At Toocog this bat occupied a partially water-filled solution chamber along with *C. perspicillata* and *M. nigricans*. There, mustached bats sought daytime retreats in pockets in the ceiling of the chamber. March-taken specimens from Puente Punta

Gordo and Jocotán were captured in mist nets stretched over streams.

Twenty-one of 25 females obtained from 12 km. NNW Chinajá on March 5, 1960, were pregnant, each with a single embryo. Embryos ranged from 3 to 26 (average 15.6) in crown-rump length. None of 34 January-taken females from Alta Verapaz and Chimaltenango was pregnant. Freshly examined testes measured 4 in males taken in January and March.

Guatemalan specimens are referable to the subspecies *P. p. fuscus* as currently understood, although Koopman (1955:112) has suggested that *fuscus* may prove to be indistinguishable from *P. p. parnellii* of South America. Based on material available in the Museum of Natural History, intergradation between *fuscus* and the larger *P. p. mexicanus* takes place in the Isthmus of Tehuantepec. All Guatemalan specimens examined are in the brownish color phase save the three from Puente Punta Gordo, which are reddish brown.

There has been disagreement (see especially Koopman, 1955:111, de la Torre, 1955:696, and Alvarez, 1963:398) as to the correct specific name of this bat—*parnellii* Gray, 1843, or *rubiginosa* (= *rubiginosus*) Wagner, 1843. As set forth by de la Torre, *parnellii* was published in October of 1843, whereas the date of publication in that year of *rubiginosus* is unknown. Under the circumstances, Article 21 of the International Code of Zoological Nomenclature dictates use of *parnellii*.

Pteronotus psilotus (Dobson, 1878)

Dobson's Mustached Bat

Specimens examined (43).—ALTA VERAPAZ: Lanquín Cave, 1022 ft., 42. CHIQUIMULA: Jocotán, 1350 ft., 1.

Additional records.—EL PETEN: Laguna de Zotz (Sanborn, 1938:1). Precise locality unknown: "Guatemala" (Dobson, 1878:451).

A female taken on March 7, 1960, at Jocotán carried a single embryo measuring 11 (crown-rump). As in other species of *Pteronotus* from Guatemala, January-taken females (14 from Alta Verapaz) evidenced no gross reproductive activity. The testes of 28 males from the same series averaged 5.7 (2-7) in length.

Color of pelage varies among the skins at hand. Most are grayish brown dorsally and buffy gray ventrally, but one is deep reddish brown dorsally and buffy orange ventrally and several are variously intermediate between the two extremes. One bat has a distinct cream-colored patch on the right side just above the wing membrane.

TABLE 2.—SELECTED MEASUREMENTS OF FOUR SPECIES OF PTERONOTUS FROM LANQUIN CAVE, ALTA VERAPAZ.

Number of specimens averaged or catalogue number, and sex	Length of forearm*	Weight in grams	Greatest length of skull**	Zygomatic breadth	Breadth of braincase	Mastoid breadth	Interorbital constriction	Length of maxillary tooth-row
Pteronotus davyi fulvus								
Average 10 (5♂, 5♀)	45.4	8.7	15.7	8.8	7.9	8.9	3.4	6.5
Minimum..........	43.8	8.0	15.5	8.6	7.7	8.7	3.3	6.4
Maximum.........	46.8	10.0	16.0	9.0	8.0	9.0	3.6	6.6
Pteronotus parnellii fuscus								
64743 KU, ♂......	59.2	20.0	22.1	12.5	10.8	11.6	4.3	9.4
64744 KU, ♀......	59.4	19.0	21.6	12.4	10.6	11.2	4.2	9.2
64745 KU, ♀......	60.4	22.0	21.5	12.1	10.5	11.3	4.3	9.3
64746 KU, ♀......	59.3	20.0	21.7	12.2	10.4	11.5	4.1	9.3
Pteronotus psilotus								
Average 10 (5♂, 5♀)	43.2	8.0	15.4	8.4	7.7	8.7	3.4	5.9
Minimum..........	42.0	7.0	15.2	8.3	7.6	8.5	3.4	5.8
Maximum.........	44.5	9.0	15.7	8.6	7.9	8.8	3.5	6.0
Pteronotus suapurensis								
64697 KU, ♀......	53.9	16.0	17.8	......	8.7	10.3	4.1	7.5
64698 KU, ♀......	52.8	17.0	17.6	10.3	8.5	9.7	4.0	7.5

* Average of both forearms for each individual measured.

** Includes incisors.

Some measurements of the four species of *Pteronotus* from Lanquín Cave, one of the few localities in North America where all four have been taken, are given in Table 2. I follow Burt and Stirton (1961:25) in use of the generic name *Pteronotus* for the species *parnellii* and *psilotus*, formerly placed in a separate genus, *Chilonycteris*.

Pteronotus suapurensis (J. A. Allen, 1904)

Suapuré Naked-backed Bat

Specimens examined (2).—ALTA VERAPAZ: Lanquín Cave, 1022 ft., 2.

Two non-pregnant females, apparently the only individuals of the species known from Guatemala, were obtained by Bee on January 13 and 14, 1955. The larger external and cranial dimensions (see Table 2) of *P. suapurensis* easily distinguish it from the other naked-backed bat of Guatemala, *P. davyi*.

Mormoops megalophylla megalophylla (Peters, 1864)

Peters' Leaf-chinned Bat

Specimens examined (78).—ALTA VERAPAZ: Lanquín Cave, 1022 ft., 76. CHIQUIMULA: Jocotán, 1350 ft., 1. EL PETEN: Laguna de Zotz, 1 (USNM).

Additional records.—EL PETEN: 2 mi. S Flores (Davis and Carter, 1962a:67). SACATEPEQUEZ: Dueñas (Dobson, 1878:456).

Details of capture of the large series from Lanquín Cave, obtained in mid-January, unfortunately are lacking. None of 28 females from there was pregnant; freshly-measured testes of 37 males averaged 2.9 (3-5) in length. The series of 76 specimens (48 males, 28 females) averaged 15.6 (12-20) grams in weight.

A March-taken female (non-pregnant) from Jocotán was captured in a mist net over a small stream. The two large series of specimens presently on record from Guatemala—from Lanquín Cave and 2 mi. S Flores (27 specimens see, Goodwin, 1955:1)—both came from caves.

Micronycteris brachyotis (Dobson, 1878)

Yellow-throated Bat

A previously unreported specimen of this bat in the U. S. National Museum (USNM 245135) from Chuntuquí in northern El Petén constitutes the first record from Guatemala and the fourth from the North American mainland. Davis *et al.* (1964:377) reported a specimen from Florida, Chiapas, and Sanborn (1949:224) listed two individuals from Volcán de Chinandega, Nicaragua. I follow Goodwin and Greenhall (1961:230-231) in using the specific name *brachyotis* rather than *platyceps* for this species.

Selected measurements of the Guatemalan bat, a male that was obtained by Harry Malleis on May 6, 1923, are: length of forearm, 40.9; greatest lenth of skull (includes incisors), 21.7; zygomatic breadth, 10.7; breadth of braincase, 8.7; interorbital constriction, 5.1; mastoid breadth, 10.0; breadth of rostrum, 6.3; length of maxillary tooth-row, 8.3; length of mandibular c-m3, 8.6.

Micronycteris megalotis mexicana Miller, 1898

Brazilian Big-eared Bat

This species is known in Guatemala only from Hda. California, San Marcos, where two individuals were taken in a building along with *Saccopteryx bilineata* (Goodwin, 1934:8), and from Dueñas, Sacatepequez (Andersen, 1906:54).

Micronycteris schmidtorum Sanborn, 1935

Schmidt's Big-eared Bat

This rare bat has been recorded from Guatemala only from the type locality, Bobós, Izabal. "The type was taken in a hollow tree in December and four months later another male was captured in the same tree" (Sanborn, 1935:82).

Macrotus waterhousii mexicanus Saussure, 1860

Leaf-nosed Bat

The occurrence in Guatemala of this species is based on the four specimens "obtained by M. Bocourt in Vera Paz" that formed the basis of Dobson's (1876:436-437) description of *Macrotus bocourtianus.* No one of the four, housed in the Paris Museum, was regarded as fully adult by Dobson. According to Stuart (1948:9), Bocourt made most of his collections in "Vera Paz" in the vicinity of Cobán.

M. bocourtianus first was relegated to synonymy under *M. w. mexicanus* by Rehn (1904:437, 439). The specific name *waterhousii* is used following Anderson and Nelson (1965).

Lonchorhina aurita aurita Tomes, 1863

Tomes' Long-eared Bat

Specimens examined (2).—CHIMALTENANGO: ¾ mi. E, 1 mi. S Yepocapa, 4280 ft., 1. IZABAL: Quebradas, 1 (USNM).

According to Sanborn (1936:96), 23 specimens of *L. aurita* were captured at Quebradas "in a tunnel of a gold mine" on April 14, 1934. The specimen from southeast of Yepocapa, a non-pregnant female, was taken on January 7, 1955.

Mimon bennettii cozumelae Goldman, 1914

Cozumel Spear-nosed Bat

This species is known only from Tikal, El Petén, where four males and two females were collected in March of 1956 (Winkelmann, 1962:112). I tentatively follow Schaldach (1965:132) in use of the specific name *bennettii* for this bat.

Phyllostomus discolor verrucosus Elliot, 1905

Pale Spear-nosed Bat

Specimens examined (2).—CHIQUIMULA: Jocotán, 1350 ft., 2.

Additional records (Sanborn, 1936:98).—IZABAL: Escobas. SUCHITEPEQUEZ: Patulul.

A male and non-pregnant female from Jocotán were netted over a small stream along with bats of six other species (see account of *Pteronotus davyi fulvus*).

Trachops cirrhosus coffini Goldman, 1925

Fringe-lipped Bat

Specimens examined (41).—EL PETEN: 12 km. NNW Chinajá, 10; El Gallo, 8 mi. W Yaxhá, 17 (USNM); Tikal, about 935 ft., 14.

The fringe-lipped bat presently is known from Guatemala only from the rainforests of the Petén. The 10 specimens from 12 km. NNW Chinajá were taken in a small limestone cave in which *Pteronotus parnellii, Carollia perspicillata,* and *Myotis nigricans* also found daytime refuge. The entrance to the cave was in a sink, approximately six feet wide, 20 feet long, and 20 feet deep, located at the bottom of a hill. The *M. nigricans* occupied a hole in the ceiling of a narrow passage that sloped downward for a distance of about 15 feet from one end of the sink, terminating in a pool of water. Above the water was a dome-shaped cavern, the ceiling of which was punctured with numerous holes and crevices in which *Trachops, Pteronotus,* and *Carollia* were found. By blocking much of the opening to the tunnel with my body, I prevented some of the bats from escaping and shot them. Some that did escape were "swatted" down or shot by my companions in the sink outside. *T. cirrhosus* was the least numerous of the three species in the dome; I estimated that no more than 20 individuals were present. When the same cave was visited a week later only a few *Pteronotus* and *Carollia* were found there.

Four of seven females from 12 km. NNW Chinajá (March 5, 1960) were pregnant, each carrying a single embryo on the left side. Embryos averaged 13.0 (6-18) in crown-rump length. Six of seven females taken at Tikal on April 5, 1955, also were pregnant. Again, each carried a single embryo on the left side, the embryos averaging 30.8 (28-34).

The specimens in the U. S. National Museum, including the holotype of *T. c. coffini,* are labeled as from a place called "Guyo" in El Petén. As de la Torre (1956:189) has pointed out, no such locality is known in the Petén. From a study of the field notes of the collector, Harry Malleis, de la Torre concluded that "Guyo" in reality is the place known as El Gallo (Galla on some maps), 8 km. W Yaxhá (also Yaxá and Yashá) on the El Cayo-Remate trail.

Davis and Carter (1962*a*:69) used the binomen, *Trachops cirrhosus* (Spix), for a specimen of the fringe-lipped bat from Costa

Rica. They noted overlap in "most measurements" when published descriptions of *T. c. cirrhosus* and *T. c. coffini* were compared, and wrote as follows: "For this reason, we question the validity of *coffini* and suspect that it will be found to be inseparable from *cirrhosus*." While the suspicions of Davis and Carter may prove to be well founded, it seems best to retain the subspecific name *coffini* until firsthand evidence to the contrary is available.

Vampyrum spectrum nelsoni (Goldman, 1917)

Linnaeus' False Vampire Bat

There seems to be no definite record of this bat from Guatemala, although it undoubtedly occurs there. Alston (1879-1882:39) indicated that Dobson had examined specimens from Guatemala, but Dobson (1878:471) simply recorded Guatemala as within the geographic range of the species—he listed no Guatemalan specimens as examined. It ought to be noted, however, that Dobson rarely if ever listed a country within the range of a species unless he had examined material therefrom or had certain evidence of occurrence there of the bat concerned.

Glossophaga commissarisi Gardner, 1962

Gardner's Long-tongued Bat

Specimens examined (13).—CHIMALTENANGO: Yepocapa, 1 (USNM). EL PROGRESO: El Progreso, 2 (AMNH). JUTIAPA: 2½ mi. W, 2¼ mi. N San Cristóbal, 2900 ft., 3. SAN MARCOS: Hda. California, 4 (AMNH). SANTA ROSA: Astillero, 25 ft., 2. SOLOLA: San Lucas, 1 (AMNH).

Additional record.—HUEHUETENANGO: La Democracia, 3300 ft. (Davis *et al.*, 1964:379).

G. commissarisi, a bat that closely resembles externally the well-known *G. soricina*, was first named and described in 1962 (type locality, 10 km. SE Tonalá, Chiapas). The species has been reported only once previously by name from Guatemala, although some specimens were listed as *G. soricina* by earlier authors. Goodwin (1934:9), for example, described the characteristics of long-tongued bats (all of which he referred to *G. s. leachii*) from Hda. California in such a manner that it was possible to predict that some would prove to be *commissarisi*. I have not seen all the specimens of *Glossophaga* reported previously from Guatemala, but 15 of the 63 individuals listed by Goodwin (*loc. cit.*) were examined, with the following results: four of six from Hda. California are referable to *commissarisi*, as are two of three from El Progreso, and the single specimen examined from San Lucas; all specimens seen from Finca Carolina (one), Finca Cipres (three), and Puebla (one) were correctly labeled as *G. s. leachii* (see, also, list of specimens above and in the account beyond). Additional specimens of *commissarisi* probably will be found among those eariler reported as *soricina*.

Actually, two morphological types that may represent distinct species are included among the specimens herein assigned to *commissarisi*. One type (represented by the five specimens examined from El Progreso and Jutiapa) differs from the other in having a longer forearm, somewhat larger skull, more inflated braincase accompanied by a more abrupt angle from rostrum to braincase, slightly less procumbent upper incisors, larger lower incisors, a distinct ridge on the ventral surface of the presphenoid, and shallower basisphenoidal pits. Bats of the type described are reminiscent of Mexican specimens of *Glossophaga soricina alticola* Davis, 1944 (type locality, 13 km. NE Tlaxcala, 7800 ft., Tlaxcala). The relationships of *commissarisi* and *alticola* currently are under study. Characters by which *commissarisi* may be distinguished from *G. soricina* were discussed by Gardner (1962).

A female taken at Astillero on February 16 carried a single embryo, which measured 18, on the left side. Little is known concerning the comparative ecology of *commissarisi* and *soricina*.

Glossophaga soricina leachii (Gray, 1844)

Pallas' Long-tongued Bat

Specimens examined (21).—ALTA VERAPAZ: Finca Chicoyou, 1 km. W Cobán, 1300 m., 7; Finca Los Alpes, 1000 m., 1. CHIQUIMULA: Jocotán, 1350 ft., 2. EL PETEN: Chuntuquí, 1 (USNM). EL PROGRESO: El Progreso, 1 (AMNH). GUATEMALA: Lake Amatitlán, 4000 ft., 1. IZABAL: Puebla, 1 (AMNH). SAN MARCOS: Hda. California, 2 (AMNH); Finca Carolina, 1 (AMNH). SANTA ROSA: Astillero, 25 ft., 1. SUCHITEPEQUEZ: Finca Cipres, 3 (AMNH).

Additional records.—ALTA VERAPAZ: Chipoc (Goodwin, 1934:9); Cobán (Dobson, 1878:501). EL PETEN: 2 mi. S Flores (Goodwin, 1955:2); La Libertad (Goodwin, 1955:2); Uaxactún (Murie, 1935:18). HUEHUETENANGO: Barillas (Goodwin, 1934:9). SACATEPEQUEZ: Dueñas (Alston, 1879-1882:44). SANTA ROSA: Finca San Gerónimo, near Chiquimulilla, 335 m. (Ryan, 1960:8).

As noted in the previous account, only one species of *Glossophaga* was recognized as occurring in Middle America prior to 1962. Records from the literature that are listed above are suspect until the specimens upon which they were based can be re-examined.

A female taken on March 7 at Jocatán carried an embryo that measured 17. Two of seven August-taken females from Alta Verapaz were pregnant, each with a single embryo on the left side. The embryos measured 4 and 12.

Anoura geoffroyi lasiopyga (Peters, 1868)

Geoffroy's Tailless Bat

Specimens examined (5).—ALTA VERAPAZ: Finca Chicoyou, 1 km. W Cobán, 1300 m., 4. CHIMALTENANGO: Santa Elena, 1 (USNM).

Additional records.—ALTA VERAPAZ: Choctum (Dobson, 1878:509). HUEHUETENANGO: Barillas (Goodwin, 1934:10).

The four specimens examined from Finca Chicoyou were captured in mist nets. Three were netted in dense vegetation in a pastured area and the other along a river. Thirteen specimens were taken at Santa Elena in a small cave (Sanborn, 1936:98), whereas the single individual reported from Barillas (Goodwin, 1934:10) was caught in a mouse trap suspended over a pile of raw sugar.

Choeronycteris mexicana Tschudi, 1844

Mexican Long-tongued Bat

This glossophagine is on record from Guatemala from three localities—Hda. California, San Marcos, and Panajachel, Sololá (Goodwin, 1934:10), and Dueñas, Sacatepequez (Dobson, 1878:511). The specimens reported by Goodwin were "taken in outbuildings where they seemed disinclined to mingle with other species."

Choeroniscus godmani (Thomas, 1903)

Godman's Bat

Godman's bat is known from the country by a single specimen, the holotype, which is from an unknown locality (see original description and Alston, 1879-1882:209).

Leptonycteris nivalis (Saussure, 1860)

Mexican Long-nosed Bat

This bat is known from Guatemala by only two specimens, one each from Dueñas and Ciudad Vieja, Sacatepequez (Hoffmeister, 1957:459), in the collections of the British Museum. These two records, the southeasternmost for the genus on the North American mainland, were mentioned also by Dobson (1878:506) and Alston (1879-1882:45) but were overlooked by Davis and Carter (1962*b*) in their recent review of *Leptonycteris*.

Carollia perspicillata azteca Saussure, 1860

Seba's Short-tailed Bat

Specimens examined (31).—EL PETEN: 12 km. NNW Chinajá, 20; Chuntuquí, 7 (USNM); Toocog, 15 km. SW La Libertad, 540 ft., 4.

Additional records.—ALTA VERAPAZ: Chipoc (Goodwin, 1934:11); Rosario, 50 m. (Ryan, 1960:8).

The 20 specimens from 12 km. NNW Chinajá were taken in a small limestone cave (see account of *Trachops cirrhosus*). At Toocog, *C. perspicillata* found daytime retreats in holes in the ceiling of a large solution chamber. Ryan (1960:8) found this species in a hollow tree along with *Saccopteryx bilineata;* the 21 bats reported by Goodwin (1934:11) from Chipoc came from caves. All specimens thus far reported from Guatemala are from the Caribbean lowlands.

Three of four March-taken females from El Petén were pregnant. Each carried a single embryo (25, 16, and 8) on the left side.

Carollia subrufa (Hahn, 1905)

Hahn's Short-tailed Bat

Specimens examined (13).—ALTA VERAPAZ: Finca Chicoyou, 1 km. W Cobán, 1300 m., 10; Finca Los Alpes, 1000 m., 1; ½ mi. W Lanquín Cave, 1330 ft., 1. CHIQUIMULA: Jocotán, 1350 ft., 1.

Additional records.—ALTA VERAPAZ: Cobán (Goodwin, 1955:2). EL PETEN: Uaxactún (Murie, 1935:18). IZABAL: Escobas (Sanborn, 1936:101); Puebla (Goodwin, 1934:11). SANTA ROSA: Finca San Gerónimo, near Chiquimulilla, 335 m. (Ryan, 1960:9). SUCHITEPEQUEZ: Mocá (Hall and Kelson, 1959:125, figs. 82-83).

Many of the specimens from Guatemala have been taken from roosts in man-made structures (see Goodwin, 1934:11 and 1955:2, and Ryan, 1960:9), frequently in company with *Glossophaga*. The specimen from Finca Los Alpes was netted in a citrus grove. At Finca Chicoyou, specimens also were netted, either in dense vegetation in a pasture or along a small river, and two were captured there in a small cave along with one *Artibeus toltecus*. One of three females from Finca Chicoyou (August 2) carried an embryo on the left side that measured 16.

Felten (1956:211) regarded *C. subrufa* as conspecific with *C. castanea,* but these two bats actually are distinct species (see, for example, Starrett and de la Torre, 1964:59). Ranges of measurements of specimens of *subrufa* examined, followed for comparison by those of Guatemalan *C. perspicillata,* are: length of forearm, 33.2-41.2 (42.8-46.5 in *perspicillata*); greatest length of skull (includes incisors), 20.5-23.2 (23.5-25.3); length of maxillary tooth-row, 6.5-7.2 (7.7-8.3). The lower limits of the range of variation in *subrufa* are measurements of a male from Jocotán that is noticeably smaller than any of the other individuals examined, but otherwise typical of the species as currently understood.

Sturnira lilium parvidens Goldman, 1917

Yellow-shouldered Bat

Specimens examined (38).—ALTA VERAPAZ: Chinajá, 550 ft., 24; Finca Chicoyou, 1 km. W Cobán, 1300 m., 1; Finca Los Alpes, 1000 m., 2. CHIQUIMULA: Jocotán, 1350 ft., 2. ESCUINTLA: km. 52 on highway S Guatemala City (approximately 4 km. NE Escuintla), 3; 4 km. W Escuintla, 800 ft., 4. SANTA ROSA: Astillero, 25 ft., 2.

Additional records.—IZABAL: Escobas and Los Amates (Sanborn, 1936: 100). Precise locality unknown: "Guatemala" (Alston, 1879-1882:50).

The yellow-shouldered bat evidently is widely distributed at lower elevations in Guatemala. The species was common in the rainforest at Chinajá where individuals were netted along trails and in small clearings in the forest. Sanborn (1936:101) reported the unusual circumstance of a specimen being "caught in a steel trap set on a bunch of bananas on a fallen tree." The same trap had previously taken a *Carollia subrufa.*

Pregnant females have been taken both in the dry season (11 of 16 examined in February and March) and in the rainy season (four of nine examined in June, July, and August). All carried a single embryo on the left side. This species seemingly breeds throughout the year.

Uroderma bilobatum bilobatum Peters, 1866

Tent-making Bat

Specimen examined (1).—SANTA ROSA: Astillero, 25 ft., 1.

A female obtained by J. W. Bee at Astillero on February 14, 1955, provides the first record of this bat from Guatemala. The specimen carried a single embryo, which had a total length of 30, on the left side.

Vampyrops helleri Peters, 1866

Heller's Broad-nosed Bat

A male of this relatively rare species, taken in a mist net 10 mi. N Sebol, 900 ft., Alta Verapaz (Davis *et al.,* 1964:383), is the only specimen known from Guatemala.

Vampyrodes major (G. M. Allen, 1908)

San Pablo Bat

Specimen examined (1).—ALTA VERAPAZ: Chinajá, 550 ft., 1.
Additional record.—IZABAL: Escobas (Sanborn, 1936:101).

The single specimen examined, a male having testes 6 mm. long, was netted on February 25, 1960, over a temporary pool in rainforest. Several *Artibeus jamaicensis* were taken in the same net. Four specimens from Escobas (Sanborn, *op. cit.*), the only other locality of record, also were netted. *V. major* is known in the northern part of its range only from the heavily forested regions of the Caribbean lowlands—in Guatemala, Chiapas, Tabasco, and southern Veracruz.

Artibeus cinereus watsoni Thomas, 1901

Cinereous Fruit-eating Bat

Specimens examined (3).—EL PETEN: Toocog, 15 km. SE La Libertad, 540 ft., 2; Remate, 1 (USNM).

Additional records.—ALTA VERAPAZ: 10 mi. N Sebol, 900 ft. (Davis and Carter, 1962*a*:71). IZABAL: Escobas (Sanborn, 1936:104); 16 km. N, 4 km. E Los Amates, 50 ft. (Davis and Carter, 1962*a*:71).

This species may be limited in Guatemala to the Caribbean lowlands. A male and female from Toocog were taken in mist nets placed across trails through the forest that led to patches of savanna. Three specimens of *Artibeus phaeotis* were trapped on the same night in the same nets, but the *cinereus* were taken early in the evening and the *phaeotis* in early morning. The female carried a single embryo (March 11) on the left side that measured 17. Testes of the male measured 6.5.

One of the two specimens (KU 82101) from Toocog has a noticeably higher braincase and more abruptly angled rostrum than the other but the two agree in other cranial details. Also, KU 82101 has but two lower molars, rather than the three characteristic of *A. cinereus*, but all the post-canine teeth in the lower jaws of this specimen are strangely aberrant, possibly relating in some way to the absence on both sides of m3.

Artibeus jamaicensis yucatanicus J. A. Allen, 1904

Jamaican Fruit-eating Bat

Specimens examined (29).—ALTA VERAPAZ: Chinajá, 550 ft., 9; Finca Chicoyou, 1 km. W. Cobán, 1300 m., 1; Finca Los Alpes, 1000 m., 1; Lanquín Cave, 1022 ft., 8. EL PETEN: no precise locality ("Petén"), 1 (USNM). ESCUINTLA: 4 km. W Escuintla, 880 ft., 1. GUATEMALA: 5 mi. S Guatemala, 4950 ft., 1. JUTIAPA: 1 mi. SE Mongoy, 3. RETALHULEU: 2 mi. SE Champerico, sea level, 1. SANTA ROSA: Astillero, 25 ft., 3.

Additional records.—EL PETEN: Uaxactún (Murie, 1935:19). SACATEPEQUEZ: Dueñas (Andersen, 1908:266). SOLOLA: Panajachel (Goodwin, 1934:12).

This species occurs widely in Guatemala and almost certainly is more abundant than the relatively few records indicate. Many of the available specimens were trapped in mist nets but some were taken in caves or from retreats in man-made structures.

Pregnant females, each with a single embryo, have been taken only in February (four of five females examined) and March (one of three)—the five embryos ranged from 31 to 36 in crown-rump length. Females obtained in January (six) and August (four) evidenced no reproductive activity. Males taken in January (two), February (three), and March (one) had testes that measured 4, 7, 8, 8, 9.5, and 7, respectively.

Pending C. O. Handley's intended revision of the genus *Artibeus*, I tentatively apply the subspecific name *A. j. yucatanicus* to members of this species from throughout Guatemala. Available specimens from the central part of the country average slightly larger than topotypes of *yucatanicus* but there is overlap in all measurements analyzed; specimens examined from elsewhere in Guatemala do not differ noticeably from topotypes. Murie (1935:19) previously applied the name *yucatanicus* to specimens from Uaxactún.

Size of the third lower molar varies among the 26 skulls studied, and one specimen (KU 82098) lacks that tooth on the left side. A third upper molar, absent as a rule in *A. jamaicensis*, is present, although minute and peglike, on the left side in KU 64918 and on both sides in KU 70811.

Artibeus lituratus palmarum Allen and Chapman, 1897

Big Fruit-eating Bat

Specimens examined (16).—ALTA VERAPAZ: Chinajá, 550 ft., 5. EL PETEN: Flores, 1 (USNM); La Libertad, 2 (USNM); Toocog, 15 km. SE La Libertad, 540 ft., 2; no precise locality ("Petén"), 1 (USNM). SANTA ROSA: Astillero, 25 ft., 5.

Additional records (Andersen, 1908:279).—ALTA VERAPAZ: Cahabón. SACATEPEQUEZ: Dueñas.

Available Guatemalan records of the big fruit-eating bat suggest that it, too, is widely distributed in the country. Two February-taken females from Astillero each carried a single embryo (25 and 30 crown-rump) on the left side as did three of four March-taken females from Toocog and Chinajá. Testes of males taken in the same two months varied in length from 7 to 11.

Artibeus phaeotis phaeotis Miller, 1902

Dwarf Fruit-eating Bat

Specimens examined (5).—EL PETEN: Toocog, 15 km. SE La Libertad, 540 ft., 3; Uaxactún, 2.

Like *Artibeus cinereus*, with which it was taken at Toocog, *A. p. phaeotis* may be limited to the Caribbean lowlands in Guatemala. A female (March 10) from Toocog carried a single, near-term embryo on the left side that measured 26. The testes of two males taken at the same time measured 6. Murie (1935:19) reported (under the name *Artibeus nanus*) 43 individuals from Uaxactún, one a pregnant female (April 15) that contained an embryo measuring 30. Murie's statement that the "amount of vaulting in the skull is variable and apparently is due to individual variation and not to age difference" suggests the possibility that more than one species of small *Artibeus* was represented among his specimens. The two I have examined, however, are clearly *phaeotis*.

The specific name *phaeotis* is used in place of *turpis* for this bat for the reasons explained by Jones and Lawlor (1965:412).

Artibeus phaeotis nanus Andersen, 1906

Dwarf Fruit-eating Bat

Specimens examined (2).—SANTA ROSA: Astillero, 25 ft., 2.

The relatively small size (see Table 3) of two subadults from Astillero leads me to refer them to *nanus* rather than *turpis* [= *phaeotis*], to which Davis (1958:164) referred them on the basis of "geographic probability."

TABLE 3.—CRANIAL MEASUREMENTS OF THREE SMALL SPECIES OF ARTIBEUS.

Number of specimens averaged or catalogue uumber, and sex	Length of forearm	Greatest length of skull*	Zygomatic breadth	Mastoid breadth	Interorbital constriction	Length of maxillary tooth-row	Breadth across upper molars
Artibeus cinereus watsoni, Toocog, El Peten							
82101 KU, ♂	38.5	20.1	11.3	10.2	4.8	6.6	8.6
82102 KU, ♀	37.7	19.8	11.2	10.1	4.5	6.4	8.3
Artibeus phaeotis phaeotis, El Peten							
Average 5 (3♂, 2♀)	38.2	19.2	11.4	10.1	4.5	5.7	8.3
Minimum	37.0	18.8	11.2	10.0	4.3	5.6	8.2
Maximum	39.0	19.4	11.7	10.5	4.7	5.8	8.5
Artibeus phaeotis nanus, Astillero, Santa Rosa							
64923 KU, ♀	34.8	18.1	11.0	9.7	4.4	5.5	8.0
64924 KU, ♂	36.5	18.9	10.9	9.8	4.5	5.8	8.2
Artibeus toltecus, Alta Verapaz							
Average 6 (5♂, 1♀)	40.6	20.4	12.0	10.7	4.8	6.5	9.2
Minimum	38.8	19.8	11.9	10.3	4.7	6.4	8.9
Maximum	43.5	21.1	12.1	11.1	5.2	6.7	9.3

* Includes incisors.

The subspecies *A. p. phaeotis* and *A. p. nanus* probably are separated in Guatemala by the highlands of the central part of the country.

Artibeus toltecus (Saussure, 1860)

Toltec Fruit-eating Bat

Specimens examined (8).—ALTA VERAPAZ: Finca Chicoyou, 1 km. W Cobán, 1300 m., 5; Finca Los Alpes, 1000 m., 1. SOLOLA: San Lucas, 1 (AMNH); Verdenango, 5173 ft., 1.

Additional record.—BAJA VERAPAZ: San Jerónimo (Andersen, 1908:300).

This species probably occurs in Guatemala principally in the central highlands. All specimens examined from Alta Verapaz were taken in mist nets save one, which was shot in the "twilight zone" of a small cave in company with *Carollia subrufa.* The specimen from San Lucas, originally reported under the name *Artibeus phaeotis* (Goodwin, 1934:12), was taken from a building along with other bats that "seemed to be *Glossophaga.*"

Guatemalan specimens of *toltecus* average larger and darker than specimens studied from western México. One specimen (KU 88187) from Finca Chicoyou has but a single pair of slightly enlarged lower incisors.

Centurio senex Gray, 1842

Wrinkle-faced Bat

Specimens examined (3).—CHIMALTENANGO: Yepocapa, 1 (USNM). SUCHITEPEQUEZ: Mocá, 2 (USNM).

Additional record.—Precise locality unknown: "Guatemala" (Alston, 1879-1882:51).

Little is known of the habits of this bat. Sanborn (1936:104) reported that 36 specimens obtained in the period January 2-12, 1934, at Mocá were brought in by Indians who refused to reveal particulars of their capture.

Family DESMODONTIDAE

Desmodus rotundus murinus Wagner, 1840

Vampire Bat

Specimens examined (48).—ALTA VERAPEZ: 9 mi. S Cobán, 4500 ft., 5; Finca Chicoyou, 1 km. W Cobán, 1300 m., 7. CHIMALTENANGO: Tecpán, 1; Yepocapa, 27 (USNM). EL PETEN: "Guyo" [= El Gallo, 8 mi. W Yaxhá], 6 (USNM); Toocog, 15 km. SE La Libertad, 540 ft., 1. SUCHITEPEQUEZ: Mocá, 2700 ft., 1 (USNM).

Additional records.—ALTA VERAPAZ (Ryan, 1960:10): Actelá; "todos partes del valle del Río Polochic"; Senahú. EL PETEN: Lago Petén Itzá (Ryan, 1960:10); Uaxactún (Murie, 1935:19). SACATEPEQUEZ: "cerca de Antigua" (Ryan, 1960:10); Dueñas (Alston, 1879-1882:53); San Antonio

(Goodwin, 1934:13). SANTA ROSA: Los Cerritos (Ryan, 1960:10). Precise locality unknown: "Vera Paz" (Dobson, 1878:550).

The vampire bat is widely distributed in Guatemala and evidently common in many places. Three March-taken females were pregnant as was one of three August-taken females examined. Each carried a single embryo.

Diphylla ecaudata Spix, 1823

Hairy-legged Vampire Bat

The only record of the hairy-legged vampire from the country seems to be the single specimen listed as from "Guatemala" by Alston (1879-1882:53). This specimen, obtained by Salvin in 1864 and housed in the Berlin Museum, was reported to Alston by Peters.

Family NATALIDAE

Natalus stramineus saturatus Dalquest and Hall, 1949

Funnel-eared Bat

Specimens examined (106).—ALTA VERAPAZ: Lanquín Cave, 1022-1098 ft., 62. EL PETEN: Flores, 11 (USNM); 3 mi. S Flores, 28 (USNM). IZABAL: Grutas de Silvino, 2 km. ENE Navajoa [= Navajo], about 60 m., 4; Quiriguá, 1 (USNM).

Additional records.—EL PROGRESO: El Progreso (Goodwin, 1959:8). SACATEPEQUEZ: Dueñas (Dobson, 1878:343).

All funnel-eared bats from Guatemala for which observations are available were taken in caves or rock shelters. Among 62 specimens taken between January 13 and 21 at Lanquín Cave, all but one of which came from a small cavern adjacent to the main cave, 37 males weighed an average of 6.3 (5-8) grams and all had testes that measured 2, whereas none of 25 females, which averaged 6.2 (5-7) grams in weight, was pregnant or lactating.

Family VESPERTILIONIDAE

Myotis cobanensis Goodwin, 1955

Guatemalan Myotis

This species is known only from the holotype, a male, which was taken in a cathedral at Cobán, Alta Verapaz, on June 21, 1946. Goodwin (1955:2) originally described *cobanensis* as a subspecies of *M. velifer*. Later, de la Torre (1958:167-170) found *cobanensis* to be so distinct morphologically from specimens of *M. v. velifer* from Guatemala that he regarded it as a separate species. "Its relationship to other named species or its possible identity with some already described species must await further study" (de la Torre, 1958:170).

Myotis nigricans extremus Miller and Allen, 1928

Black Myotis

Specimens examined (7).—EL PETEN: 12 km. NNW Chinajá, 7.

Specimens of this species reported from the central and southern parts of Guatemala have been referred to the subspecies *nigricans* (Miller and Allen, 1928:180, and Goodwin, 1934:14). The seven specimens from the Caribbean lowlands of El Petén listed above are referred to *M. n. extremus,* pending a systematic review of the species, because they agree with the original description of *extremus* given by Miller and Allen (*op. cit.*:182). Ranges of selected measurements of four females are: length of forearm, 34.6-36.8; greatest length of skull (includes incisors), 12.9-13.5; interorbital constriction, 2.9-3.1; breadth of braincase, 6.0-6.2; length of maxillary tooth-row, 4.6-4.8.

Four specimens were shot in a small limestone cavern that was occupied also by a few individuals of *Peropteryx macrotis.* The other three were found roosting in a pocket in the ceiling of a limestone cave described in the account of *Trachops cirrhosus.* None of four females examined (two taken on February 28 and the other two on March 5) evidenced reproductive activity.

Myotis nigricans nigricans (Schinz, 1821)

Black Myotis

Dobson (1878:230) recorded this bat from Dueñas, Sacatepequez, and Goodwin (1934:14) listed specimens from Finca Carolina, San Marcos, and Finca Cipres, Suchitepequez. Bats examined by Goodwin were "taken in . . . warehouses, where hundreds were hanging from the roof beams."

Myotis velifer velifer (J. A. Allen, 1890)

Cave Myotis

Specimens examined (9).—CHIMALTENANGO: Chocoyos, 9.

Additional records.—CHIMALTENANGO: Sierra Santa Elena (Miller and Allen, 1928:91). SACATEPEQUEZ: Ciudad Vieja (Miller and Allen, 1928:91). SOLOLA: Panajachel (de la Torre, 1958:167). ZACAPA: Santa Clara (de la Torre, 1958:167).

The cave myotis evidently is restricted in Guatemala to the highlands that bisect the central part of the country. The species reaches the southeasternmost limit of its range in adjacent Honduras

(Davis *et al.*, 1964:386). Dobson (1878:327) and Alston (1879-1882:25) recorded this bat from Guatemala under the name *Vespertilio albescens.*

Eptesicus fuscus miradorensis (H. Allen, 1866)

Big Brown Bat

Specimens examined (15).—ALTA VERAPAZ: 9 mi. S Cobán, 4500 ft., 10. GUATEMALA: 5 mi. S Guatemala, 4950 ft., 4. QUEZALTENANGO: Zunil, 1 (USNM).

Additional records.—ALTA VERAPAZ: Cobán (Goodwin, 1955:4). CHIMALTENANGO (Goodwin, 1934:15): Chichivac; Tecpán. EL PETEN (Goodwin, 1955:4): Flores; La Libertad. SACATEPEQUEZ: Dueñas (Alston, 1879-1882:20).

The big brown bat probably occurs mainly in the interior highlands in Guatemala, although Goodwin (1955:4) recorded the species from the central Petén. Ten females from 9 mi. S Cobán were netted at the entrance to a cave; *Desmodus rotundus* and *Tadarida brasiliensis* were taken in the same net. Eight of the 10 were pregnant (March 12), two with a single embryo and six with two embryos. Crown-rump lengths of embryos ranged from 7 to 17. None of four females from 5 mi. S Guatemala (March 11 and 13) was pregnant.

Eptesicus gaumeri gaumeri (J. A. Allen, 1897)

Gaumer's Brown Bat

This bat presently is known in Guatemala only from 2 km. E Taxisco, 700 ft., Santa Rosa (Davis, 1965:234), although it probably is widely distributed in lowlands throughout the country. Davis noted that most of the specimens examined by him from throughout the range of *E. g. gaumeri* were from elevations below 1000 feet.

Prior to 1965, this bat was known as *Eptesicus brasiliensis propinquus.* Davis (*op. cit.*) demonstrated that *gaumeri* was a species distinct from *brasiliensis,* and that *Vesperus propinquus* of Peters was a synonym of the Old World *Eptesicus nilssonii.* The specimen on which the description of *propinquus* was based was mistakenly said to have come from "Ysabel de Guatemala."

Lasiurus borealis frantzii (Peters, 1871)

Red Bat

The red bat is known only from Barillas, Huehuetenango (Goodwin, 1934:15), where a specimen was caught in a mouse trap suspended above a pile of raw sugar, and from Dueñas, Sacatepequez (Alston, 1879-1882:22). The subspecific name *frantzii* is applied on the basis of Handley's (1960:469-472) remarks on geographic variation in red bats.

Rhogeessa tumida tumida H. Allen, 1866

Little Yellow Bat

Specimens examined (3).—SANTA ROSA: Astillero, 25 ft., 2; 3 mi. S Astillero, sea level, 1.

Additional records.—EL PETEN: La Libertad (Goodwin, 1958:3). SUCHITEPEQUEZ: Mocá (Goodwin, 1958:3). Precise locality unknown: "Vera Paz" (Alston, 1879-1882:21).

Two of three females from Astillero, obtained on March 1, were pregnant, each with a single embryo on the left side. The embryos measured 7 and 14 in crown-rump length.

Family MOLOSSIDAE

Tadarida brasiliensis intermedia Shamel, 1931

Brazilian Free-tailed Bat

Specimens examined (27).—ALTA VERAPAZ: 9 mi. S Cobán, 4500 ft., 11. CHIMALTENANGO: Chocoyos, 14. HUEHUETENANGO: Jacaltenango, 2 (USNM).

Additional records.—ALTA VERAPAZ: Cobán (Schwartz, 1955:108). CHIMALTENANGO: Chimaltenango (Schwartz, 1955:108). SACATEPEQUEZ: Dueñas (Alston, 1879-1882:34).

Available records from Guatemala suggest that this species may be restricted to the highlands of the central part of the country. Specimens examined from Chocoyos, all males, were shot at dusk on August 4, 1956, as they emerged from holes in a cliff, which they occupied with *Myotis velifer.* Those from 9 mi. S Cobán were netted on the night of March 12-13, 1960, along with *Eptesicus fuscus* and *Desmodus rotundus*, at the entrance to a cave. Four of 11 bats thus taken were females, none of which was pregnant or lactating.

Tadarida laticaudata yucatanica (Miller, 1902)

Brown Free-tailed Bat

Specimens examined (70).—EL PETEN: Flores, 39 (4 AMNH, 35 USNM); La Libertad, 31.

Additional records.—ALTA VERAPAZ: Cobán (Goodwin, 1955:4). EL PETEN: San Andrés (Goodwin, 1955:4); Uaxactún (Murie, 1935:19). SACATEPEQUEZ: Dueñas (Alston, 1879-1882:33).

This bat is known in Guatemala from several localities in the lowlands of the Petén, by a single specimen from Cobán (Goodwin, 1955:4), and by two specimens from Dueñas (Dobson, 1878:437). Colonies frequently inhabit man-made structures. Ryan (1960:10), for example, found 400 in the attic of a public school in Flores, and

I located about 200 in the tower of the Catholic church in La Libertad where the bats roosted between a corrugated tin roof and the two-by-four beams that supported the roof. No gross indication of reproductive activity was evident in six females (March 9) from La Libertad.

Eumops auripendulus milleri (J. A. Allen, 1900)

Shaw's Mastiff Bat

This mastiff bat is known from Guatemala only from Cobán, Alta Verapaz (Alston, 1879-1882:32), and Finca Cipres, Suchitepequez, where a specimen was taken under a loose piece of bark (Goodwin, 1934:16).

Promops centralis Thomas, 1915

Thomas' Mastiff Bat

This species has been thrice reported from Guatemala—from Salamá, Baja Verapaz (Sanborn, 1936:105), where two females were taken, from La Libertad, El Petén, where a single female was found in a hollow tree (Sanborn, 1938:5), and from Dueñas, Sacatepequez, under the name "*Molossus nasutus*" (Dobson, 1878:415, and Alston, 1879-1882:32).

Molossus sinaloae J. A. Allen, 1906

Allen's Mastiff Bat

A male and female from Bobós, 200 ft., Izabal, in the U. S. National Museum are the only specimens known to me from Guatemala. The specimen label attached to the male indicates it was taken in a house.

Molossus ater nigricans Miller, 1902

Black Mastiff Bat

Specimens examined (11).—ALTA VERAPAZ: Chinajá, 550 ft., 5. EL PETEN: Toocog, 15 km. SE La Libertad, 540 ft., 2. JUTIAPA: 6 mi. S Asunción Mita, 1. SANTA ROSA: Astillero, 25 ft., 3.

Additional record.—Precise locality unknown: "Vera Paz" (Alston, 1879-1882:31).

This common molossid seems not to have been reported previously from Guatemala save for mention of a single specimen from "Vera Paz" by Dobson (1878:413) and Alston (*loc. cit.*). Specimens examined from Alta Verapaz and El Petén were netted over a small pond (three of those from Chinajá) or shot as they foraged early in the evening.

None of four February-taken females was pregnant but a female taken at Toocog on March 10 carried a single small embryo. Testes of February-taken males measured 5 to 7.

UNREPORTED SPECIES THAT PROBABLY OCCUR IN GUATEMALA

Fifty-six species of bats are recorded in the foregoing accounts as occurring in Guatemala. In addition to these, at least the 33 species listed below likely will be found there as a result of further collecting, especially in the highlands of the interior and in the Caribbean lowlands.

- Family Emballonuridae
  - *Saccopteryx leptura*
- Family Noctilionidae
  - *Noctilio leporinus*
- Family Phyllostomatidae
  - *Micronycteris sylvestris*
  - *Macrophyllum macrophyllum*
  - *Tonatia sylvicola*
  - *Mimon crenulatum*
  - *Phyllostomus hastatus*
  - *Phylloderma septentrionalis*
  - *Chrotopterus auritus*
  - *Hylonycteris underwoodi*
  - *Carollia castanea*
  - *Sturnira ludovici (sensu lato)*
  - *Vampyressa pusilla*
  - *Chiroderma salvini*
  - *Chiroderma villosum*
  - *Artibeus aztecus*
  - *Artibeus hirsutus*
  - *Enchistenes hartii*
- Family Desmodonitidae
  - *Diaemus youngi*
- Family Thyropteridae
  - *Thyroptera discifera*
  - *Thyroptera tricolor*
- Family Vespertilionidae
  - *Myotis fortidens*
  - *Pipistrellus subflavus*
  - *Lasiurus cinereus*
  - *Lasiurus intermedius*
  - *Lasiurus ega*
  - *Rhogeessa parvula*
- Family Molossidae
  - *Tadarida macrotis*
  - *Eumops underwoodi*
  - *Eumops glaucinus*
  - *Molossops greenhalli*
  - *Molossus bondae*
  - *Molossus aztecus*

PLACE-NAMES

All place-names mentioned in the preceding text are identified with the department in which they are located. One reason for doing this is to avoid possible confusion owing to changes in recent years in some departmental boundaries and the creation of one new department. As a result, some oft-mentioned localities no longer are in the departments in which those localities previously were listed. For example, Mocá and Patulul, formerly in the Departamento de Sololá, are now in Suchitepequez, and El Progreso, formerly in the Departamento de Guatemala, now is the capital of the Departamento de El Progreso. Most of the localities from which bats are listed are well known and can be found on any of several maps of Guatemala. The following maps (in order of probable usefulness) will be of aid in locating place-names: "Mapa Preliminar de la República de Guatemala," 1:750,000, published in 1959 by the Dirección General de Cartografía de Guatemala; "Map of Hispanic America" (sheets ND 15 and 16, NE 15 and 16), 1:1,000,000, published 1935-38 by the American Geographical Society and accompanied by a gazetteer ("Geographical Names in Central America") published in 1943; "Mapa de la República de Guatemala," 1:600,000, compiled by F. P. de Torroella and published in Guatemala in 1948; "Mapa de la República de Guatemala," approximately 1:900,000, published in 1960 by Esso Central America, S. A.

Griscom's (1932:413-425) gazetteer, accompanied by a map showing stations where birds were collected in Guatemala, is especially useful in locating place-names recorded by early collectors that appear infrequently if at all on modern maps. Gazetteers in several papers by L. C. Stuart (see especially 1948, 1951, 1954) also are helpful. The place-names listed immediately below do not appear on at least some modern maps, have been listed in the literature under an alternate spelling or name, or for other reasons might be difficult for future investigators to locate precisely. Latitude (north) and longitude (west) are given for each locality, along with departmental designation. Alternate spellings are in parentheses.

Alpes, Alta Verapaz—15°20′, 89°56′.

Astillero, Santa Rosa—13°21′, 90°21′.

Barillas (Barrillos), Huehuetenango—15°48′, 91°19′.

Bobós, Izabal—15°25′, 88°48′.

Chichivac (Chichavac), Chimaltenango—approximately 14°47′, 91°00′; an Indian name for a station above Tecpán according to Goodwin (1934:15); about 5 km. N Tecpán according to Stuart, 1951:43 and map 2.

Chinajá, Alta Verapaz—16°02′, 90°13′.

Chipoc, Alta Verapaz—15°30′, 89°51′.

Choctum, Alta Verapaz—15°37′, 90°21′ (see Stuart, 1948:map 1).

Chuntuquí (Chantuquí), El Petén—17°31′, 90°09′.

El Gallo (Galla, "Guyo"), El Petén—17°05′, 89°31′.

El Rancho, El Progreso—14°54′, 90°01′.

Escobas, Izabal—15°41′, 88°51′.

Finca Carolina, San Marcos—approximately 14°45′, 91°57′ (see Griscom, 1932:416).

Finca Cipres, Suchitepequez—approximately 14°40′, 91°28′ (see Griscom, 1932:416).

Finca Los Alpes, Alta Verapaz—see Alpes

Finca San Gerónimo, Santa Rosa—approximately 14°05′, 90°23′ (see Ryan, 1960:6).

Hda. California, San Marcos—approximately 14°35′, 92°09′ (see Griscom, 1932:417).

Laguna de Zotz (or Sotz), El Petén—16°57′, 90°08′.

Mongoy (Monogoy), Jutiapa—14°14′, 89°42′.

Navajo (locally Navajoa), Izabal—15°32′, 88°43′.

Puebla, Izabal—15°19′, 89°04′.

Puente Punta Gordo, El Progreso—approximately 14°48′, 90°12′; a bridge at Km. 51 on the highway from Guatemala City to Puerto Barrios.

Quebradas (Quebrados), Izabal—15°23′, 88°46′.

(El) Rosario, Alta Verapaz—15°21′, 89°45′.

San Cristóbal (Frontera), Jutiapa—14°12′, 89°40′.

Santa Clara, Zacapa—not exactly located; placed in Zacapa following de la Torre (1958:169) but, judging from his map, possibly in eastern part of what is now El Progreso.

Sebol (Sebal), Alta Verapaz—15°50′, 89°55′.

Sierra Santa Elena, Chimaltenango—14°51′, 91°02′.

Toocog (also Sojio), El Petén—16°41′, 90°02′.

Verdenango, Sololá—not exactly located; on Lago de Atitlán near Panajachel.

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CONTENTS

INTRODUCTION

When C. Hart Merriam wrote his monograph of the subfamily Geomyinae in 1895, he had no opportunity to examine fossil specimens. No doubt his phylogenetic conclusions and classification would have been greatly influenced had he enjoyed that opportunity because study of fossil geomyids reveals the historic sequence of phyletic development, and this sequence provides a firm basis for distinguishing specialized from primitive characters. The history of the Geomyinae has been characterized by the evolution of specializations. These evolutionary trends begin, as we presently know them, with a generalized ancestral stock in the early Miocene. The direction, degree, and rate of change, beginning with the primitive morphotype of the subfamily, has not been the same in the various lineages. The classification within the subfamily is based upon the phyletic interpretations of available data and the relationships they disclose. In turn, a new, and I hope more realistic, phylogeny and classification is offered.

MATERIALS AND ACKNOWLEDGMENTS

Recent specimens were studied of all the known genera, subgenera and 29 of the 36 living species. Most of the species not studied are monotypic and have restricted geographic ranges. They are: *Geomys colonus, G. fontanellus,* and *G. cumberlandicus, Orthogeomys cuniculus* and *O. pygacanthus* of the subgenus *Orthogeomys,* and *O. dariensis* and *O. matagalpae* of the subgenus *Macrogeomys.* Examination of these modern species would not radically change the estimation of the degree of phyletic development of the genera and subgenera involved. All of the major polytypic and widespread species were studied.

Specimens of the extinct genera *Dikkomys, Pliosacccomys, Pliogeomys, Nerterogeomys,* and *Parageomys* also were studied, as were examples of the extinct species *Geomys quinni, Geomys tobinensis,* and *Orthogeomys onerosus.* Considerable fossil material of living species, especially of the genera *Geomys* and *Pappogeomys,* was used.

Inasmuch as the present account concerns mainly structural changes in the subfamily Geomyinae at the level of subgenera and above, and the temporal sequence of those changes, no attempt is made in the present account to revise taxonomy below the level of subgenera. Considerable modification of the classification below that level (for species and subspecies) is to be expected in *Orthogeomys* and Pleistocene taxa of *Geomys* when available specimens are studied.

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TAXONOMIC CHARACTERS

Morphological features of the fossils and their stratigraphic provenience provide the information upon which phylogenetic interpretations are based. Although the most critical sequences of the fossil record are lacking, and although the existing fossils are mostly fragmentary and therefore seldom furnish ideally suitable data for the interpretations that have been made, phylogenetic conclusions drawn from fossil materials are superior to those drawn on other bases. The especially relevant characters are those disclosing primary trends in the evolution of the modern assemblages. The higher systematic categories recognized in the following account are based primarily upon such characters.

The most important characters found are in the teeth, although several structural changes in the lower jaw, especially those associated with the insertion of cranial musculature, are almost as important.

Prismatic Character of Molars

In primitive geomyines the molar consisted of two columns united at their mid-points and forming a figure 8 or H-pattern (see Fig. 4B). Both labial and lingual re-entrant folds were formed between the two columns. The primitive pattern is retained in the premolars of all known Geomyinae. Therefore, in the earliest (Miocene) members of the subfamily, the pattern of the molars was essentially like that of the premolars.

In Pliocene Geomyinae the two columns of the molars tend to merge into one. This is evident on the worn occlusal surface of the teeth; the lateral re-entrant folds are shallow vertically and progressively recede laterally until only a slight inflection remains. In the final stages of attrition, the inflection disappears and the tooth is a simple elliptical column. In the Pleistocene the monoprismatic pattern appears at earlier stages of wear owing to the decrease in depth of the re-entrant folds, and in Geomyinae of Recent time the initial stages of wear on the enamel cap of infants erase the last vestiges of two columns in the molar teeth.

The general trend in evolution, therefore, has been from a bicolumnar to a monocolumnar pattern. The particular patterns of wear characterizing each genus are described in detail beyond.

The third upper molar has evolved less rapidly than the first and second and in one of the modern lineages (tribe Geomyini) tends to retain at least a vestige of the primitive bicolumnar pattern in the final stage of wear. Therefore, the loss of any trace of the bicolumnar pattern in M3 is considered to be a much specialized condition. Unfortunately, the fossil record of the third upper molar is less complete than that for the first molar and second molar; the tooth drops out of its alveolus more often than does any one of the other molariform teeth and is seldom recovered.

Character of Enamel Patterns

In the primitive genera the enamel pattern is bilophate and the enamel loop (see Fig. 4B) is continuous on the occlusal surface of a worn molar. Concomitant with the union of the double columns, the bilophodont pattern is reduced to a single loph, but the enamel still completely encircles the dentine.

In the molars of modern geomyines, the enamel loop is not continuous but is interrupted on the sides of the crown by vertical tracts of dentine that are exposed at the occlusal surface of the tooth during early stages of wear. Therefore, a continuous enamel band is to be found only in a juvenal individual whose teeth have been subjected to only slight attrition on the enamel cap. In molars lacking enamel on the labial and lingual sides, anterior and posterior enamel plates, or blades, are found on each molar. The premolar also has an enamel plate on the anterior surface and another on the posterior surface, and in addition both re-entrant angles are protected by a V-shaped investment of enamel. One or the other of the various plates can be reduced or lost accounting for the several distinctive tooth-patterns of the modern geomyines. If loss occurs, it usually is the anterior plate in the lower dentition and the posterior plate in the upper dentition, including the upper premolar. When reduction of the posterior plate of the upper cheek teeth occurs, enamel is first lost from the labial side of the tooth, thus leaving only a short vestigial plate on the lingual end of the crown.

Grooving of Incisors

The incisors are smooth with no trace of a groove in the ancestral lineage. In the specialized assemblage (tribe Geomyini) pronounced grooves are always developed on the anterior face of the upper incisor. The pattern of grooving is constant in each species and thus provides characters of taxonomic worth for grouping species into genera. The only inconstancy noted was an incisor of *Geomys* from the Tobin local fauna of the middle Pleistocene which has three grooves rather than the normal two (No. 6718 KU). The extra groove is an obvious abnormality, and the tooth was associated with others of the same species from the same quarry that were normally grooved.

Grooves on the lower incisors are unknown. The functional significance of grooving has been debated on numerous occasions in the literature. Grooves appear in a number of only distantly related rodents and in lagomorphs. The grooving occurs always in small herbivorous mammals, and in some way may be related to feeding habits.

The grooves provide a serrated cutting edge on the occlusal edge of the upper incisor. In the genus *Geomys,* for example, the two incisors, including the slight space between them, present a total of five serrations, which may facilitate cutting and piercing tuberous and fibrous roots upon which *Geomys* feeds. Also the sulci would perform the same function as the longitudinal groove on the side of a bayonet, and would aid the animal in extracting its upper incisors from coarse, fibrous material. In gathering food, the gopher sinks its upper incisors into a root, and then, with the upper incisors firmly anchored, slices off small chunks by means of the lower incisors. Therefore, in pocket gophers, grooving may be an adaptation for feeding on fibrous or woody material. Finally, grooves increase the enamel surface of the incisor without additional broadening of the tooth itself. There could be a selective advantage for sulcation if the extra enamel and the serrate pattern strengthen the incisors, which are under heavy stress while penetrating or prying off pieces of coarse material. Few broken incisors of pocket gophers are found.

Masseteric Ridge and Fossa

This ridge and fossa are on the lateral surface of the ramus. The crest on the ridge begins at the base of the angular process and terminates slightly anterior to the plane of the lower premolar. The masseteric fossa receives the insertion of the rostral or superficial division of the masseter muscle. The mental foramen lies immediately anterior, or anteroventral, to the fossa.

In the ancestral lineage, the ridge is distinct but relatively low; the masseteric fossa is shallow and is a poorly developed area for attachment of the superficial masseter muscle. In modern Geomyinae the ridge is massive and forms a high crest, especially anteriorly, and the masseteric fossa is a deep, prominent cup along the dorsal side of the crest. The elaboration of the crest and fossa evidently is associated with an increase in size of the superficial masseter muscle, which enlarges and provides increased power for the propalinal type of mastication. A high crest has evolved independently in both modern lineages, Thomomyini and Geomyini.

Basitemporal Fossa

The name basitemporal fossa is suggested here to denote the deep pit that lies between the lingual base of the coronoid process and the third lower molar. The basitemporal fossa receives the insertion of the temporal muscle. The fossa, which until now has not been named, is a unique feature in advanced Geomyinae, being unknown in either primitive Geomyinae or in other rodents.

The temporal is one of several muscles holding the occlusal surface of the lower molariform dentition firmly against the upper cheek teeth during mastication. In primitive geomyines that masticate food by a planing action, the temporal muscle also moves the mandible posteriorly and food is ground between the enamel plates when the lower jaw is retracted as well as when it is moved forward.

The basitemporal fossa appears in late Pliocene geomyines and increases the attachment surface of the temporal muscles that powers the planing action important in utilizing woody and fibrous foods. The basitemporal fossa developed in only one of the modern lineages (tribe Geomyini), the same lineage in which grooved incisors evolved. Both features probably are adaptations for feeding on coarse food. The fossa is not greatly developed in either the ancestral tribe Dikkomyini or the modern tribe Thomomyini, although in some specimens a slight depression marks the site of the basitemporal fossa.

Specializations of Skull

The skull in most geomyines is generalized, being neither extremely long and narrow nor short, broad and flat as in specialized skulls (see Fig. 1). In Pleistocene lineages of the modern tribe

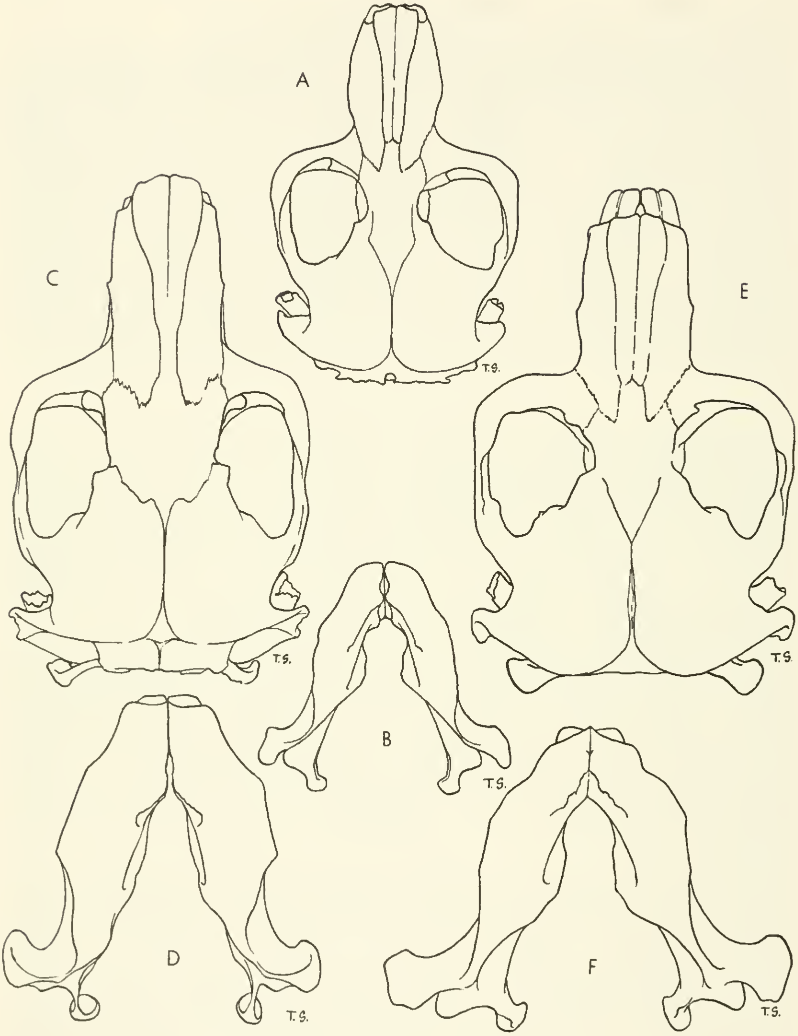


FIG. 1. Types of skulls in the subfamily Geomyinae. × 1.

A. and B. Generalized type of skull. *Geomys bursarius lutescens,* adult, male, No. 77955 KU, 10 mi. N Springview, Keya Paha Co., Nebraska.
 A. Dorsal view of skull.
 B. Ventral view of lower jaw.

C. and D. Dolichocephalic type of skull. *Orthogeomys (Orthogeomys) grandis guerrerensis,* adult, female, No. 39807 KU, ½ mi. E La Mira, 300 ft., Michoacán, México.
 C. Dorsal view of skull.
 D. Ventral view of lower jaw.

E. and F. Platycephalic type of skull. *Pappogeomys (Cratogeomys) gymnurus tellus,* adult, female, No. 33454 KU, 3 mi. W Tala, 4300 ft., Jalisco, México.
 E. Dorsal view of skull.
 F. Ventral view of lower jaw.

Geomyini, long skulls and broad skulls evolved and have been termed dolichocephalic and platycephalic specializations, respectively by Merriam (1895:88-101). He correlated them with two diametrically different mechanical methods of mastication.

In animals with dolichocephalic skulls the principal movements of the mandible in the masticatory process are anteroposterior. The resulting propalinal action of enamel plates in opposition to each other characterizes also animals with a generalized skull, and evidently is the method of mastication in the primitive geomyines, but in animals with a dolichocephalic skull the method is developed to a high degree by elongation of the cranium, mandible, and teeth. Both the mandibular and maxillary tooth-rows are relatively longer than in the generalized skull, providing a longer block for the planing action of the lower molariform teeth. All teeth, especially P4 and M3, are longer. In M3 the heel (posterior loph) in particular is elongated. Both the anterior and posterior enamel plates usually are retained in M1 and M2.

The superficial (or rostral) masseter muscle, originates on the side of the rostrum and inserts in the masseteric fossa and on the masseteric ridge. The deep masseter, especially the zygomatic part having its origin along the zygomatic arch, inserts on the angular process of the lower jaw. These two divisions of the masseter muscle have a longer pull (forward) in the dolichocephalic skull than in a non-dolichocephalic skull. The temporal and diagastric muscles retract the lower jaws.

Other, secondary, modifications of the dolichocephalic skull are shortening of the angular process of the mandible, broadening of the rostrum, and narrowing of the cranium and zygomata. Depth of the posterior part of the skull is unchanged. The skull appears to be deep and of nearly equal breadth from nasals to occiput. A good example of a dolichocephalic skull is that of *Orthogeomys* (see Fig. 1, C and D).

In the platycephalic skull, the principal masticatory movement of the mandible is antero-oblique, to one side and then to the other. The oblique passage of the enamel blades of the lower teeth across those of the upper teeth produces a shearing rather than planing action (Fig. 1E, F). The antero-oblique movement of the lower jaw is possible because of major architectural changes in the cranium and mandible. These changes include: (1) Broadening of the post-rostral part of the skull, especially the occiput (mastoidal breadth equals or exceeds zygomatic breadth in skulls of some taxa); (2) flattening of the skull; (3) anteroposterior compression of the molariform teeth, especially the molars. Therefore, the entire maxillary tooth-row is relatively shorter than in the dolichocephalic skull. Only a vestige of the heel ordinarily remains on M3. The loss of the posterior enamel blades of P4, M1, and M2 eliminates unnecessary friction, and each of these teeth is wider than long. The distance between the posterior ends of the lower jaws is increased approximately in proportion to the extent that the occiput is widened. As a result of the flattening of the skull the angular processes of the lower jaws are lateral to the zygomatic arches, and approximately on the same vertical level with them. Consequently the insertions of masticatory muscles are shifted laterally. This is especially true of the zygomatic division of the deep masseter, which inserts on the angular process. Contraction of that muscle division of one side of the skull moves the lower jaws obliquely forward. The diagastric and temporal muscles of course retract the lower jaws.

The platycephalic skull is the most specialized skull in the Geomyinae and is a result of the new (for the Geomyinae) method of mastication. The subgenus *Cratogeomys* (see Fig. 1, E and F) has a platycephalic skull. The trend toward platycephalic specialization has been the major feature of evolution in *Cratogeomys*.

FOSSIL RECORD

The fossil record of the subfamily Geomyinae begins in the early Miocene of western North America. No geomyids have been recovered from beds of the late Miocene age. Beginning with the early Pliocene the fossil record becomes progressively more complete, and geomyines are relatively abundant in deposits of late Pliocene and Pleistocene age. Although pocket gophers of the subfamily Geomyinae are rare in lower Miocene deposits, members of the subfamily Entoptychinae are relatively common and highly diversified. Four genera and a number of species have been described (see Wood, 1936:4-25), and the subfamily ranged widely in western North America. I interpret this to mean that the geomyines were indeed uncommon in the early Miocene and their distribution restricted since so few of their remains have been recovered in comparison with entoptychines and the known records are only from the northern part of the Great Plains. On the other hand, entoptychines enjoyed a widespread distribution in western North America (see discussion beyond). Probably the geographic range of the geomyines was largely allopatric to that of the more specialized entoptychines. The zone of fossoral adaptation for herbivorous rodents is ecologically narrow, and as a result competition is severe. As a rule, the outcome of episodes of intergroup competition is geographic exclusion. If these rodents were fossorial in the early Miocene—their morphology suggests they were at least semi-fossorial—mutually exclusive patterns of distribution are to be expected.

Miocene

Dikkomys is the only genus of the Geomyinae known from the early and middle Miocene. *Dikkomys matthewi* was described by Wood (1936) on the basis of isolated teeth from lower Harrison deposits (Arikareean in age) near Agate, Sioux County, Nebraska. Later, Galbreath (1948:316-317) described the features of an almost complete mandible recovered from the younger upper Rosebud deposits, now considered by MacDonald (1963:149-150) to be middle Miocene, near Wounded Knee, Shannon County, South Dakota. More recently Black (1961:13) has described a new species, *Dikkomys woodi*, from the Deep River Formation, Meagher County, Montana. The Deep River Formation is late Hemingfordian (middle Miocene) in age. No remains of *Dikkomys* have been identified in the extensive rodent fauna of the John Day beds of the lower Miocene of Oregon, although entoptychines are abundant in these deposits.

In the present account, *Dikkomys* is regarded as the ancestor from which the Pliocene and modern geomyines were derived. These probably did not evolve from the subfamily Entoptychinae because the dentition of entoptychines, especially the premolars and third molars, was already highly specialized by Miocene time.

The numerous records of *Thomomys* and especially *Geomys* reported from supposed Miocene or Pliocene deposits are without foundation (see Matthew, 1899:66; 1909:114, 116, 119; 1910:67, 72; 1923a:369; 1924:66; Matthew and Cook, 1909:382; Cook and Cook, 1933:49; and Simpson, 1945:80). Most of the records of *Geomys* date back to the description of *Geomys bisculcatus* Marsh (1871:121) from the Loup Fork beds of Nebraska (near Camp Thomas on the Middle Loup River). At first Marsh and other investigators thought these beds were of the late Miocene age. Subsequently the Loup Fork fauna was determined by Matthew (1923b) to be mostly early Pliocene (Clarendonian), but with a later Pleistocene element. Recently, Schultz and Stout (1948:560) have shown that the various Loup River faunas and also those from along the Niobrara River (Hay Springs, Rushville, Gordon local faunas) are of middle Pleistocene age, the fossil-bearing beds occurring just below the Pearlette Ash. These beds are those termed the Loup Fork or North Prong of Middle Loup by the earlier workers who supposed them to be of Miocene or Pliocene age. Both *Geomys* and *Thomomys* have been recovered from most of these deposits, but they are no older than middle Pleistocene. This is not surprising in view of the primitive structure of the geomyids known from Miocene and Pliocene beds, but the supposed early appearance of *Geomys* and *Thomomys* led to much confusion concerning geomyid evolution in the late Tertiary.

The dearth of geomyines in the Miocene is counterbalanced by the relatively abundant and highly differentiated gophers of the subfamily Entoptychinae. They reached the zenith of their development in this period. Four genera and a number of species are known from the western part of the United States, mostly from beds along the Pacific Coast and in the northern part of the Great Plains. The great diversification of the group in a relatively short period suggests prior movement into a new adaptive zone and subsequent specialization in different subzones and therefore an episode of radial adaptation. The radiation of the entoptychines is discussed elsewhere in the account of geomyid phylogeny, but it should be noted here that both the Geomyinae and the Entoptychinae appear in the fossil record at about the same time in the early Miocene. The principal distinguishing features of each of the two lineages were well developed at the time of their first occurrence, and the entoptychines were the more successful in early Miocene. The Entoptychinae are known only from the early and middle Miocene, unless the earlier deposits of the John Day Formation of Oregon from which mammals have been recovered are considered to be latest Whitneyan (latest Oligocene); for correlations, see Wilson (1949:75). Both lineages likely had an earlier history extending back to their divergence in the Oligocene.

Pliocene

The oldest and most primitive Pliocene geomyine is *Pliosaccomys dubius* Wilson (1936:20) from the Smith Valley local fauna of middle Pliocene (Hemphillian) age in Nevada. According to Wilson (*op. cit.*:15) the beds probably were deposited near the middle of Hemphillian time. Shotwell (1956:730) recorded *Pliosaccomys dubius* from the McKay Reservoir and from the Otis Basin (1963:73) local faunas of the middle Pliocene (Hemphillian) of Oregon, and Green (1956:155) has recovered remains of *Pliosaccomys* (cf. *dubius*) from the Wolf Creek local fauna, uppermost part of the lower Pliocene (late Claredonian in age), of Shannon County, South Dakota. Recently, James (1963:101) has described a second species, *Pliosaccomys wilsoni*, of this primitive genus. The new species was found in early Pliocene deposits (late Clarendonian) from the Nettle Spring local fauna (Apache Canyon), in the Cuyama Valley, Ventura County, California. *Pliosaccomys wilsoni* does not differ greatly from P. *dubius;* however, the few differences in dental characters seem to warrant specific recognition. The reduction of cusps on the metalophid of p4 from three (*dubius*) to two (*wilsoni*) and the lack of accessory cuspules on the protolophid of p4 in *wilsoni* are probably specializations, suggesting that *P. dubius* even though the more recent in age is the less advanced of the two. *P. wilsoni* is known only from a lower jaw of a young individual that had dp4 in place, along with m1 and m2. The permanent premolar was in the process of erupting, and the deciduous tooth was removed so that the unworn surface of p4 could be examined.

Pliosaccomys occurred geographically in the area that the Entoptychinae had occupied in the early Miocene. The Smith Valley material includes dentitions in almost all stages of wear and the chronological sequences in the development of the patterns of wear can be reconstructed. An understanding of the dental patterns of the primitive geomyines is based mostly on the interpretation of the stages of wear in *Pliosaccomys.*

No other pocket gopher is known from the area in which *Pliosaccomys* occurred, and it is unknown after middle Hemphillian age. *Pliosaccomys* has closer affinities with *Dikkomys* of the early Miocene than with any geomyid of the modern assemblage and gives no clue to the origin of the lineage culminating in the modern pocket gophers of the tribe Geomyini.

Pliogeomys buisi Hibbard (1954:353) was found in the Buis Ranch local fauna, of latest middle Pliocene, on the west side of Buckshot Arroyo, Beaver County, Oklahoma. The original material included a right ramus bearing the premolar and first two molars (the holotype) and five isolated premolars and molars. One of the molars is slightly worn and from an immature individual. One premolar is a deciduous tooth. Hibbard (*op. cit.*:342) identified the beds from which he obtained the Buis Ranch local fauna as from the lowermost part of the Upper Pliocene. Moreover, he judged the Buis Ranch local fauna to be only slightly older than the Saw Rock Canyon local fauna of Seward County in southwestern Kansas. Previously (Hibbard, 1953:408-410), the Saw Rock Canyon local fauna had been assessed as older than the Rexroad local faunas (latest late Pliocene) and, therefore, representative of the early part of the late Pliocene. More recently, Hibbard (1956:164) identified the Buis Ranch beds as part of the Ogallala Formation, which here occurs unconformably just beneath the Rexroad Formation (composed of strata nearly all of late Pliocene age). Therefore, he regarded the Buis Ranch beds as latest middle Pliocene in age.

Hibbard (1954:356) suggested that pocket gopher remains from the Saw Rock Canyon local fauna were referable to *Pliogeomys buisi,* and, in effect, tentatively assigned them to *Pliogeomys* (in his description of the genus Hibbard remarked that the upper incisor is bisulcate as in *Geomys,* and the only upper incisor that he mentions was one of the Saw Rock Canyon fossils and not part of the Buis Ranch material). *Pliogeomys* has closer affinities with modern pocket gophers of the tribe Geomyini than it does with the middle Pliocene genus *Pliosaccomys.*

The pocket gopher fauna known from the late Pliocene was more varied than the faunas known from any earlier time. In addition to the extinct *Pliogeomys,* which occurs in early late Pliocene (see discussion above), the living genera *Zygogeomys, Geomys, Pappogeomys* (in the sense used on p. 534), and *Thomomys* first appear in the late Pliocene. The only other living genus, *Orthogeomys,* makes its first appearance in the late Pleistocene.

The earliest record of the genus *Thomomys* is based on a fragment of a left mandibular ramus bearing p4 and m1, *Thomomys gidleyi* Wilson (1933b:122), from the Hagerman local fauna of Twin Falls County, Idaho. Wilson (*loc. cit.*) was uncertain as to age (late Pliocene or early Pleistocene) but subsequently (1937:38 and 67-70) settled on the middle part of the late Pliocene. Hibbard (1958:11) later considered the age as early Pleistocene (suggesting that the deposits accumulated in the Aftonian interglacial interval) but subsequently (Hibbard *et al.*, 1965:512), on the basis of potassium argon age determinations, also settled on late Pliocene.

Remains of *Nerterogeomys [=Zygogeomys]* have been found in the Benson local fauna, Cochise County, Arizona, and the Rexroad local fauna of Kansas. This early Blancan gopher first was described as *Geomys minor* by Gidley (1922:123), and was later referred by Gazin (1942:487) to his new genus *Nerterogeomys.* Hibbard (1950:138) identified specimens from the Fox Canyon locality, one of the localities of Meade County, Kansas, where the Rexroad local fauna is preserved, as *Nerterogeomys,* and tentatively referred them to the species *N. minor. Neterogeomys* cf. *minor* has been recovered also from Locality 3 of the Rexroad local fauna (Hibbard, 1950:171) of Meade County, Kansas. Apparently these are also the small gophers about which Franzen (1947:58) wrote. She assigned them to the genus *Geomys,* and they may actually be a primitive form of *Geomys* that represents an intermediate stage in the development of the enamel pattern from the uninterrupted loops of the ancestor to the discontinuous pattern of modern *Geomys.* I favor this interpretation; the evidence, however, is inconclusive, and I have, therefore, reluctantly allocated them, along with the other specimens of *Nerterogeomys,* to the genus *Zygogeomys.* In an early paper, Hibbard (1938:244) erroneously referred the same specimens, two upper premolars of a young individual, to the genus *Thomomys,* and the same material was identified with the genus *Geomys,* also without specific assignment, in a later paper (Hibbard, 1941b:278). *Thomomys* is unknown from the late Pliocene of the Great Plains. The specimens previously referred to *Nerterogeomys* are assigned to the genus *Zygogeomys* for the first time in this report; for a discussion of the systematic arrangement see the accounts beyond. The type and paratype of *Nerterogeomys* from the Benson local fauna of Arizona have no indication of enamel reduction.

Specimens of the genus *Geomys* from the late Pliocene were referred to the large *Geomys quinni* McGrew, first by Franzen (1947:55) and later by Hibbard and Riggs (1949:835) and Hibbard (1950:171). *Geomys quinni* has been obtained from the Fox Canyon locality and Locality 3 of the Rexroad local fauna. At Locality 3, both *Zygogeomys* (cf. *minor*) and *Geomys quinni* have been found together, but *Geomys quinni* can be distinguished by its much larger size and the advanced enamel pattern of the cheek-teeth (see systematic accounts beyond). All age classes are represented among the specimens of *Geomys quinni;* therefore, it seems unlikely that the smaller gophers referred to *Zygogeomys* are actually the young of *Geomys quinni.* Hibbard (personal communication, May, 1966) informed me that specimens of *Geomys* from the late Pliocene (Fox Canyon and Rexroad Locality 3) are erroneously referred to *G. quinni.* According to Hibbard, this material represents instead two distinct undescribed species, descriptions of which have been submitted by him for publication. Allocation of late Pliocene specimens of *Geomys quinni* to other species will restrict *quinni* to the early Pleistocene.

Cratogeomys bensoni Gidley (1922:123) was of medium size. The name was based on an upper incisor bearing a single median sulcus and an associated lower jaw containing all of the cheek-teeth from the Benson local fauna, Cochise County, Arizona. Additional lower jaws carrying various teeth also were recovered. The specimens might just as well have been assigned to the genus *Pappogeomys* since the lower dentitions of all the genera of the tribe Geomyini have the same enamel pattern, and the subgenera *Pappo-*

geomys and *Cratogeomys* have upper incisors with median grooves. The specimens are too fragmentary to warrant more than generic identification. Mainly because of their late Pliocene age and primitive traits the specimens are here regarded as early representatives of the subgenus *Papopgeomys.* Discovery of the upper molariform dentition would make a more precise assignment possible.

Pleistocene

Numerous specimens of geomyids from many localities and horizons are available from the Pleistocene of North America. Specimens of the genera *Geomys* and *Thomomys* are especially common. Few specimens are known of the genera *Orthogeomys* and *Pappogeomys,* especially from the early and middle Pleistocene, owing, probably, to slight knowledge of the early Pleistocene of México were these two genera are thought to have evolved (see map, Figure 2). This lack of knowledge about early Pleistocene deposits in México is a handicap in the present instance since the center of differentiation for several of the modern genera is judged to have been in México, probably on, and at the edge of, the Central Plateau. The relative abundance of the remains of *Geomys* and *Thomomys* from Pleistocene deposits farther north, and the marked absence of other genera, may mean that *Orthogeomys* and *Pappogeomys* did not range northward from southern and central México in most of the Pleistocene. One species of *Pappogeomys* eventually ranged into the southwestern United States in the late Pleistocene (toward the end of the Wisconsin) and it occurs there today, but the genus is essentially Mexican.

The fossil record of *Zygogeomys,* as the genus is here understood, evidently continued in the United States will into the Middle Pleistocene, depending upon the stratigraphic interpretation of the age of the Curtis Ranch local fauna from southeastern Arizona. Hibbard (1958:25) regarded the Curtis Ranch local fauna as Irvingtonian in age, a local fauna that lived either in the late Kansan glacial or the Yarmouthian interglacial, and his correlation is tentatively followed here. In deposits laid down later than those of Irvingtonian age no remains of *Zygogeomys* have been found. Today a single species exists as a relic in the mountains of central México and *Zygogeomys* may have retreated southward to its present refugium in the late Pleistocene. Perhaps, *Zygogeomys* occurred in northern México and the southwestern United States in the early and middle Pleistocene (see Fig. 2), occupying the area between the ranges of *Pappogeomys* to the south and *Geomys* to the

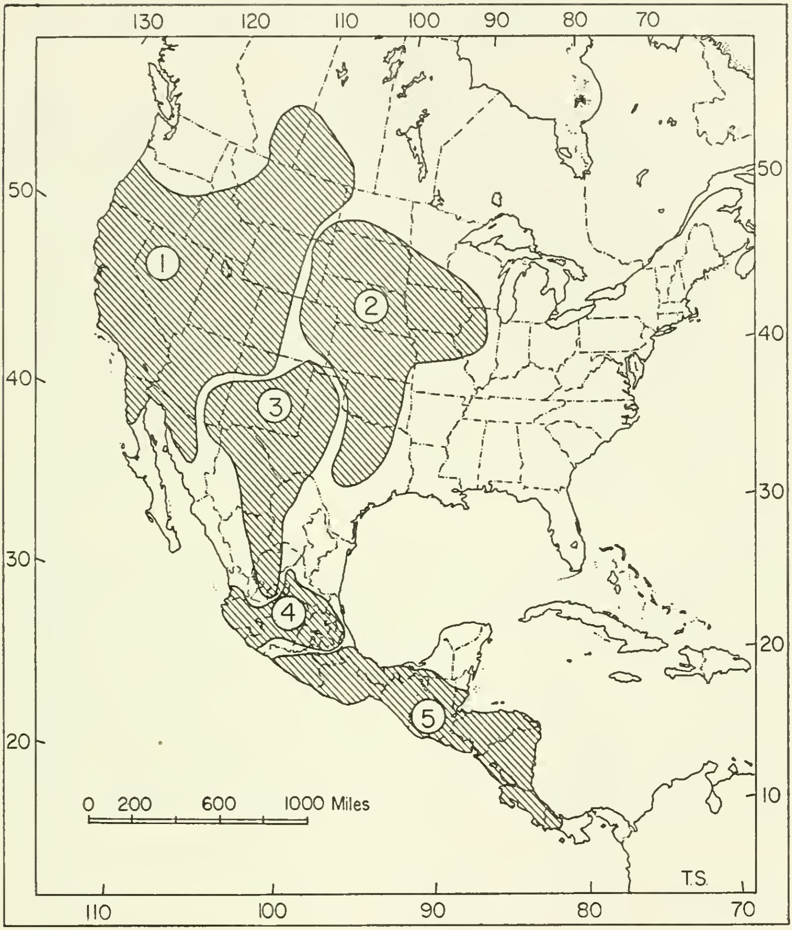


FIG. 2. Probable distribution of the Subfamily Geomyinae in the early Pleistocene (late Blancan), depicting major areas of differentiation of the modern genera.

1. *Thomomys*
2. *Geomys*
3. *Zygogeomys*
4. *Pappogeomys*
5. *Orthogeomys*

north. Competition with *Pappogeomys*, and especially *Geomys*, during Irvingtonian time may have extirpated *Zygogeomys* over most of this area, and by late Pleistocene (Sangamon) much of the former range of *Zygogeomys* came to be occupied by one or the other of its competitors. The occurrence of *Geomys garbanii* in southern California (see White and Downs, 1961) and the unidentified species of *Geomys* in Aguascalientes (Mooser, 1959; for faunal correlation, see Hibbard and Mooser, 1963), both from deposits of Irvingtonian age, supports this suggestion.

Thomomys

The earliest Pleistocene records of *Thomomys* are mostly isolated teeth. Although they can be identified as genus *Thomomys*, most of the materials are too fragmentary to be identified to species. In *Thomomys* two distinct patterns of occlusal surfaces of the molars can be recognized: the generalized elliptical pattern in the subgenus *Pleisothomomys*, not unlike the pattern in other geomyids, and the pear-shaped pattern in the subgenus *Thomomys*, which results from constriction of the upper molars on the labial side and constriction of the lower molars on the lingual side. Some fossils assigned to *Thomomys* were not examined with this distinction in mind by the persons who made the assignments. Consequently some of the identifications now in the literature may be subject to change.

Three occurrences of *Thomomys* are from the early and middle Pleistocene, with a possible fourth (depending upon the age of the Hay Springs local fauna of Nebraska). The earliest Pleistocene record is from the Broadwater-Lisco beds along the North Platte River in Morrill County, western Nebraska. Possibly the specimen from there was misidentified. Those beds are Lower Pleistocene, and are regarded by Schultz and Stout (1948:560-561, 573) and by Hibbard (1958:11), as having been deposited mostly during the Aftonian interglacial. There is also some indication that some of the strata were deposited late in the Nebraskan glaciation. There are no other early Pleistocene records of *Thomomys*. Savage (1951: 228) reported the genus from the Irvington local fauna, Alameda County, California. The specimens were not identified to species, although they were described as indistinguishable from *Thomomys bottae*. Paulson (1961:137) recorded specimens from the Cudahy local fauna, Meade County, Kansas. These fragmentary specimens are referable to the subgenus *Thomomys*, owing to the strong constriction of the molars, but have not been identified to species. The Cudahy is an Irvingtonian local fauna, and is considered to have been deposited during the late Kansan glaciation. The stratum containing the Cudahy local fauna immediately underlies the Pearlette Ash. The Cudahy material includes five isolated molars and a fragmentary ramus bearing only the premolar. The genus *Thomomys* has been recovered also from the Hay Springs local fauna in Sheridan County, northwestern Nebraska, by Shultz and Tanner (1957:71). The Hay Springs local fauna is considered to have been deposited in late Kansan glaciation or in early Yarmouth interglacial by Shultz and Tanner (*op. cit.*:69), or of Irvingtonian age; however, Hibbard (1958:25) regarded the beds containing this fauna as Illinoian (thus post-Irvingtonian in age), and equivalent in age to the Berends local fauna of Oklahoma and the Butler Springs and Mt. Scott local faunas of Kansas. The *Thomomys* from Hay Springs local fauna has not been referred to species.

The relative abundance of *Geomys*, and rarity of *Thomomys*, in Great Plains fossil beds of early and middle Pleistocene is probably due to allopatric distributions of the two genera. The Great Plains area was evidently the center of distribution and differentiation of *Geomys*. Perhaps *Thomomys* evolved earlier to the west, in the Great Basin and Pacific Coastal regions, and not on the Great Plains.

Upper Pleistocene records of *Thomomys* are more common. The genus was widespread in beds identified with the Illinoian and Sangamon and extended its range eastward to the Atlantic Coast. Stephens (1960:1961) reported *Thomomys* from the Doby Springs local fauna, Harper County, northwestern Oklahoma. The material (34 isolated teeth) was too fragmentary to permit assignment to species. The molars are constricted on one side, indicative of the subgenus *Thomomys*, like the Cudahy specimens reported by Paulson (see discussion above). Stephens erroneously mentioned that the enamel plate on the posterior face of the upper premolar is unique in *Thomomys;* this plate occurs also in *Zygogeomys.* The Doby Springs local fauna was recovered from beds that have been identified as Illinoian deposits, and it is correlated with the Berends local fauna in Beaver County, Oklahoma, and the Butler Springs local fauna in Meade County, Kansas (see Stephens, *op. cit.*:1700).

Local faunas in Maryland and Florida of Rancholabrean age include *Thomomys*, in every instance referable to the subgenus *Pleisothomomys* on the basis of unconstricted molars. *Thomomys potomacensis* (Gidley and Gazin, 1933), from Cumberland Cave local fauna, Allegany County in western Maryland, is the type of the genus *Pleisothomomys* Gidley and Gazin (1933:354). *Pleisothomomys* is here regarded as a subgenus. The material used in the original description included four lower jaws, one with a complete dentition. Hibbard (1958:25) pointed out that the Cumberland Cave assemblage is a composite fauna including both glacial and interglacial forms. He placed the stratigraphic position of the fauna as definitely Upper Pleistocene, probably deposited in both Illinoian glaciation and during the Sangamon interglacial. *T. potomacensis* is significantly larger than *T. orientalis* Simpson (1928:6), from the Saber-tooth Cave local fauna, Citrus County, Florida. Simpson's material included a rostral fragment with an incisor, premolar, and first molar. The Saber-tooth Cave local fauna is regarded by Kurten (1965:219) as having been recovered from Sangamon deposits. *Thomomys* is unknown from Wisconsin deposits in the eastern United States, and today the genus does not occur east of the Great Plains.

Thomomys of Rancholabrean provincial age from the western United States and México is known only from Wisconsin beds.

Three extinct species of *Thomomys*, all referable to the subgenus *Thomomys*, have been described. *Thomomys microdon* Sinclair (1905:146), based on the rostral portion of a skull without a mandible, is from the Potter Creek Cave local fauna, Shasta County, California, and has been recovered also from Samwel Cave, Shasta County, California. *T. microdon* closely resembles *Thomomys monticola* that lives in he area today. *Thomomys scudderi* Hay (1921:614) is from the Fossil Lake (or Christmas Lake) local fauna in central Oregon. Elftman (1931:10-11) referred these specimens to *Thomomys townsendii*, and he considered *T. scudderi* to be a synonym of *T. townsendii*. Davis (1937:156-158) disagreed with Elftman concerning the taxonomic status of *T. scudderi*, which he regarded as a valid species. According to Davis, *T. scudderi* is more closely allied to *Thomomys bottae* than to *T. townsendii*. Cope (1878:389; 1889:160-165) had referred the same specimens to *Thomomys clusius* (now *Thomomys talpoides clusius*). Cope considered the beds to be Pliocene in age. In all accounts of the Fossil Lake local fauna up to Hay (1921), the specimens of *Thomomys* were referred to the species *clusius*, *talpoides*, or *bulbivorus* (see Elftman, *loc. cit.*). The Fossil Lake local fauna is currently considered as being of Rancholabrean provincial age, probably dating from the Wisconsin glacial maximum when the lake reached its greatest size. The third extinct species described from the Wisconsin is *Thomomys vetus* Davis (1937:156), also from the Fossil Lake local fauna in Lake County, Oregon. Davis pointed out that *T. vetus* differs from *T. scudderi* Hay, of the same fauna, in larger size and other cranial details, and that it is closely allied to the living species *Thomomys townsendii*, and not to *Thomomys talpoides*, which is the only species of *Thomomys* living in the area today.

Thomomys townsendii was recovered by Gazin (1935:299) from the American Falls beds (probably Wisconsin deposits) in Idaho.

Thomomys talpoides is reported from the Howard Ranch local fauna in Hardeman County, western Texas, by Dalquest (1965:69-70), who referred the isolated teeth to *T. talpoides* on geographic grounds, apparently on the erroneous assumption that *T. talpoides* was the species of *Thomomys* nearest geographically to Hardeman County. Hay (1927:259) reported *Thomomys fuscus* [= *Thomomys talpoides*] from late Pleistocene beds near Wenatchee, Chelan County, Washington. Hibbard (1951:229) recorded *Thomomys talpoides* from late Pleistocene deposits in Greeley County, Kansas, and Walters (1957:540) reported the same species from late Pleistocene deposits in Clark County, Kansas. According to Hibbard (1958:14) other remains reported as *T. talpoides* have been recovered from numerous areas of Wisconsin glacial drift in western North America.

Thomomys bottae has been identified from Wisconsin age deposits in western North America, as follows: Burnet Cave, Gaudalupe Mt., New Mexico (Schultz and Howard, 1935:280); Carpinteria Asphalt, California (Wilson, 1933a:70); McKittrick Asphalt, Kern County, California (J. R. Schultz, 1938:206); Rancho La Brea, Los Angeles County, California (Dice, 1925:125—specimens described as a new subspecies, *T. b. occipitalis*); Papago Springs Cave, Santa Cruz County, Arizona (Skinner, 1942:150 and 158—probably *bottae,* but possibly *umbrinus* on the assumption that the two are specifically instead of subspecifically distinct); Isleta Cave, Bernalillo County, New Mexico (Harris and Findley, 1964:115—some of these fossils may be post-Wisconsin in age); Potter Creek Cave and Samwel Cave, Shasta County, California (Sinclair, 1905:146—identified as *T. leucodon,* now a subspecies of *T. bottae;* also see Hay, 1927:214-215).

Thomomys umbrinus has been reported from San Josecito Cave, Nuevo León, México (Russell, 1960:542); Upper Bercerra, México (Hibbard, 1955a:51—identified only as *Thomomys* sp., but undoubtedly referable to *T. umbrinus*). Post-Wisconsin remains of *Thomomys umbrinus* are reported by Alvarez (1964:6) from capa II and capa III of the Cueva La Nopalera, southwestern Hidalgo. Hay (1927:222-223) reported specimens of the genus *Thomomys* from Wisconsin deposits in Hawver Cave, Eldorado County, California, but did not assign them to species. Gilmore (1947:158) found the remains of *Thomomys umbrinus* in cave deposits near Quatro Ciénegas in central Coahuila. These cave deposits may have been laid down during the Wisconsin, but more likely accumulated in the post-Wisconsin.

Zygogeomys

Remains found in the Curtis Ranch local fauna, Cochise County, in southeastern Arizona are regarded as of middle Pleistocene age. See Gazin (1942:481-484), Wilson (1937:39-40), Hibbard (1958: 25), and Hibbard *et al.* (1965:510-511). Although some question as to the exact age of the Curtis Ranch local fauna still seems to exist, most authorities on the Pleistocene agree that the age is not Pliocene and that it is older than Rancholabrean. Gidley (1922:122) described the pocket gopher found in the Curtis Ranch beds as *Geomys parvidens,* which is preoccupied by *Geomys parvidens* Brown (1908:194), a name proposed for the pocket gopher from the Conard Fissure of Arkansas; therefore, Hay (1927:136) proposed the name *Geomys persimilis* for the Curtis Ranch species to replace *Geomys parvidens* Gidley. *Geomys persimilis* Hay became the type species of Gazin's genus *Nerterogeomys* (1942:507). In this paper, *Nerterogeomys* is considered to be a junior synonym of *Zygogeomys.*

Zygogeomys persimilis is represented by a rostral fragment bearing all the cheek teeth on the left side and the upper incisors. In addition, two lower jaws, one with the first three cheek teeth, are referred to the species (see Gazin, 1942:507). The fossils identified as *Geomys* from the Arroyo San Francisco, Cedazo fauna, in Aguascalientes, México, by Mooser (1959:413) may be referable instead to *Zygogeomys.* I have not seen the specimens and no figures are available; Mooser states that a cranium was recovered. If either the upper premolar or third molar is in place, generic identification could be made with reasonable certainty. No other fossils of *Zygogeomys* have been uncovered in late Pleistocene deposits and the significance of the absence of *Zygogeomys* has been discussed in an earlier paragraph of this section. *Geomys* has not been found so far south as Aguascalientes, but *Zygogeomys* occurs farther south now and presumably had a more extensive range on the plateau to the north in the Pleistocene.

Geomys

Geomys is common in Pleistocene deposits, especially on the Great Plains. Certainly the center of differentiation for *Geomys* was in this region, although at times, probably when conditions were favorable, *Geomys* expanded its range into adjacent areas, reaching the Pacific Coast in Irvingtonian times and the Atlantic Coast at the time of the Illinoian glaciation. The earliest Pleistocene records of the genus are from the Great Plains. McGrew (1944:49) described *Geomys quinni* from the Sand Draw local fauna, Brown County, Nebraska, considered by Hibbard (1958:11) to be Nebraskan in age. As mentioned in the account of Pliocene geomyids, *Geomys quinni* occurs also in the late Pliocene deposits of southwestern Kansas. Also, *Geomys quinni* occurs in the Broadwater-Lisco local fauna of Morrill and Garden counties, western Nebraska (Barbour and Schultz, 1937:3; Schultz and Stout, 1948:560-563; Schultz *et al.*, 1951: table 1). The Broadwater-Lisco is currently regarded as Aftonian deposits (Schultz and Stout, *loc. cit.;* Hibbard, 1958:11). Hibbard (1956:174) identified *Geomys quinni* from the Deer Park local fauna, probably deposited during the early Aftonian interglacial, of Meade County, Kansas. Strain (1966:36) described *Geomys paenebursarius* on the basis of fossils obtained from early Pleistocene deposits of the Hudspeth local fauna from western Hudspeth County in the Trans-Pecos of Texas. The Hudspeth fossils were probably deposited during the Aftonian interglacial. From Kingman County, Kansas, Hibbard (*op. cit.*:164) recovered isolated teeth of *Geomys* from the Dixon local fauna, regarded by him (*op. cit.*:153-154) as deposited during the latest Nebraskan glaciation, and correlated by him with the Sand Draw local fauna of Nebraska. Hibbard (1958:11) later regarded the Dixon as a transitional fauna between Nebraskan and Aftonian. The remains of *Geomys* from the Dixon are known only from isolated teeth. The teeth are small, and suggest that a smaller species of *Geomys* may have occurred along with the more common and larger *G. quinni* during the early Pleistocene (see discussion beyond of the Saunders *Geomys*). *Geomys quinni* was widespread and common throughout the central Great Plains from the late Pliocene (Rexroad fauna) through the early Pleistocene (Nebraskan and Aftonian deposits).

Hibbard (1956:179) referred the pocket gopher remains taken from the Saunders local fauna in Meade County, Kansas, to *Geomys tobinensis,* a small species having continuous enamel bands around the lower premolar in younger specimens. The Saunders local fauna was deposited in the late Aftonian and is younger than the Deer Park local fauna discussed above. Paulson (1961:138) later pointed out that the Saunders *Geomys* is distinct from *Geomys tobinensis;* hence, the small pocket gopher from the Saunders local fauna is probably an unnamed species, perhaps more closely allied to *paenebursarius* than to *quinni.* The small *Geomys* reported from the Aftonian Broadwater-Lisco local fauna of Nebraska (Schultz and Stout, 1948:563) may also be the same as the Saunders pocket gopher, but the smaller adult specimens occurring in the same bed with larger specimens probably are females and the larger specimens males. In all living Geomyini females have smaller skulls than males.

The Irvingtonian provincial age is currently regarded as Middle Pleistocene and includes the late Kansan glaciation (that part occurring after the glacial maximum) and the Yarmouthian interglacial (see Hibbard *et al.*, 1965:512-514). The Irvintonian provincial age, therefore, follows the late Blancan provincial age of the early Pleistocene and is succeeded by the Rancholabrean provincial age of the late Pleistocene. No specimen of an Irvingtonian *Geomys* is referable to any living species. Two Irvingtonian species have been described. Hibbard (1944:735) named *Parageomys tobinensis* [= *Geomys tobinensis*] from the Tobin local fauna of Russell County, Kansas. This species since has been reported from the Cudahy local fauna of Meade County, Kansas (Paulson, 1961: 137). Hibbard (1956:183) also identified as *Geomys tobinensis* the pocket gopher recovered from the Saunders local fauna, a late Aftonian deposit of Meade County, Kansas, and reduced the technical name *Parageomys* from generic to subgeneric rank. Paulson (*op. cit.*:138) pointed out that the Saunders specimens differ from *G. tobinensis*, and he, therefore, restricted the name to the small *Geomys* of the Cudahy and Tobin local faunas of Irvingtonian provincial age. *G. tobinensis* is markedly smaller than the Blancan *G. quinni.* The Cudahy and Tobin local faunas are of approximately the same age, and presently both are included in one unit, the Cudahy fauna. The Cudahy fauna is considered to have been deposited in late Kansan as it occurs in strata immediately below the Pearlette ash.

Recently, White and Downs (1961:8) described a new Irvingtonian species, *Geomys garbanii*, from the middle Pleistocene Vallecito Creek local fauna of San Diego County, California. Many well preserved fossils of the new species were recovered. *Geomys garbanii* is of medium size (approximately the size of one of the larger subspecies of *G. bursarius*), and significantly larger than the Irvingtonian *Geomys tobinensis* of the Great Plains. The Valelcito Creek occurrence of *Geomys* is the first authenticated record from the Pacific Coast region. Matthew (1902:320) erroneously referred remains of *Thomomys* to the genus *Geomys* in his revised list of Cope's earlier report on the Fossil Lake (or Silver Lake) fauna (see discussion of *Thomomys* above).

A number of Irvingtonian fossil remains of *Geomys* have not been identified with particular species. Hibbard (1941a:206) found *Geomys* in the Borchers local fauna (deposited in the time of the Yarmouthian interglacial) of Meade County, Kansas. Also, *Geomys* has been reported from several sites in Nebraska. Schultz and Tanner (1957:67) reported *Geomys* from the Angus fossil quarry in Nuckolls County, south-central Nebraska. The Angus fossils were found in sediments of the Sappa Formation considered by Schultz and Tanner to be a Yarmouthian deposit. Fossil quarries (Hay Springs, Rushville, and Gordon) along the south side of the Niobrara River Valley in Sheridan County, Nebraska, have also provided records of geomyids. Both a large and small species of *Geomys* have been reported from the more recently excavated Rushville and Gordon sites (Schultz and Stout, 1948:562-567, and table 3). In view of the great disparity in size owing to sex, these may actually be males and females of the same species, as mentioned above. The name Hay Springs has been used in reference to all three sites. The ages of the Hay Springs sites are approximately the same, but their correlation is presently under debate. Schultz and Tanner (1957:68-71) maintain that the fossils are distinctly middle Pleistocene, and that they were deposited during late Kansan glaciation, or perhaps from early Yarmouthian into early Illinoian, with the largest concentration coming from the Sappa sands of pre-Illinoian (Yarmouth) age. Hibbard (1958:25), basing his opinion on the presence of *Microtus pennsylvanicus,* and the stage of evolution of other species in the assemblage, regards the Hay Springs sites as probably Illinoian deposits, but certainly no older than that.

Mooser (1959:413) identified as *Geomys* the pocket gopher from Irvingtonian deposits in Arroyo San Francisco (loc. no. 5) near the city of Aguascalientes, México. As suggested elsewhere in this account, these fossils may be referable to *Zygogeomys* rather than *Geomys.* The Irvingtonian provincial age of this fauna was established by Hibbard and Mooser (1963:245-250). Other alleged occurrences have recently been compiled by Alvarez (1965:19-20). Maldonado-Koerdell (1948:20) noted four fossil occurrences of the genus *Geomys* in México. Two of these from San Josecito Cave in Nuevo León have since been identified with the genera *Orthogeomys* and *Pappogeomys* (Russell, 1960:543-548); the third listed by Maldonado-Koerdell from "near Ameca, Jalisco," was based on Brown's (1912:167) mention of some bones supposedly of the family "Geomyidae," and the fourth refers to pocket gopher remains from the "Hochtals von Mexiko" listed as *Geomys* by Freudenberg (1921:139). His generic identification is doubtful and the specimens should be compared with Mexican genera of the Geomyinae.

Upper Pleistocene records of *Geomys* also are common. Upper Pleistocene is here understood to include late Illinoian, Sangamon and Wisconsin deposits; all are considered to be of Rancholabrean provincial age (see Hibbard *et al.*, 1965:512-515) and post-Irvingtonian. The presence of remains of *Bison* and/or *Microtus pennsylvanicus* are currently considered mammalian index fossils of Rancholabrean faunas. In the Illinoian, *Geomys* extended its range to the Atlantic Coast in the southeastern United States. The eastern and western species-groups evidently were isolated throughout much of the late Pleistocene, and, therefore, evolved separately. Of the two, the eastern, or *pinetis,* species-group seems to have remained somewhat more generalized, and the western, or *bursarius,* species-group has become more specialized. The Rancholabrean *Geomys* from deposits in the southeastern United States are referable (see Ray, 1963:325) to *Geomys pinetis.*

Marsh (1871:121) described *Geomys bisulcatus* from the North Prong of the Loup River (near Camp Thomas), Nebraska. These beds are also termed the Loup Fork or Loup River fossil beds (see discussion on p. 485), and they lie along the upper reaches of the Middle Loup River in Thomas County (near Senea), Hooker County (near Mullen), and southeastern Cherry County (probably the North Prong beds northwest of Mullen). These beds were at first though to be of Miocene age, but later were regarded as early Pliocene (see Schultz and Stout, 1948:562-566 for a historical account of expeditions to these fossil sites). Schultz and Tanner (1957:71-72) pointed out that the principal fossiliferous beds in the Middle Loup region are of middle to late Pleistocene age, with most of the fossils coming from the Crete sand and silt beds which are probably early Illinoian deposits, and, therefore, younger than the Hay Springs faunas. Some fossils may have come from the Sappa deposits dated by Schultz and Tanner (*loc. cit.*) as mostly Yarmouthian deposits. *Geomys bisulcatus,* judging from the original description and Hibbard's discussion of the cotypes (1954:357), does not differ significantly from *Geomys bursarius.* However, *Geomys bisulcatus* is tentatively retained as a valid species. Based on the evidence cited above it seems unlikely that *Geomys bisulcatus* occurred in pre-Irvingtonian times as often suggested in the literature.

The genus *Geomys* has been identified in several faunas of

Illinoian age, all from the Great Plains. Stephens (1960:1961) reported the genus from the Doby Springs local fauna in Harper County, Oklahoma, and Starrett (1956:1188) reported it from the Berends local fauna in Beaver County, Oklahoma. Schultz (1965: 249) assigned 21 isolated teeth, including six incisors, from Butler Springs local fauna (considered by him to be late Illinoian, following the glacial maximum) to *Geomys* cf. *bursarius.* Hibbard and Taylor (1960:167) reported a baculum tentatively identified as that of *Geomys* from the early Illinoian Butler Springs local fauna (including the Adams fauna) of Meade County, Kansas. Hibbard (1963:206) recorded the genus *Geomys* from the Mt. Scott local fauna (late Illinoian deposits) of Meade County, Kansas; the specimens probably are referable to the living species *bursarius.* From McPherson County, Kansas, Hibbard (1952:7) reported the genus *Geomys* from the Kentuck Assemblage, which he (1958:25) regarded as a composite of Illinoian and Sangamon species. Specific identification of the Illinoian pocket gophers is uncertain, primarily due to the fragmentary nature of the material. On the basis of dental characters alone most specimens could be referred to *G. bursarius;* however the taxonomic status of *G. bisulcatus* is in doubt, and more complete material may indicate that the Illinoian gophers are specifically distinct from the living species. Consequently, most authors, including myself, have made no attempt to refer these specimens to species. Nevertheless, the Illinoian *Geomys* from the Great Plains is more closely allied to the living species of *Geomys* than it is to the earlier Irvingtonian species.

Geomys bursarius has been collected from a number of Sangamon fossil sites on the Great Plains. Although specific identification of specimens of *Geomys* from Illinoian faunas is uncertain, the Great Plains *Geomys* from Sangamon and later deposits probably is referable to the living species as Hibbard and Taylor (1960:165) pointed out. They found no difference between *Geomys* recovered from the Cragin Quarry local fauna (early Sangamon) of Meade County, Kansas, and the living species *Geomys bursarius.* Isolated teeth of the same species were collected from the Jinglebob local fauna of Meade County, Kansas (Hibbard, 1955b:206), a fauna of the late Sangamon. Hibbard (1943:240) also recorded the genus *Geomys* (referable to *G. bursarius*) from the Rezabek local fauna of Lincoln County, Kansas. According to Schultz *et al.* (1951:6 and table 1) the genus *Geomys* occurs in buried or "fossil" soils of Sangamon age, lying just above the Loveland Loess, in Nebraska. No specific localities were given by them, nor were any particular specimens mentioned. Dalquest reported *Geomys bursarius* from two Sangamon faunas in northern Texas. The species is represented in the Ward Quarry local fauna of Cooke County, Texas (1962a:42), and the Good Creek local fauna of Foard County, Texas (1962b:575).

Geomys bursarius has been reported from Wisconsin fossil deposits of the Great Plains and adjacent areas as follows: Jones local fauna, Meade County, Kansas (Hibbard and Taylor, 1960:64-66); Two Creeks Forest beds of the third interstadial soils formed between Cary and Mankato glaciations, late Wisconsin (Schultz *et al.*, 1951:8 and table 1); Cita Canyon local fauna in the northern part of the Panhandle of Texas (Johnson and Savage, 1955:39); Howard Ranch local fauna of Hardeman County in northwestern Texas (Dalquest, 1965:70); Quitaque local fauna of Motley County, Texas (Dalquest, 1964:501); Clear Creek local fauna of Denton County in north-central Texas (Slaughter and Ritchie, 1963:120); Ben Franklin local fauna, of late Wisconsin beds along the North Sulphur River in Delta County, NE Texas (Slaughter and Hoover, 1963:137); Bulverde Cave (Hay, 1920:140; 1924:247) and Friesenhahn Cave (Tamsitt, 1957:321), both in Bexar County, south-central Texas; Alton, Illinois (Hay, 1923:338-339); Wisconsin drift of Illinois, without mention of specific locality (Bader and Techter, 1959:172); Wisconsin drift of southwestern Wisconsin and northeastern Iowa (Hay, *op. cit.*:343); Wisconsin drift near Galena, Illinois, and mouth of Platte River in eastern Nebraska (Leidy, 1869:406).

Brown (1908:194) described *Geomys parvidens* from the Conard Fissure, in northern Arkansas. Hibbard (1958:25) concluded that the Conard Fissure fauna represents a glacial stage, probably the Illinoian, and Hibbard *et al.* (1965:510-511) regarded the fauna as a composite including both Irvingtonian and Rancholabrean elements. White and Downs (1961:21) considered *G. parvidens* to be a subspecies of *Geomys bursarius.*

The first Pleistocene occurrence of *Geomys* in the southeastern United States is from the Reddick I deposits reported by Gut and Ray (1963:325), who found the remains of *Geomys pinetis* among the fossils comprising the "rodent beds" of Marion County, Florida. Gut and Ray tentatively identified the beds as Illinoian, but Kurten (1965:219) regarded the Reddick I fauna as early Sangamon. Simpson (1928:2) reported *Geomys floridanus* [= *pinetis*] from Saber-tooth Cave deposits of Citrus County, Florida. The Saber-tooth Cave (or Lecanto Cave) local fauna is considered by Kurten (*op. cit.*:219) also to be a Sangamon deposit. *Geomys floridanus*

[=*pinetis*] was reported from the Seminole Field deposits by Simpson (1929:563); both Simpson and Kurten (*op. cit.*:221) agreed that the Seminole Field fauna is mainly late Wisconsin, although sub-Recent fossils occur at the tops of the beds. Ray (1958:430) collected remains of *Geomys pinetis* from the Melbourne Bone Bed of Brevard County, Florida. The Melbourne local fauna is considered to be from Wisconsin deposits by Kurten (*op. cit.*:220). The eastern species of *Geomys* were probably derived from Great Plains stock that reached the southeastern Coastal Plains in early Rancholabrean (Illinoian) time. Presently there is no contact between the eastern and western populations of the genus, and it is assumed that disjunction occurred as a result of Wisconsin glaciation. It is interesting to note that the genus *Thomomys* occurred in this region at approximately the same time; both genera occur in Sabertooth Cave deposits.

Pappogeomys

The genus *Pappogeomys* is not known from Pleistocene deposits older than the Wisconsin glaciation, but a pre-Pleistocene occurrence in the Benson beds of Arizona (see discussion of the Pliocene above) shows that *Pappogeomys* had been differentiated by late Pliocene time. The absence of *Pappogeomys,* beginning in the early Pleistocene and continuing well into the late Pleistocene, is attributed to the southern distribution of the genus, where its range probably was centered on the Central Plateau of México. The paucity of early and middle Pleistocene deposits from this critical region prevents any definite statements about phyletic development within the genus. All of the late Pleistocene records pertain to the subgenus *Cratogeomys* (long in use as a generic name but in the present paper reduced to subgeneric rank in the genus *Pappogeomys*). Schultz and Howard (1935:280) found *Cratogeomys* [=*Pappogeomys*] *castanops* in Burnett Cave in the Guadalupe Mountains of south-central New Mexico. The Burnett deposits are probably late Wisconsin (see Schultz and Tanner, 1957:75, for discussion of the age of these deposits based on carbon-14 tests). These writers (*loc. cit.*) also referred the mandible of a small pocket gopher to the genus *Pappogeomys* [=subgenus *Pappogeomys*]. However, neither genera nor subgenera of the tribe Geomyini can be distinguished on the basis of their inferior dentitions. Judging from the distribution of the modern geomyines, it seems unlikely that the subgenus *Pappogeomys* has occurred beyond its present range in the late Pleistocene; therefore the small mandible is most likely that of a young individual of *Pappogeomys castanops.* Russell

(1960:543) referred specimens collected at San Josecito Cave in Nuevo León, México, to the group of small subspecies *Cratogeomys* [= *Pappogeomys*] *castanops.* Also, Russell (*loc. cit.*) identified a rostral fragment as of the genus *Cratogeomys* [= subgenus *Cratogeomys*] although the fragment had a combination of features different than in any named species of the genus; he did not name the fragment as a new species, preferring to wait for additional material that could clarify its taxonomic relationships.

Hibbard (1955a:52-53) identified *Cratogeomys* [= *Pappogeomys*] *tylorhinus* from the Becerra Superior deposits in the valley of Tequixquic in the northern part of the state of México. The Wisconsin age of these beds suggests an earlier Pleistocene derivation of the *gymnurus*-group of species.

Several specimens of the subgenus *Cratogeomys* have been reported from beds of latest Wisconsin (certainly after the glacial maximum) or post-Wisconsin age. Gilmore (1947:158) found fossil remains of *Cratogeomys* [= *Pappogeomys*] *castanops* commonly in Quaternary cave deposits on the mountain slopes in the vicinity of Cuatro Cienegas, in central Coahuila. These deposits actually may be of post-Wisconsin origin (see discussion above). Alvarez (1964:8) obtained fragments of *Cratogeomys* [= *Pappogeomys*] *tylorhinus* from sub-Recent deposits of Capa III in the Cueva La Nopalera in southwestern Hidalgo, México. *Pappogeomys merriami* lives in the area today. Mayer-Oakes (1959:373) reported remains of *Cratogeomys* [= *Pappogeomys*] *merriami* from levels eight and eleven of the excavations at El Risco II, in the northern part of Mexico City. The ages of these deposits are unknown to me, but they probably are no older than late Wisconsin with most of the beds dating from the post-Wisconsin.

Orthogeomys

This genus is not known from the Pleistocene, except for its occurrence in the San Josecito cave deposits of southwestern Nuevo León, México (Russell, 1960:544). Although *Orthogeomys* does not occur in the immediate vicinity of the cave at the present time, the northern limits of its range is nearby in southern Tamaulipas. The *Orthogeomys* from San Josecito Cave differs from living species, and has been named *Heterogeomys* [= *Orthogeomys*] *onerosus* Russell (*loc. cit.*), and is evidently referable to the subgenus *Heterogeomys.* As mentioned before, the San Josecito Cave local fauna represents deposits of Wisconsin glaciation.

HISTORY OF CLASSIFICATION

The account of the Tucan or Indian mole by Hernandez (sometimes listed as Fernandez) in 1651 probably is the earliest published one of a geomyid (see Merriam, 1895:201; Coues, 1877:607-608). Linnaeus in 1758 did not mention geomyids. In 1772, Kerr described Hernandez's Tucan under the name *Sorex mexicana* on the basis of Hernandez's account without having seen any specimens. Lichtenstein in 1827 applied the technical name *Ascomys mexicana* to three specimens collected by Deppe from unknown localities on the tableland of México. Merriam (*loc. cit.*) pointed out that the name *mexicanus* of Lichtenstein in 1827 is a *nomen nudum*, and that it is preoccupied by *mexicanus* used by Kerr in 1792. The latter can not be technically identified with any particular species of geomyid.

Bartram in 1791 wrote of the pocket gopher of Florida, without formally describing it. The first available technical name is *Mus bursarius* of Shaw in 1800. Rafinesque in 1817 proposed the first generic names for the geomyids when he described *Geomys* and *Diplostoma*. In 1839, Waterhouse referred the genus *Geomys* to his family Arvicolidae, considered by him to be a subgroup of muroids. In 1841, he suggested that *Geomys* was related to *Bathyergus* and *Spalax*. Waterhouse in 1848 (p. 8) treated the pocket gophers as a subgroup of rodents under the group name Saccomyina, in which he included the genera *Heteromys, Saccomys, Perognathus,* and *Dipodomys*. Hence, Waterhouse was the first to recognize the relationship between the heteromyids and geomyids. In the next year Gervais erected the family Pseudostomidae for a group of specialized squirrels to include *Geomys* and *Thomomys* and the same genera (at least in part) of heteromyids that Waterhouse classified in the "family" Saccomyina.

In 1839 the name *Thomomys* was proposed by Maximilian (Wied-Neuwied). All of the generic names previously proposed for pocket gophers were considered by subsequent authors to be synonyms of *Geomys*.

A third family name, Sciurospalacoides, was proposed by Brandt (1855:188) who referred *Geomys* and *Thomomys* to that family. He placed his new family phylogenetically between the family Sciuridae and the family Spalacoides (a group in which Brandt included the genera *Spalax, Sipheus,* and *Ellobius*). Brandt took exception to the classification of Waterhouse (1848), who united the geomyids and heteromyids in one family. Brandt placed the heteromyid genera in other groups: *Perognathus* in the Muridae, and *Macrocolus* [= *Dipodomys*] in the Macrolini, a subfamily of the family Dipodoides.

Modern classification of the pocket gophers begins with Baird in 1858. The important classifications are summarized in Table 1; a few that do not depart essentially from those listed have been omitted owing to limited space for the tabular arrangement, but are discussed in the following account.

Baird probably was strongly influenced by the arrangement proposed by Waterhouse in 1848, but was opposed to separating geomyids from heteromyids as was done by Brandt. Baird was convinced of the close relationship of the geomyids and heteromyids, and referred both groups to one family, the Saccomyidae, as Waterhouse had done earlier. In order to recognize the morphological specializations he used two subfamilies, Geomyinae and the Saccomyinae. In the 20 years that followed, some authors followed Brandt and others followed Baird.

Gill, in 1872 (p. 71), proposed a classification essentially like Baird's of 1858, but Gill raised Baird's subfamilies to the rank of family (see Table 1). In referring all pocket gophers to the Geomyidae, Gill used that name as a family term for the first time. Also he established the superfamily Saccomyoidea to include his two families, Geomyidae and Saccomyidae; therefore, the Saccomyoidea was equivalent to the group Saccomyina of Waterhouse (1848) and the Saccomyidae of Baird (1858). Coues (1877), in his classic monograph of the Geomyidae followed the arrangement proposed by Gill in treating the pocket gophers as a family. Alston in 1876 proposed another classification based on Baird (1858), with two subfamilies, the Geomyinae and the Heteromyinae, united together in the family Geomyidae; thus, he recognized that the genus *Saccomys* Frédéric Cuvier, 1823, was a synonym of *Heteromys* Desmarest, 1817, as had been pointed out by Gray (1868:201) and Peters (1874:356). Coues (1877:487-490) acknowledged the invalidity of the genus *Saccomys,* but refused to give up the name in supergeneric classification. Winge, first in 1887 and subsequently in 1924, classified the geomyids and heteromyids together in the family Saccomyidae as did Baird in 1858, and like Coues, Winge too ignored the synonymy of *Saccomys* with *Heteromys* and insisted on retaining the technical terms Saccomyidae and Saccomyini.

Up to the time of Merriam's classic revision of the Recent Geomyidae in 1895 all the known species of living pocket gophers were referred to two genera, *Geomys* and *Thomomys*. Merriam described much new material, especially from México and Central America, and proposed seven new genera (see Table 1). His complete and detailed study of the dentitions and osteology of the skull remains today as the definitive work on this subject, and is the point where most studies of the Geomyidae must begin. His treatment of the Recent genera survived for 52 years without change until Hooper (1946:397) arranged *Platygeomys* as a synonym of *Cratogeomys*. However, Merriam's genera have been recognized in all subsequent classifications except for the current review (see Table 1).

Cope described the first known fossil geomyids in 1878, and published an excellent review of the two genera, *Pleurolicus* and *Entoptycus*, in 1884 (pp. 855-870, pl. 64, figs. 1-9). Both genera were recovered from the John Day Miocene deposits of Oregon. Cope did not propose a new systematic arrangement of these geomyids, but referred them to the family Saccomyidae and mentioned that the Saccomyidae was equivalent to the family Geomyidae of Alston. Winge, in 1887, followed Cope in referring *Pleurolicus* and *Entoptycus* to the Saccomyidae along with the living genera *Thomomys* and *Geomys*. Miller and Gidley (1918), in their synopsis of the supergeneric groups of rodents, proposed a new subfamily, Entoptychinae, to include the divergent Miocene pocket gophers. Miller and Gidley also revived the old subfamily Geomyinae of Baird (1858), but restricted its application to the modern pocket gophers and their immediate ancestors. In 1936, A. E. Wood revised the taxa of the subfamily Entoptychinae, and described the first Miocene genus, *Dikkomys*, of the Geomyinae. He followed the supergeneric classification of Miller and Gidley (1918).

The recent classifications of Simpson (1945) and Wood (1955) have combined the classifications of Merriam (1895) and Wood (1936). Wood (1955) brought up to date the list of genera, including those that were described after the publication of Simpson's classification (1945). In Table 1, the list of genera is principally from Simpson (1945) but generic names used by Wood (1955) are included. This is the currently accepted classification.

The new classification proposed in this paper (see Table 1) includes three tribes proposed as vertical units; they are intended to stress the phyletic trends in the known evolutionary sequences by placing immediate ancestors together with their descendants.

Pliogeomys is placed in the same tribe (Geomyini) as *Zygogeomys, Geomys, Orthogeomys*, and *Pappogeomys*. That tribe includes the most specialized Geomyinae. *Zygogeomys, Geomys, Orthogeomys*, and *Pappogeomys* are lineages resulting from a Pleistocene

TABLE 1.—History of the classification of the Superfamily Geomyoidea

Baird 1858	Gill 1872 Coues 1877	Winge 1887 and 1924	Merriam 1895 Ellerman 1940	Wood 1935 Wood 1936	Simpson 1945 Wood 1955	Names used in present paper
Family Saccomyidae	Family Geomyidae	Family Saccomyidae	Family Geomyidae	Family Geomyidae	Family Geomyidae	Family Geomyidae
Subfamily Geomyinae		"Group" Geomyini		Subfamily Geomyinae	Subfamily Geomyinae	Subfamily Geomyinae
						Tribe Dikkomyini
				**Dikkomys*	**Dikkomys*	**Dikkomys*
					**Pliosaccomys*	**Pliosaccomys*
						Tribe Thomomyini
				**Pleisothomomys*	**Pleisothomomys*	*Thomomys*
Thomomys	*Thomomys*	*Thomomys*	*Thomomys*	*Thomomys*	*Thomomys*	
						Tribe Geomyini
					**Pliogeomys*	**Pliogeomys*
			Zygogeomys	*Zygggeomys*	*Zygogeomys*	*Zygogeomys*
					**Nerterogeomys*	
Geomys	*Geomys*	*Geomys*	*Geomys*	*Geomys*	*Geomys*	*Geomys*
					**Parageomys*	

			Orthogeomys *Heterogeomys* *Macrogeomys* *Pappogeomys* *Cratogeomys* *Platygeomys*	*Orthogeomys* *Heterogeomys* *Macrogeomys* *Pappogeomys* *Cratogeomys* *Platygeomys*	*Orthogeomys* *Heterogeomys* *Macrogeomys* *Pappogeomys* *Cratogeomys* *Platygeomys*	*Orthogeomys* *Pappogeomys*
		**Pleurolicus* **Entoptychus*		Subfamily Entoptychinae **Pleurolicus* **Gregorymys* **Grangerimus* **Entoptychus*	Subfamily Entoptychinae **Pleurolicus* **Gregorymys* **Grangerimus* **Entoptychus*	Subfamily Entoptychinae **Pleurolicus* **Gregorymys* **Grangerimus* **Entoptychus*
		"Group" Gymnoptychine** *Gymnoptychus*		**Gidleumys*	Geomyidae *incertae sedis* **Diplolophus* **Griphomys*	Geomyidae *incertae sedis* **Diplolophus* **Griphomys*
Subfamily Saccomyinae	Family Saccomyidae	"Group" Saccomyini		Family Heteromyidae	Family Heteromyidae	Family Heteromyidae

* Denotes extinct genera.

** Winge included in his family Saccomyidae the "group" Gymnoptychine and the contained genus *Gymnoptychus* Cope, 1873, which genus currently is placed in the family Eomyidae. The type of *Gymnoptychus* Cope, 1873, is synonymous with *Ischyromys* Leidy, 1856, and the valid name for the genus is *Adjidaumo* Hay, 1899.

radiation in which all the lineages diverged from a common Pliocene ancestor. The radiation of the Geomyini was well under way by the close of the late Pliocene. Although *Pliogeomys* may not be the actual ancestor, it closely resembles the primitive morphotype.

Pliosaccomys, on the other hand, represents the terminal stages of a long trend that began with the *Dikkomys*-like Geomyinae of the early Miocene. In this lineage, the rate of evolution in the dentition and the skull was slow; therefore, the differences between early Miocene (*Dikkomys*) and middle Pliocene (*Pliosaccomys*) are not great and the two are united into the tribe Dikkomyini. The Dikkomyini is the ancestral geomyinen trunk from which the modern groups have diverged.

The Pliocene ancestor of *Thomomys* is unknown but probably resembled *Pliosaccomys,* with which it may have been a contemporary. *Thomomys* is the least specialized of the modern Geomyinae, and, consequently, shows the most resemblance to the ancestral tribe. The specializations of *Thomomys,* however, clearly preclude its reference to the tribe Dikkomyini; therefore, it is set apart in the monotypic tribe Thomomyini. That tribe has not undergone an adaptive radiation comparable to that of the tribe Geomyini or that of the Entoptychinae in the early Miocene. Here, for the first time, *Thomomys* is set apart in classification from the other living pocket gophers.

Merriam's genera *Orthogeomys, Heterogeomys,* and *Macrogeomys* are closely related. Each of these taxa is retained as a subgenus of a single genus, *Orthogeomys.* Some species of *Macrogeomys* seem to be more closely allied to the subgenus *Orthogeomys* and others to the subgenus *Heterogeomys.* A revision of the genus is needed; it might show that the currently recognized subgenera are artificial, and that a different arrangement of the species would more clearly express their evolutionary relationships. The subgenus *Heterogeomys* seems to be the most nearly uniform of the subgenera, and it is the least specialized. Radiation within the genus may have begun relatively recently, but the many special adaptations for tropical environments suggest that the genus has been in the Neotropical Zone a long time. Therefore, discovery of an early dichotomy from the common ancestral stock of the tribe would come as no surprise.

Nerterogeomys Gazin here is arranged as a junior synonym of *Zygogeomys.* Both are less specialized than any of the other Geomyini, except *Pliogeomys.* The single living species (*Zygogeomys tricopus*) is obviously a relic. Its range is small. The two subspecies differ only in minor features. The living species does have a few unique characteristics, only to be expected in the surviving species of a long phyletic lineage. Some of these are specializations. Otherwise, *Zygogeomys* and *Nertergeomys* are closely related and the latter is best placed as a synonym of the former. Both are admittedly closely related to *Geomys*. *Zygogeomys* and *Geomys* share several characters, particularly primitive ones; there is considerable parallelism, especially marked in Irvingtonian species of *Geomys*. Nevertheless, *Geomys* is more specialized, particularly in the dentition, and it has developed some *Pappogeomys*-like specializations. *Zygogeomys* has retained more of the primitive characters of the tribe. A strong case could be made for recognizing only one genus, *Geomys*, containing *Zygogeomys* as one of two subgenera. Nevertheless, the characters separating *Zygogeomys* and *Geomys* are of considerable importance and I consider the two kinds to be distinct genera.

The species of *Geomys*, both living and extinct, form a distinct and well-marked group. The genus is less primitive in most respects than *Zygogeomys* and *Orthogeomys* and it is less specialized than *Pappogeomys*, excluding the ancestral stock (subgenus *Pappogeomys*). Some specimens of species of Irvingtonian age (*Geomys tobinensis* and *Geomys garbanii*, especially the former) retain primitive enamel plates as does *Zygogeomys;* but this is true of only a small percentage of the individuals. Also the adult dental pattern developed somewhat later in ontogeny in these middle Pleistocene species of *Geomys* than in either Recent or late Pliocene and early Pleistocene representatives (*Geomys paenebursarius*, *Geomys quinni*) of the genus. Whether these features represent a stage in the evolution of the late Pleistocene and Recent species or a terminal stage in members of a sterile and primitive branch of the main line of evolution of *Geomys* is uncertain. At present I favor the latter explanation, and view *G. paenebursarius* and *G. quinni* as early progressive species that evolved dental specializations that were maintained in the main line of phylogeny.

Hibbard proposed the generic name *Parageomys* (1944:55), but later regarded it as a subgenus of *Geomys* (1956:182) that includes those species retaining continuous enamel bands until relatively late in ontogeny; no other differences have been noted. When the early phylogeny of *Geomys* is better understood, *Parageomys* may serve as a subgeneric taxon in which the primitive species of *Geomys* can be grouped, but as of now *Parageomys* is arranged as a synonym of *Geomys*.

Pappogeomys and *Cratogeomys* also form a natural group. Their close relationship is best reflected in formal taxonomy by including them in the same genus. Their dissimilarities are of the sort that separate a primitive ancestral lineage from a divergent and progressively more specialized assemblage. The fossil record is inadequate, and I can only speculate that *Cratogeomys* diverged from primitive *Pappogeomys*-stock in the earlier Pleistocene, at least before the end of the Irvingtonian. *Cratogeomys* probably originated on the Mexican Plateau and probably underwent its subsequent evolution there. The living species of the subgenus *Pappogeomys* are evidently relics of the ancestral stock of the genus. Hooper (1946:397), I think correctly, considered *Platygeomys* as congeneric with *Cratogeomys*, although the highest degree of specialization of the genus is attained in those species formerly classed in the genus *Platygeomys*. Even so, in my opinion, the differences are insufficient to warrant even subgeneric recognition.

CLASSIFICATION

Family GEOMYIDAE Gill, 1872

Rodents of the superfamily Geomyoidea specialized for completely fossorial life (early Pliocene to Recent); specialized earlier (late? Oligocene and early Miocene) for semi-fossorial habits; body thickset, fusiform without apparent neck (in modern geomyids); legs short; forelegs especially stout; eyes and ears small (pinna reduced to inconspicuous crest concealed beneath pelage); tail tactile, shorter than head and body; lips closing behind incisors; cheek pouches external, fur-lined; baculum rodlike, arched, having expanded quadriform platelike base; pelage long, soft without underfur, covering body in thick coat (in some species of *Orthogeomys* scant, harsh or scattered bristles); color varying from pale tints of buffy (almost white) to metallic black.

Skull thick-walled, massive, angular, relatively broad, and flattened; distinctly murine form, but having zygomasseteric structure of advanced sciuromorphs, including small infraorbital canal (that transmits no part of masseter muscle) and well-developed, broad zygomatic plate; zygomata massive and widely flaring, jugals stout; rostrum robust, relatively broad and deep, and without evidence of transverse canal (as in Heteromyidae); anterior projection of nasals only slightly exceeding that of upper incisors; interorbital region usually constricted, narrower than rostrum; anterior opening of infraorbital canal far forward on side of rostrum, about half way between zygomatic plate and upper incisor and just behind premaxillary-maxillary suture, its opening countersunk in oblique sulcus (for protection from muscle contraction); postorbital process lacking, except for rudimentary knoblike projection in subgenus *Macrogeomys;* palate relatively narrow, its deeply sculptured surface sloping steeply downward posteriorly causing region supporting maxillary tooth-row to be markedly depressed; palatine bone reduced, forming, on two abruptly different levels, posterior margin of hard palate behind tooth-rows; parietals compressed and narrow, and most of cerebral cavity roofed by squamosals (in some species squamosals overlap lateral parts of parietals); tympanic bullae completely inferior in position and fully ossified, external meatus being developed laterally as elongated tube; mastoid not inflated, but broadly exposed at posterolateral margin of the skull; occiput large, its surface usually rugose, and paroccipital processes large and flangelike, at least in advanced groups (early Pliocene to Recent); ramus relatively short and stout, having distinct crest and ridges for muscle attachments; coronoid process well developed, erect; articular condyle prominent; angular process prominent, reflected laterally, and in modern groups lateral extension protruding from posterior border of ramus nearly at right angle; capsule for root of lower incisor, prominent between angular process and articular condyle.

Anterior surface of incisors broad and flat, always smooth on lower teeth, but either smooth or grooved on upper teeth depending on taxon; cheek teeth hypsodont, becoming progressively higher crowned in modern groups, rooted in primitive groups (late? Oligocene to middle Pliocene), rootless and ever-growing in modern groups (late Pliocene to Recent); upper and lower premolars persistently bicolumnar; upper and lower molars bicolumnar only in primitive groups (late? Oligocene and early Miocene), becoming progressively monocolumnar in advanced groups (early Pliocene to Recent), primitive bicolumnar pattern being retained on occlusal surface only in early stages of ontogeny and in third molar throughout life; enamel pattern of occlusal surface of cheek teeth based on sextituberculate prototype (see Wood and Wilson, 1936:388-391), having cusps arranged in two transverse rows of three cusps each, excepting three anterior cusps of premolars that are arranged in trefoil, especially on p4 (sometimes only one or two, rather than three, cusps develop in a particular set, especially in p4), conules absent; protostyle and endostyle in upper teeth and protostylid and hypostylid in lower teeth formed from cingulum; cusps of each row uniting with wear into transverse enamel lophs (or lophids), each tooth having two lophs, one on anterior column, protoloph and protolophid, and one on posterior column, hypoloph and hypolophid, that unite with additional wear forming continuous enamel band; enamel lacking on sides of each column in advanced lineages, thereby restricting enamel to anterior and posterior walls; with extreme reduction, posterior plates of upper teeth and, more commonly, anterior plates of lower molars, missing. Dental formula: $\frac{1}{1}$, $\frac{0}{0}$, $\frac{1}{1}$ $\frac{3}{3}$.

Key to the Subfamilies of Geomyidae

A Angular process of ramus mostly below alveolar level of mandibular tooth-row; pattern of premolar like that of molars, consisting of two subequal crests united at one or both margins of tooth; molars persistently bicolumnar; molariform teeth always rooted. Subfamily Entoptychinae . . . . p. 513

A′ Angular process of ramus mostly above level of mandibular tooth-row; pattern of permolar unlike that of molars, consisting of two prisms differing in size and united at their midpoints but never at either margin; molars progressively monocolumnar, except for early Miocene forms; molariform teeth rooted only in primitive genera (late? Oligocene to middle Pliocene), and rootless and ever-growing in later genera (late Pliocene to Recent). Subfamily Geomyinae . . . . p. 514

Subfamily ENTOPTYCHINAE Miller and Gidley, 1918

Anterior face of upper incisor usually smooth, sometimes bearing faint groove in center or near medial margin of tooth, at least in *Gregorymys;* cheek teeth hypsodont, medium to high crowned, and rooted in all but *Entoptychus* (has rootless, ever-growing teeth); cheek teeth identical in form, premolars resembling molars and lower cheek teeth mirror images of upper teeth; crowns biprismatic, having two columns joined at edge of protomeres (for description of term, see discussion of primitive morphotype on page 537) and with persistent lateral fissure between them; lateral re-entrant fold deep, penetrating at least half width of crown, from external side in upper teeth and internal side in lower teeth (in specialized genus *Entoptychus* lophs, upon additional wear, join also at edge of parameres, thus uniting columns at both ends and thereby enclosing interior part of lateral fissure as a transverse fossette in center of tooth); enamel investment of prisms usually complete, including inflection bordering re-entrant folds, occlusal pattern becoming interrupted with wear only in *Entoptychus,* where enamel disappears first from sides of crowns (following union of anterior and posterior columns at both sides) and later, in final stages of attrition, from anterior wall of lower molars and posterior wall of upper molars.

Maxillary bone without pronounced vertical depth in part supporting cheek teeth, its inferior border only slightly lower than inferior border of premaxillary and alveolar lips of molariform teeth consequently approximately level with, or slightly below, alveolar lip of upper incisor; squamosal without lateral expansion, therefore, meatal tube of auditory bulla separated from zygomatic process of squamosal by deep, well-developed postglenoid notch; angular part of mandible below alveolar level of mandibular cheek teeth; angular process only slightly reflected laterally; coronoid process low, tip only slightly above condyle.

For information concerning the structure and relationships of the known genera, and for accounts of species, see Wood (1936). A list of the named genera in order of specialization is as follows:

***Pleurolicus* Cope, 1878. Proc. Amer. Phil. Soc., 18:66.
***Gregorymys* Wood, 1936. Amer. Mus. Novit., 866:9.
***Grangerimus* Wood, 1936. Amer. Mus. Novit., 866:13.
***Entoptychus* Cope, 1878. Proc. Amer. Phil. Soc., 18:64.

Five new species have been described since Wood's (1936) revision. They are: *Pleurolicus clasoni* MacDonald (1963:180); *Gregorymys kayi* Wood (1950:335); *Gregorymys montanensis* Hibbard and Keenmon (1950:198); *Grangerimus dakotensis* MacDonald (1963:182); *Grangerimus sellardsi* Hibbard and Wilson (1950:623).

Subfamily GEOMYINAE Baird, 1858

Anterior face of upper incisor primitively smooth, grooves consistently developed only in one modern lineage (Geomyini); cheek teeth hypsodont, primitively rooted and having crown of medium height (late Oligocene to middle Pliocene), being higher crowned, rootless and every-growing in modern lineages (late Pliocene to Recent); primitively crowns of cheek teeth biprismatic, having two columns joined at mid-points by narrow isthmus and entire crown sheathed in continuous band of enamel; premolars retaining primitive biprismatic form, anterior and posterior columns never uniting at edge of protomeres or parameres, and with both lateral re-entrant folds persistent throughout life; primitive biprismatic pattern becoming decidely modified in molars (except in M3), having two prisms progressively uniting into one column by reduction and loss of lateral inflections, primitive biprismatic patterns being retained only in early stages of ontogeny; third upper molars retaining, at least partially, primitive bicolumnar pattern (except in Thomomyini), with relatively broad isthmus and horizontially shallow re-entrant folds, lingual fold sometimes wanting; enamel pattern becoming discontinuous (late Pliocene to Recent) owing to loss of enamel from sides of each column; remaining enamel restricted to anterior and posterior plates, or cutting blades, and enamel bordering lateral inflections in premolars (considering both sides together, these plates constitute esssentially two transverse cutting blades); enamel pattern of M3 varying, depending on taxon; with specialization, anterior plates of lower molars and posterior plates of upper premolar and molars may be reduced or lost; except in primitive species (early Miocene), no enamel fossettes retained in adult dentitions.

Maxillary bone having pronounced vertical depth in part supporting cheek teeth, inferior border arching downward well below inferior border of premaxillary; consequently, alveolar lips of molariform teeth decidedly below level of alveolar lip of upper incisor; squamosal with marked lateral expansion at expense of postglenoid notch; notch compressed and reduced between meatal tube of auditory bulla and zygomatic process of squamosal; angular part of mandible mostly above alveolar level of mandibular cheek teeth; angular process reflected laterally at right angles to axis of ramus and developed into heavy knoblike projection; coronoid process well developed, tip decidedly higher than condyle; fossorial specializations remarkably well developed in advanced lineages, degree of specialization of primitive Miocene species unknown but probably only semi-fossorial as in Entoptychinae.

Key to the Tribes of the Geomyinae

A Enamel investment complete and uninterrupted, even in final (adult) stages of wear; cheek teeth rooted, with crowns of medium height; third lower molar biprismatic, the two columns separated by inner and outer re-entrant folds as in lower premolar. Tribe Dikkomyini .... p. 515

A′ Enamel investment incomplete and discontinuous, reduced, at least in final (adult) stages of wear, to interrupted enamel-plates; cheek teeth rootless and ever-growing (except in extinct genus *Pliogeomys*), crowns of maximum height; third lower molar monoprismatic, without trace of inner and outer re-entrant folds as in first and second lower molars.

  B Upper incisors smooth, occasionally with a fine indistinct groove near inner margin of tooth; form of third upper molar same as M1 and M2, monoprismatic, antero-posteriorly compressed, and having transverse enamel plates on both anterior and posterior faces, and without suggestion of either labial or lingual re-entrant folds; basitemporal fossa absent (except for a shallow depression in one Recent species, *T. townsendii*); forefoot small and narrow with claws not elongated for digging. Tribe Thomomyini .... p. 518

  B′ Upper incisors grooved, bearing either one or two sulci; form of third upper molar distinctly different from M1 and M2, fully or partially biprismatic (with a few exceptions discussed beyond), without marked anteoposterior compression (either subtriangular, elongated, suborbicular or quadriform in cross-section, but not elliptical as in M1 and M2), and having typical transverse anterior plate and two lateral plates (varying in their development, depending on taxa), but no posterior plate, and with lateral re-entrant folds usually developed, especially labial inflection (although sometimes minute in a few species, as described beyond); basitemporal fossa well-developed, although occasionally shallow or absent (primitive species of *Zygogeomys*); forefoot large and broad, with elongated claws for digging. Tribe Geomyini .... p. 521

Tribe DIKKOMYINI, new tribe

Genotype.—Dikkomys Wood, 1936.

Chronologic and geographic range.—Early to Middle Pliocene (early Arikareean to mid-Hemphillian) in western United States. Known from Miocene fossil sites in Montana, South Dakota, and Nebraska and Pliocene sites in South Dakota, Oregon, Nevada, and southern California. For precise localities see accounts of *Dikkomys* and *Pliosaccomys* beyond.

Diagnosis.—Small Geomyinae; lacking specializations of more advanced tribes; upper incisors smooth, at least in *Pliosaccomys;* molariform teeth always rooted and having crowns of medium height; enamel investment of cheek teeth complete and uninterrupted in all stages of wear; crowns of molars primitively biprismatic, having two columns united at mid-points, thus forming narrow isthmus separating lateral re-entrant folds as in premolars, and, with wear, also uniting secondarily at protomeres (with exception of third lower molars), consequently, isolating remnant of that inflection as shallow fossette (columns uniting first at protomeres in *Pliosaccomys*); anterior and posterior columns of first and second molars, both above and below, becoming progressively united into one column in advanced Dikkomyini (early and middle Pliocene), but m3 (M3 unknown) retaining primitive biprismatic pattern, with columns joined at centers but never at protomeres (for details of dentition see generic accounts); mandible stout, its angle mostly above mandibular tooth-row; masseteric ridge low; basitemporal fossa barely discernable in some fragments of *Pliosaccomys;* postcranial skeleton unknown.

Key to the Genera of the Tribe Dikkomyini

A Molars biprismatic throughout life; anterior and posterior lophs of first and second molars in pre-final stages of wear uniting first at their mid-points and later at edge of protomeres; anterior lophid of lower premolar having distinct anteroexternal inflection. Genus *Dikkomys* . . . . p. 516

A′ First and second molars becoming monoprismatic in final (adult?) stages of wear, biprismatic only in pre-final stages of wear; third molars persistently biprismatic; anterior and posterior lophs of first and second molars uniting first at edge of protomeres; anterior lophid of lower premolar lacking anteroexternal inflection. Genus *Pliosaccomys* . . . . p. 517

Genus Dikkomys Wood

1936. *Dikkomys* Wood, Amer. Mus. Novit., 866:26, July 2.

Type.—*Dikkomys matthewi* Wood, 1936, from Lower Harrison deposits near Agate, Sioux County, Nebraska.

Chronologic range.—Early Miocene, from early Arikareean (Lower Harrison local fauna of Nebraska) to middle Miocene, late Hemingfordian (Upper Rosebud local fauna, South Dakota, and the Deep River Formation, Montana). According to MacDonald (1963:149-150), the Upper Rosebud is middle Miocene rather than early Miocene.

Description.—Size small, about as in small kinds of *Thomomys;* known only from fragmentary mandible, including molariform dentition in place, and isolated cheek teeth, including M1 (see Wood, 1936:26-28 and fig. 32; Galbreath, 1948:316-317 and fig. 1; and Black, 1961:13-14 and fig. 58); upper incisors unknown; cheek-teeth hyposodont, persistently rooted, and having crowns of medium height compared with Recent geomyids; enamel investment complete and uninterrupted in all molariform teeth in all stages of wear; P4 unknown, but probably formed like p4; p4 persistently biprismatic, two crowns joined at mid-points by relatively narrow isthmus separating lateral re-entrant folds; anterior lophid of p4 having distinct anterioexternal inflection; molars also biprismatic throughout life; two lophids of lower molars first uniting at mid-points as in p4, and, with additional wear, m1 and m2 secondarily uniting at edge of protomeres and forming isolated enamel fossette between point of, connection (detailed description of stages of wear discussed in account of phylogeny of subfamily); m3 permanently joined at mid-point only, without lateral union at edge of protomeres; upper molars, judging by M1 (M2 and M3 unknown), having same pattern as lower molars, but first union of lophs decidedly on lingual side of center, consequently, lingual re-entrant fold small; M1 probably developing U-pattern in advanced stages of wear by union of protomeres, with minute lingual fossette developing in transition as lophs secondarily become united at lingual edge of columns; mandible stout and geomyidlike; masseteric ridge weakly developed; basitemporal fossa absent.

Evidently, *Dikkomys matthewi* is more primitive than *Dikkomys woodi.* The modified H-pattern in m1 and m2, with the metalophid and hypolophid joined at both their mid-points and also at their protomeres (by union of the protostylid and hypostylid in the lower dentition), is persistent throughout life. Therefore, the enclosed enamel fossette is not eradicated with wear. In m1 and m2 of *Dikkomys woodi,* the fossette is shallower, and, at least in advanced stages of wear, it would disappear, therefore, forming a U-pattern on the occlusal surface, as in M1 and M2, but laterial inflection horizontally shallow rather than deep as in entoptychines.

Specimen (No. P 26284 FMNH) reported as *Dikkomys matthewi* by Galbreath (1948:316) is referable to the recently described species *Dikkomys woodi* Black, 1961.

Specimens examined.—One, no. P 26284, Field Mus. Nat. Hist., from upper Rosebud, Shannon Co., South Dakota.

Referred species.—two:

Dikkomys matthewi Wood, 1936. Amer. Mus. Novit., 866:26, July. Type from early Arikareean Lower Harrison deposits (early Miocene) near Agate, Sioux County, Nebraska.

Dikkomys woodi Black, 1961. Postilla, Yale Peabody Museum, 48:13, January 16. Type from Deep River Formation, late Hemingfordian (middle Miocene), Meagher County, Montana; also known from Upper Rosebud deposits (middle Miocene) near Wounded Knee, Shannon County, South Dakota.

Genus Pliosaccomys Wilson

1936. *Pliosaccomys* Wilson, Carnegie Inst. Washington Publ., 473:20, May 21.

Type.—*Pliosaccomys dubius* Wilson, 1936, from Smiths Valley local fauna in Lyon County, Nevada.

Chronologic range.—Early Pliocene, late Clarendonian (Wolf Creek local fauna, South Dakota, and Nettle Springs local fauna, California) to Middle Pliocene, middle part of Hemphillian (Smiths Valley local fauna, Nevada, and McKay Reservoir and Otis Basin local faunas, Oregon).

Description.—Size small (alveolar length of mandibular tooth-row measuring 6.0 in holotype), about as in *Thomomys monticola;* upper incisor relatively broad and flat, having anterior face smooth, without trace of grooving; crowns of cheek teeth of medium height and rooted; enamel investment continuous and uninterrupted in all stages of wear; premolars permanently, biprismatic; P4 having anterior prism subtriangular and decidedly smaller that subcrescentic posterior prism, and joined near centers by narrow, obliquely oriented isthmus; p4 having anterior prism subovate, posterior prism strongly compressed anteroposteriorly, and joined at mid-points by relatively broad and straight isthmus; first and second molars, both above and below, monoprismatic in final (?adult) stage of wear, derived ontogenetically from primitive bilophate pattern by coalescence of two columns into one; M1 and M2 mirror images of m1 and m2 in pre-final stages of wear, two columns first uniting at edge of protomeres forming U-pattern, and primitive H-pattern never developing in either series (for detailed description of stages of wear, see account of phylogeny, p. 546); m3 (M3 unknown, but probably with same form as in Geomyini, see p. 552) persistently biprismatic, two columns joined by relatively broad isthmus at centers, consequently, forming H-pattern of primitive ancestors; rostrum heavy and broad as in modern geomyids; palate narrow and strongly ribbed; mandible stout; masseteric ridge and fossa well developed; basitemporal fossa absent.

Specimens examined.—Six, nos. 1796 (holotype)—1799, 1804 and 1806 (CIT) now in the Los Angeles County Museum, all from Smiths Valley local fauna, Middle Pliocene, Nevada.

Referred species.—two:

**Pliosaccomys dubius* Wilson, 1936. Carnegie Inst. Washington Publ., 743:20, May 21. Known from early and middle Pliocene faunas including Wolf Creek local fauna (late Clarendonian), Shannon County, South Dakota; McKay Reservoir local fauna and Otis Basin local fauna (Hemphillian), Oregon; type from Smiths Valley local fauna (probably middle Hemphillian), Lyon County, Nevada.

Pliosaccomys wilsoni James, 1963. Univ. California Publ. Geol. Sci., 45:101, June 26. Type from Nettle Springs local fauna of late Clarendonian (early Pliocene), Ventura County, California.

Tribe THOMOMYINI, new tribe

Type.—*Thomomys* Wied-Neuwied, 1839.

Chronologic and geographic range.—Known from late Pliocene (early Blancan) to Recent. Known primarily from western North America from southern Canada south to Central México in Pliocene, Pleistocene and Recent and in middle and late Pleistocene of Maryland and Florida.

Diagnosis.—Size small to medium (basilar length exclusive of *T. bulbivorus*, measuring from approximately 24 to 45, including both males and females); upper incisors without grooving, excepting fine, indistinct sulcus rarely near inner margin (grooving more common in *T. monticola* than in other Recent species); crowns of cheek teeth high, rooted and ever-growing; all molars, including M3, monoprismatic and anteroposteriorly compressed, sometimes (especially in subadults) having slight inflection on labial side in upper teeth and lingual side in lower teeth; molars bicolumnar in pre-final stages of wear (seen in juvenal teeth only), patterns of wear in both upper and lower molars resembling those of *Pliosaccomys*, except that crowns of m3 and M3 unite into single column in final stages of wear; enamel pattern interrupted in all cheek teeth, loss occurring only at sides of each column; transverse enamel blade completely covering posterior face of both P4 and p4; all upper and lower molars with two transverse enamel blades, one on anterior surface and one on posterior surface, of each tooth, including M3; small third plate sometimes persistent on broad side of tooth, labial side in upper molars and lingual side in lower molars (*T. bulbivorous*); skull generalized, neither unusually narrow and deep or broad and flat; usually without marked cresting or rugosity; masseteric ridge well developed and massive; basitemporal fossa absent, sometimes shallow depression forming in *T. townsendii;* pelage soft, never harsh or hispid, covering body with thick coat of hair; forefoot exceptionally small for fossorial mammal, claws not especially long; body form remarkably fossorial.

The tribe Thomomyini is monotypic, including only the genus *Thomomys*.

Genus Thomomys Wied-Neuwied

1839. *Thomomys* Wied-Neuwied, Nova Acta Phys. Med. Acad. Caesar. Leop.-Carol., 19(1):377.

1836. *Oryctomys* Eydoux and Gervais (in part), Mag. de Zool., 6:20, pl. 21. Type: *Oryctomys* (*Saccophorus*) *bottae*, from coast of California, probably near Monterey.

1903. *Megascapheus* Elliot, Field Columb. Mus., Publ. 76, Zool. Ser., 3(11):190, July 25. Type: *Diplostoma bulbivorum* Richardson, from Columbia River, probably near Portland, Ore.

1933. *Pleisothomomys* Gidley and Gazin, Jour. Mamm. 14:354. Type: *Pleisothomomys potomacensis* Gidley and Gazin, from Pleistocene, Cumberland Cave local fauna, Allegany County, Maryland.

Chronologic range.—Known from late Pliocene to Recent.

Description.—Same as that given for the tribe Thomomyini above.

Discussion.—Features characterizing *Thomomys* and the tribe Thomomyini are more advanced than those characterizing the tribe Dikkomyini. Also, the

Thomomyini retain more of the primitive features of the Geomyinae than do the more specialized tribe Geomyini.

Specializations are few, but include the third molar being a single column both above and below, enamel plates, and a masseteric ridge.

Key to the Subgenera of *Thomomys*

A Molars sub-crescent or ovate in cross-section, not becoming abruptly narrower at one end of tooth. Subgenus *Pleisothomomys*.......... p. 519

A′ Molars pear-shaped, not sub-crescent or ovate, in cross-section, crown becoming abruptly narrow at one end of tooth. Subgenus *Thomomys*, p. 520

Subgenus **Pleisothomomys** Gidley and Gazin

1933. *Pleisothomomys* Gidley and Gazin, Jour. Mamm., 14:354, November 13.

Type.—Pleisothomomys potomacensis Gidley and Gazin, 1933.

Chronologic range.—Late Pliocene (Hagerman local fauna, Idaho) to late Pleistocene. The latest records are from the fauna of Saber-tooth Cave, Florida, a late Pleistocene assemblage that probably was deposited in the Sangamon. The middle and late Pleistocene records are from the eastern United States, suggesting that the subgenus *Pleisothomomys* was restricted to that region while the subgenus *Thomomys* occupied the western United States and parts of Canada and México as it does today.

Description and Comparison.—Separated from subgenus *Thomomys* only on basis of sub-crescentic shaped molars (only jaw fragments and isolated teeth known), seemingly a primitive feature of the genus. This dental structure continued into the late Pleistocene; none of the Recent species expresses this feature of the molars, although the molars of *Thomomys vetus* of the late Pleistocene (Wisconsin deposits), referred to the subgenus *Thomomys* on the basis of its alleged relationship to *Thomomys townsendii* (see Davis, 1937: 156-158), are less distinctly pear-shaped, and are more sub-crescentic, than in any other known species of the subgenus *Thomomys*. *Pleisothomomys* Gidley and Gazin (*loc. cit.*) was proposed as a genus but is here considered as of no more than subgeneric worth, and is recognized because of the apparent constancy of the sub-crescentic molars in the earlier members of the genus and in those populations of *Thomomys* occurring in Pleistocene times in the eastern United States.

Referred species.—Three (all extinct):

**Thomomys gidleyi* Wilson, 1933. Carnegie Inst. Washington Publ. 440:122, December. Type from Hagerman beds, late Pliocene, Idaho.

**Thomomys potomacensis* Gidley and Gazin, 1933. Jour. Mamm., 14:354, November 13. Type from Cumberland Cave, middle and late Pleistocene, Maryland.

**Thomomys orientalis* Simpson, 1928. Amer. Mus. Novit., 328:6, October 26. Type from Saber-tooth Cave, late Pleistocene, Florida.

Subgenus Thomomys Wied-Neuwied

1839. *Thomomys* Wied-Neuwied, Nova Acta Phys.-Med. Acad. Caesar. Leop. Carol., 19(1):377.

1903. *Megascapheus* Elliot, Field Columb. Mus., Publ. 76, Zool. Ser., 3 (11):190, July 25. Type: *Diplostoma bulbivorum* Richardson, from Columbia River, probably near Portland, Oregon.

Type.—*Thomomys rufescens* Wied-Neuwied, 1839.

Chronologic range.—Early Pleistocene (Broadwater-Lisco local fauna, Nebraska) to Recent. Numerous records, mostly isolated teeth, from nearly all stratigraphic levels of the Pleistocene (for details, see account of fossil record).

Description.—Molars pear-shaped in cross-section, becoming abruptly narrow at one end of the tooth. The teeth of the late Pleistocene species *Thomomys vetus* are less distinctly pear-shaped than other referred species (see remarks in the description of the subgenus *Pleisothomomys*).

Essentially on the basis of its significantly larger size and details of the skull, Elliott (1903:190) proposed subgeneric recognition of *Thomomys bulbivorus* and described the subgenus *Megascapheus* to include it. Also the molars of *Thomomys bulbivorus* usually have a small enamel plate, both above and below, bordering the persistent inflection on the protomere end of the tooth; each lateral plate is isolated from the transverse plates on the anterior and posterior walls of the tooth. In my opinion these features do not warrant subgeneric recognition; however, these characters do distinctly separate *Thomomys bulbivorus* from other groups of species, and the character of the molars suggests retention of a primitive trait. Therefore, I propose that the unique structure of this species be recognized by setting it apart in the *bulbivorus* species-group.

Referred species.—Ten species, three extinct, placed in three species-groups (the numerous subspecies of this genus are listed in Miller and Kellogg, 1955: 276-332, and Hall and Kelson, 1959:412-447).

bulbivorus species-group

Thomomys bulbivorus (Richardson, 1829). Fauna Boreali-Americana, 1:206. Type from Columbia River, probably near Portland, Oregon.

umbrinus species-group

**Thomomys scudderi* Hay, 1921. Proc. U. S. Nat. Mus., 49:614. Type from Fossil Lake beds, late Pleistocene, Oregon.

Thomomys umbrinus (Richardson, 1829). Fauna Boreali-Americana, 1:202. Type from southern México, probably near Boca de Monte, Veracruz.

Thomomys bottae (Eydoux and Gervais, 1836). Mag. de Zool., Paris, 6:23. Type from coast of California, probably near Monterey.

**Thomomys vetus* Davis, 1937. Jour. Mamm., 18:156, May 12. Type from Fossil Lake beds, late Pleistocene, Oregon.

Thomomys townsendii (Bachman, 1839). Jour. Acad. Nat. Sci. Philadelphia, 8:105. Type probably from near Nampa, Canyon Co., Idaho (erroneously given as "Columbia River").

talpoides species-group

**Thomomys microdon* Sinclair, 1905. Bull. Dept. Geol. Univ. California, 4:145-161. Type from Potter Creek Cave, late Pleistocene, California.

Thomomys monticola J. A. Allen, 1893. Bull. Amer. Mus. Nat. Hist., 5:48, April 28. Type from Mt. Tallac, 7500 ft., El Dorado Co., California.

Thomomys talpoides (Richardson, 1828). Zool. Jour., 3:518. Type locality fixed at near Fort Carlton (Carlton House), Saskatchewan River, Saskatchewan, Canada.

Thomomys mazama Merriam, 1897. Proc. Biol. Soc. Washington, 11:214, July 15. Type from Anna Creek, 6000 ft., near Crater Lake, Mt. Mazama, Klamath Co., Washington.

Tribe GEOMYINI, new tribe

Genotype.—Geomys Rafinesque, 1817.

Chronologic and geographic range.—Known from late middle Pliocene deposits to Recent. The range of living members extends from extreme southern Manitoba and the southeastern United States south to southern Panamá, and probably northern Colombia, South America.

Diagnosis.—Size small to large (condylobasal length of skull 33.0 to 73.0 in adults, including both sexes); sexual dimorphism marked, sometimes strongly, females being smaller than males, especially in cranial dimensions; upper incisors invariably grooved, number and position of grooves varying according to genus; cheek teeth high-crowned and ever-growing, except in one primitive genus (*Pliogeomys*); all three lower molars and M1 and M2 monoprismatic, and elliptical in cross-section in final stages of wear (teeth of young, subadult, and adult animals); primitive biprismatic patterns (as known from Recent specimens) occurring only in pre-final stages of wear (teeth of juveniles only); biprismatic patterns of lower molars as in *Dikkomys*, and upper molars as in *Pliosaccomys* (for detailed description of these patterns, see account beyond of the phylogeny of the Geomyinae); m3 becoming monoprismatic, anteroposteriorly compressed and elliptical in cross-section like m1 and m2, but M3 remaining, with rare exceptions (see accounts of *Geomys* and *Pappogeomys* beyond), at least partially biprismatic throughout life, having one or both lateral inflections usually persisting (with exceptions) and developing various occlusal shapes (subtriangular, elongate, obcordate, suborbiculate, or quadriform) but never elliptical.

Enamel of cheek teeth reduced to interrupted plates, with exception of p4 in *Pliogeomys;* plate on posterior wall of P4 variable, occurring completely across posterior surface in primitive members, but progressively reduced to lingual side only or completely lost in modern genera (see generic accounts beyond for detailed description); both anterior and posterior plates usually retained in M1 and M2, posterior plate sometimes reduced to lingual side or completely lost (as in *Pappogeomys*) but anterior plate always completely retained; M3 usually having three plates, one anterior and two lateral; posterior plate wanting (sometimes lingual plate moved to posterior position); plates retained completely across posterior walls of all lower cheek teeth with no reduction, but anterior plates of m1-3 always lacking, except in primitive genus *Pliogeomys* (only Geomyini having both anterior and posterior enamel plates on lower molars.

Skull primitively generalized, but becoming specialized towards either dolichocephly (*Orthogeomys*) or platycephaly (*Pappogeomys*) in two modern genera; skull highly specialized for fossorial life; mandible stout and deep, angular process being high and diverging laterally at right angles to ramus; masseteric ridge and fossa weakly developed in primitive members, becoming well developed and massive in modern genera; basitemporal fossa absent in primitive forms (*Pliogeomys* and early members of *Zygogeomys*); pelage usually soft, but harsh and hispid in some genera; forefeet broad and massive, claws long and stout for digging; body form remarkably fossorial.

The tribe Geomyini includes the most highly specialized members of the subfamily Geomyinae.

Key to the Genera of the Tribe Geomyini

A Cheek teeth rooted; p4 with uninterrupted enamel loop; enamel plates on both anterior and posterior walls of m1 and m2; masseteric ridge weakly developed, low, not massive. Genus *Pliogeomys* .... p. 522

A′ Cheek teeth rootless, ever-growing; p4 with enamel investment interrupted at ends of columns, consequently, forming four islated plates; enamel plate retained only on posterior wall of m1 and m2, anterior wall without trace of enamel (except rarely in pre-final stage of wear in *Geomys tobinensis* of middle Pleistocene); masseteric crest strongly developed and massive.

  B Enamel plate on posterior wall of P4, but usually restricted to lingual end of tooth (usually absent in subgenus *Orthogeomys* of genus *Orthogeomys*); M3 conspicuously bicolumnar, longer than wide owing to elongation of posterior loph.

    C Upper incisor bisulcate; skull generalized; rostrum relatively narrow; length of labial enamel plate of M3 decidedly less than length of lingual plate; pelage soft and thick. Genus *Zygogeomys* ... p. 523

    C′ Upper incisor unisulcate; skull strongly dolichocephalic; rostrum remarkably broad and massive; length of lingual plate of M3 approximately equal to, or greater than, length of labial plate; pelage harsh, often hispid and scant. Genus *Orthogeomys* .... p. 528

  B′ Posterior wall of P4 without trace of enamel; M3 not strongly bicolumnar, having shallow re-entrant fold on labial side, and crown no longer than wide owing to shortness of posterior loph.

    D Upper incisor bisulcate; skull generalized; both anterior and posterior walls of M1 and M2 having complete enamel plates. Genus *Geomys* .... p. 525

    D′ Upper incisor unisulcate; skull generalized or tending towards platycephaly; enamel plate on posterior wall of M1 usually reduced to lingual side or absent (complete only in one species, *Pappogeomys bulleri*); enamel plate on posterior wall of M2 also absent in advanced species (subgenus *Cratogeomys*). Genus *Pappogeomys* .... p. 532

Genus Pliogeomys Hibbard

1954. *Pliogeomys* Hibbard, Michigan Acad. Sci., Arts and Letters, 39:353.

Genotype.—*Pliogeomys buisi* Hibbard, 1954, from Buis Ranch local fauna (middle Pliocene), Beaver County, Oklahoma.

Chronologic range.—Latest Middle Pliocene, known only from the highest part of the Hemphillian mammalian fauna (Buis Ranch local fauna, Oklahoma). Professor Hibbard informs me (personal communication) that he found the type, a right ramus, lying on the surface near the base of the fossil beds. The isolated teeth of small geomyids from the Saw Rock Canyon local fauna (see Hibbard, 1953:392) may also be referable to this genus. The Saw Rock Canyon local fauna may also be middle Pliocene in age but is considered to be from the later part of the late Pliocene, and, therefore, somewhat younger than the Buis Ranch local fauna (Hibbard, *op. cit.*:342).

Description and discussion.—The size of members of this small genus of the Geomyinae is about the same as in smaller adults of *Geomys bursarius*. According to Hibbard (*op. cit.*:353), the holotype is smaller than specimens from the Rexroad local fauna referred to *Geomys quinni* and larger than specimens referred to *Zygogeomys* cf. *minor*. The cheek teeth are rooted, and the crowns are as high as those of living geomyids. The upper incisor is bisulcate, and the inner groove is fine and indistinct in places.

Of the molariform dentition only the lower premolar and first two lower molars are known. The enamel investment of p4 is complete, and would not be subject to interruption at any stage of wear; the two prisms are joined at their mid-points, and the isthmus of dentine is relatively broad (as in *Pliossacomys*) when compared with modern pocket gophers of this tribe. Also, the re-entrant folds, rather than having parallel sides, diverge broadly to the sides. The divergence is especially noticeable in the labial fold. The lower deciduous premolar would have formed essentially the same enamel pattern with wear as observed in *Nerterogeomys* [= *Zygogeomys*] cf. *minor* (see Hibbard, 1954: fig. 5, A and B) and *Pliosaccomys dubius* (see Wilson, 1936; pl. 1, fig. 1). Each molar is a single column in the final stages of wear; pre-final stages are unknown. Anterior and posterior enamel plates are present on m1 and m2 (m3 has not been recovered). The dentine tracts of m1 are exposed over a relatively wide surface; therefore, the enamel plates are distinctly separated. The tracts of dentine of m2 are much narrower than in m1 and the enamel plates are barely separated at the anterolateral margin of the tooth. Possibly the enamel band of m2 was continuous in an earlier stage of wear.

The mandible is stout and its general construction not unlike that in modern geomyines. The capsule at the base of the angular process that receives the terminal end of the lower incisor is well developed. The base of the angular processes is preserved, and suggests that the process was short and decidedly smaller than in living examples of the tribe. The masseteric ridge is distinct but weakly developed, and not at all massive as in living pocket gophers. The mental foramen is immediately anterior, and slightly ventral, to the anterior extension of the crest. The basitemporal fossa is absent as such, but its position is marked by a slight depression.

Specimens examined.—Two rami; nos. 29147 (holotype) and 33446; several isolated teeth 30194 and 30195, including an upper incisor and a dp4 (deciduous lower premolar), all from Univ. Michigan Mus. Paleo.

Referred species.—One.

**Pliogeomys buisi* Hibbard, 1954. Papers Michigan Acad. Sci., Arts, and Letters, 39:353. Type from Buis local fauna, latest middle Pliocene, Beaver County, Oklahoma.

Genus Zygogeomys Merriam

1895. *Zygogeomys* Merriam, N. Amer. Fauna, 8:195, January 31.

1942. *Nerterogeomys* Gazin, Proc. U. S. Nat. Mus., 92:507 (type, *Geomys persimilis* Hay, 1927).

Type.—*Zygogeomys trichopus* Merriam, 1895, from Nahuatzen, Michoacán.

Chronologic range.—Late Pliocene (Benson and Curtis Ranch local faunas, Arizona, and ?Rexroad Formation, Kansas) to Recent.

Description and discussion.—The size is small to medium for the subfamily Geomyinae. This genus is distinguished principally by the retention of primitive features. In the living species, the skull is generalized, rather than specialized toward either extreme dolichocephaly or platycephaly. The angular process is short, barely exceeding the lateral extensions of the mastoid process of the squamosal. The rostrum is remarkably narrow in relation to its length. The jugal is reduced and displaced ventrally, causing the maxillary arm of the zygomata to articulate with the squamosal arm of the zygomata along the dorsal border of the zygomatic arch (a feature observed also in *Orthogeomys cherriei costaricensis*).

The upper incisor, recovered in material from the late Pliocene and middle Pleistocene, is bisulcate as in the genus *Geomys* and the primitive genus *Pliogeomys.* The enamel plate across the posterior wall of P4 is either complete (late Pliocene to late Pleistocene) or restricted to the lingual half of the tooth (always restricted in living species). The Pliocene specimens of the Rexroad local fauna referred to *Nerterogeomys* cf. *minor* by Hibbard (1950:138-139) are exceptional. In these specimens the length and position of the posterior enamel plate is variable; however, all but one specimen had persistant enamel. Evidently, in approximately 43 per cent of the specimens, a complete enamel blade was present (see Paulson, 1961:139), and in the others (except the one without any enamel) the plate was restricted to a small area of the ventral surface, usually on the lingual side of the loph. Hibbard suggested that the decrease in size of the plate, and its restriction to the lingual side, may be a function of age. Hence, most adults would be characterized by the reduced posterior plate on the upper premolar. Although age may be the important factor, intragroup variation cannot be ruled out. It is of interest to note that in all specimens from the Benson (type series of *P. minor*) and Curtis Ranch local faunas, the former of late Pliocene age and the latter of middle Pleistocene age, the enamel plates are complete on the posterior face of the upper premolar. As mentioned before, the specimens from Kansas may actually represent the transitional stages of the early evolution of *Geomys* in which the posterior plate of P4 is entirely lost. The enamel pattern of p4 is like that in other members of the tribe (excepting the genus *Pliogeomys*). The re-entrant angles of P4 and p4 are widely open (obtuse) in the examples recovered from late Pliocene and middle Pleistocene deposits, representing retention of a trait that is primitive in the Geomyini (see account of phylogeny).

M1 and M2 are elliptical in cross-section and each has an enamel plate on both the anterior and posterior surface. In the living species (*Z. trichopus*), the posterior enamel plate fails to reach the labial margin of the tooth and is restricted to the lingual two-thirds of the posterior surface; however, the enamel plates are complete in the late Pliocene species (*Z. minor*) and the middle Pleistocene species (*Z. persimilis*), being only slightly separated from the anterior plate by narrow tracts of dentine on the ends of the tooth. M3 is partly biprismatic in the living species, the two incompletely divided lophs being separated by a distinct outer sulcus. The posterior loph is elongated and forms a conspicuous heel paralleling the evolution of this trait in the genus *Orthogeomys;* therefore, the crown is longer than wide. The posterior part of the tooth is protected by two lateral enamel plates; of the two, the lingual plate is especially long and extends to the end of the heel. M3 has not been recovered in the Pliocene species, but in the middle Pleistocene species (*Z. persimilis*) M3 is subtriangular, no longer than wide, and the lateral inflections are weakly developed. The trend towards elongation of M3 evidently occurred in late Pleistocene evolution of the genus. All three of the inferior molars are elliptical, and only the posterior enamel plate is present (as in all other genera of the tribe except *Pliogeomys*).

The masseteric ridge of the mandible is well developed. In the late Pliocene species *Z. persimilis* and *Z. minor* the mental foramen is directly beneath the anterior extension of the masseteric ridge, but in the living species, *Z. trichopus,* the foramen lies well anterior to the ridge. The basitemporal fossa in the living species is well developed and deep; in the Pliocene species it is usually distinct but shallow (late Pliocene specimens of *Z. minor*).

Referred species.—Three (two extinct and one living; the last has two subspecies):

**Zygogeomys minor* (Gidley), 1922. U. S. Geol. Surv. Prof. Paper, 131: 123, December 26. Type from Benson local fauna (late Pliocene), Cochise County, Arizona; also known from the Rexroad local fauna, Meade County, Kansas.

**Zygogeomys persimilis* Hay, 1927. Carnegie Inst. Washington Publ., 136. Originally described by Gidley, 1922 (U. S. Geol. Surv. Prof. Papers, 131:123, December 26) as *Geomys parvidens* which was preoccupied by *G. parvidens* Brown, 1908. Type from Curtis Ranch local fauna (middle Pleistocene), Cochise County, Arizona.

Zygogeomys trichopus trichopus Merriam, 1895. N. Amer. Fauna, 8:196, January 31. Type from Nahuatzen, Michoacán.

Zygogeomys trichopus tarascensis Goldman, 1938. Proc. Biol. Soc. Washington, 51:211, December 23. Type from 6 mi. SE Pátzcuaro, 8,000 ft., Michoacán.

Genus Geomys Rafinesque

1817. *Geomys* Rafinesque, Amer. Monthly Mag., 2(1):45, November.

1817. *Diplostoma* Rafinesque, Amer. Monthly Mag., 2(1):44-45, November. Included species: *Diplostoma fusca* Rafinesque [= *Mus bursarius* Shaw] and *Diplostoma alba* Rafinesque [= *Mus bursarius* Shaw] from the Missouri River region.

1820. *Saccophorus* Kuhl, Beitr. Zool. und Vergl. Anat., pp. 65, 66. Type: *Mus bursarius* Shaw, from upper Mississippi Valley.

1823. *Pseudostoma* Say, Long's Expd. Rocky Mts., I, pp. 406. Type: *Pseudostoma bursaria* [= *Mus bursarius* Shaw], from upper Mississippi Valley.

1825. *Ascomys* Lichtenstein, Abh. K. Akad. Wiss. Berlin (1822), p. 20., fig. 2. Type: *Ascomys canadensis* Lichtenstein [= *Mus bursarius* Say], probably from upper Mississippi Valley.

1944. *Parageomys* Hibbard, Bull. Geol. Soc. Amer., 55:735, June. Type: *Parageomys tobinensis* Hibbard, from Pleistocene, Cudahy (Tobin) local fauna, Russell Co., Kansas.

Type.—*Geomys pinetis* Rafinesque, 1817, restricted to Screven County, Georgia, in region of the pines.

Chronologic range.—Late Pliocene faunas of Blancan age (Rexroad, Kansas, and Sand Draw, Nebraska, local faunas) to Recent. Reported from numerous Pleistocene deposits of all stratigraphic levels, especially from the Great Plains, where common today.

Description and discussion.—Pocket gophers of this genus are medium-sized geomyids; none is so small as the average-sized *Thomomys.* The skull is generalized and lacks the dolichocephalic and platycephalic specializations seen in the genera *Orthogeomys* and *Pappogeomys,* respectively. *Geomys* closely resembles *Zygogeomys,* but retains fewer of the primitive characters of the ancestral stock. At the same time, *Geomys* has several specializations. Even so, a considerable amount of parallelism is evident in the phyletic trends of the two genera.

The upper incisor of *Geomys* is bisulcate as in *Pliogeomys* and *Zygogeomys;* the deeper grove is medial and the shallower grove lies near the inner border of the tooth. The premolar, above and below, is bicolumnar; and two columns are joined at their mid-points (deep re-entrant angles separate the columns at the sides). A permanent enamel plate protects the anterior face of the anterior loph, and enamel bands outline each of the re-entrant folds. In p4 a complete enamel plate covers the posterior surface of the posterior loph. All of the enamel bands are interrupted by tracts of dentine, except in the initial stages of wear of the occlusal surface of the newly erupted tooth. For a short time in living *Geomys*, the enamel bands are continuous as observed in juveniles of *Geomys bursarius major* (KU 5628, 8531, and 41540). But, the enamel cap is thin and the dentine tracts, which are high on the sides of the tooth, are soon revealed by a minimum of wear on the crown. Therefore, the adult, or final, pattern characterized by interrupted enamel plates emerges early in life and remains throughout the life of the individual. Evidence from fossil *Geomys*, especially from specimens from early and late Pleistocene deposits, suggests that the final adult pattern appears later, ontogenetically, than in Recent specimens. Some of the fossil premolars in initial stages of wear have continuous and uninterrupted bands of enamel. *Geomys quinni* of the late Pliocene and early Pleistocene has the interrupted pattern seen in late Pleistocene and Recent *Geomys*. Also, in late Pliocene and early Pleistocene species, the re-entrant folds diverge laterally and form "open" angles. In later taxa (middle Pleistocene to Recent) the folds are compressed and parallel-sided, and the "open" folds are found only in the early stages of wear.

The posterior enamel plate of P4 disappears in the final stages of wear as the interrupted enamel pattern is formed. In the late Pleistocene and Recent *Geomys*, the loss of the posterior plate occurs early in life, usually in the first phases of wear on the occlusal surface of the newly erupted tooth, but in fossils of *Geomys* of corresponding ontogenetic age from the early and middle Pleistocene, the posterior plate is retained in some individuals until a later phase of wear, thereby delaying the appearance of the final patern. Indeed, in five or fewer per cent of the individuals (see Paulson, 1961:138-139; and White and Downs, 1961:18) a vestige of enamel is retained throughout life or at least until late in adulthood. In *Geomys tobinensis*, for example, a thin, but transversely complete, plate of enamel occurs all the way down to the base of the loph (Paulson, *loc. cit.*) and would persist throughout life. In *Geomys garbanii*, a vestige on the lingual side of the posterior surface of a fully adult specimen was noted by White and Downs (*loc. cit.*). Vestiges of the posterior plate occur less frequently in living geomyids. Paulson (*loc. cit.*) found a posterior plate in one of 75 specimens of *Geomys bursarius dutcheri*. A young (suture present between exoccipitals and supraoccipital) female of *Geomys pinetis austrinus* (KU 23358) has a vestige of the posterior plate on the lingual side of the tooth as White and Downs (*loc. cit.*) observed in a specimen of *Geomys garbanii*. The enamel, I suspect, tends to be thicker on the lingual than on the labial side of the loph and extends farther down the lingual surface in some individuals; therefore, wear on the occlusal surface erodes it down to the dentine more rapidly on the labial than on the lingual side. The tendency of enamel to be retained is a primitive feature.

A lower molar of *Geomys* is a single elliptical column, and enamel is restricted to the posterior surface as in *Zygogeomys*, *Orthogeomys*, and *Pappogeomys*. Paulson (*loc. cit.*) found a thin enamel plate on the anterior surfaces of the lower molars in about five per cent of the individuals of *Geomys tobinen-*

sis from the Cudahy local fauna (middle Pleistocene, deposits of the late Kansan glaciation). An anterior plate is unknown in other members of the tribe Geomyini, except in the primitive genus *Pliogeomys* of the middle Pliocene. Occurrence of the plate in *Geomys tobinensis* is an atavistic trait. Primitive dental patterns occur occasionally in geomyids, as pointed out above, but the frequency of occurrence in *G. tobinensis* is higher than would be expected.

M1 and M2, like the lower molars, are elliptical in cross-section. Complete enamel plates on the anterior and posterior surfaces are separated by tracts of dentine on the sides of each tooth. M3 is usually suborbicular (sometimes subtriangular) in cross-section. The tooth is not especially elongated posteriorly and usually has no definite heel; therefore, it is not significantly longer than wide. Living species of *Geomys* rarely have a well defined outer re-entrant fold on M3; less than 10 per cent of the individuals (and usually only one side in each individual in which it occurs) have it, although a shallow inconspicuous groove occurs more frequently. The biprismatic molar characteristic of the ancestral morphotype is less often found in *Geomys* than in any other living member of the tribe Geomyini. The outer re-entrant fold and biprismatic pattern are more often present in the extinct species *Geomys garbanii* of the Middle Pleistocene than in other species. Less than 24 per cent of the third upper molars in *Geomys garbanii* lack a tract of the re-entrant fold and more than 38 per cent have a well developed outer fold (see White and Downs, 1961:13, 18). The bicolumnar pattern, although incomplete, would be clearly evident in those teeth having a well marked re-entrant fold; the pattern occurs less frequently in those teeth with no fold or only a slight one. M3 of geomyids is not usually recovered and, therefore, the occlusal pattern of M3 is unknown in most extinct kinds of *Geomys*. In Recent *Geomys* the fold is more common in the eastern *pinetis* species-group than in the western *bursarius* species-group.

The masseteric ridge on the outer side of the mandible is well developed in all species of the genus. The position of the mental foramen relative to the anterior part of the ridge varies with individuals and according to species. The basitemporal fossa is always present, but is shallower in the late Pliocene and Pleistocene species than in Recent species. The angular process is short.

Referred species.—The twelve species, five of which are extinct, are as follows:

quinni species-group

**Geomys quinni* McGrew, 1944. Geol. Ser., Field Mus. Nat. Hist., 9 (546):49, January 20. Type from Sand Draw local fauna (late Pliocene), Brown County, Nebraska; also known from Broadwater-Lisco local faunas (early Pleistocene), Morrill and Garden counties, Nebraska, Deer Peark local fauna (early Pleistocene), Meade County, Kansas.

**Geomys paenebursarius* Strain, 1966. Bull. Texas Memorial Mus., 10:36. Type from Hudspeth local fauna (early Pleistocene), Hudspeth County, Texas.

**Geomys tobinensis* Hibbard, 1944. Bull. Geol. Soc. Amer., 55:736. Type from Tobin local fauna (middle Pleistocene), Russell County, Kansas; also known from Cudahy local fauna (middle Pleitocene), Meade County, Kansas.

**Geomys garbanii* White and Downs, 1961. Contrib. Sci., Los Angeles Co. Mus., 42:1-34, June 30. Type from Vallecito Creek local fauna (middle Pleistocene), San Diego County, California.

**Geomys bisulcatus* Marsh, 1871. Amer. Jour. Sci., 3:121. Type from Loup River fossil beds, near Camp Thomas, Nebraska (probably late Pleistocene).

bursarius species-group

Geomys parvidens Brown, 1908. Mem. Amer. Mus. Nat. Hist., 9:194. (An extinct subspecies of *Geomys bursarius* according to White and Downs, 1961:6). Type from Conard Fissure local fauna (late Pleistocene), northern Arkansas.

Geomys bursarius (Shaw, 1800). Trans. Linn. Soc. London, 5:227. Type from somewhere in Upper Mississippi Valley, North America.

Geomys arenarius Merriam, 1895. N. Amer. Fauna, 8:139, January 31. Type from El Paso, El Paso County, Texas.

Geomys personatus True, 1889. Proc. U. S. Nat. Mus., 11:159, January 5. Type from Padre Island, Cameron County, Texas.

pinetis species-group

Geomys pinetis Rafinesque, 1806. Amer. Monthly Mag., 2 (1):45, November. Type locality restricted to Screven County, Georgia.

Geomys colonus Bangs, 1898. Proc. Boston Soc. Nat. Hist., 28:178, March. Type from Arnot Plantation, about 4 mi. W St. Marys, Camden County, Georgia.

Geomys cumberlandius Bangs, 1898. Proc. Boston Soc. Nat. Hist., 28: 180, March. Type from Stafford Place, Cumberland Island, Camden County, Georgia.

Geomys fontanelus Sherman, 1940. Jour. Mamm., 21:341, August 13. Type from 7 mi. NW Savannah, Chatham County, Georgia.

Genus **Orthogeomys** Merriam

1895. *Orthogeomys* Merriam, N. Amer. Fauna 8:172, January 31.

1895. *Heterogeomys* Merriam, N. Amer. Fauna 8:179, January 31 (type, *Geomys hispidus* Le Conte, 1862).

1895. *Macrogeomys* Merriam, N. Amer. Fauna 8:185, January 31 (type, *Geomys heterodus* Peters, 1865).

Type.—*Geomys scalops* Thomas, 1894, from Tehuantepec, Oaxaca, México.

Chronologic range.—Late Pleistocene Wisconsin deposits (San Josecito Cave local fauna, Nuevo León, México) to Recent.

Description and discussion.—Species of this genus are of medium to large size. The skull is strongly dolichocephalic in most species; the posterior part of the skull is especially narrow. The angular processes are remarkably short, especially in relation to the length of the mandible. The nasals and rostrum are relatively broad and heavy. The pelage is coarse, and often hispid. In some species the hairs are so sparsely distributed that the body appears almost naked, and none has so dense a covering of hair as do other genera. The genus occurs entirely within the tropical life-zones, and most of the external features seem to be associated with adaptation to tropical conditions.

The upper incisor is unisulcate; the sulcus is usually near the inner border of the tooth, but in some species (subgenus *Orthogeomys*) it is more medial, and in a few individuals with an extremely wide groove the outer lip of the sulcus may actually reach the middle of the tooth. The groove is compressed or open. The premolar is a double column united at the mid-point. The two prisms are of approximately equal size, and the lateral re-entrant folds are so compressed that their sides are parallel. Enamel plates cover the anterior surface and border the re-entrant angles in both upper and lower premolars. As in other members of the tribe, the lower premolar has a fourth enamel plate on the posterior surface of the posterior lophid. In the upper premolar, the enamel plate is reduced to a narrow blade on the lingual side of the loph as in the living species of the genus *Zygogeomys*. In the subgenus *Orthogeomys* the posterior plate is usually absent, and otherwise is narrow and near the lingual border of the tooth.

Each lower molar, in the final stage of wear, consists of a single elliptical column having an enamel plate only on the posterior surface. The first and second upper molars are single elliptical columns having one enamel plate on the anterior surface and another on the posterior surface. The plates are separated by a tract of dentine on each side of the tooth. The third upper molar is partly bilophodont, and the two lophs are separated by a deep outer re-entrant fold. In many of the species an inner re-entrant fold also is retained, but in the adult tooth it is less distinct than the outer. In all of the species the posterior loph is long and forms a conspicuous heel; consequently the crown is significantly longer then wide. Moreover, the posterior loph has an enamel plate on each side. The labial plate always borders the outer re-entrant fold, and in the subgenus *Orthogeomys* is infrequently separated into two small plates.

The mandible is relatively long. Its masseteric ridge is well developed and massive. The basitemporal fossa is usually deep and well defined; it tends to be shallow in the subgenus *Orthogeomys*, and in young individuals is hardly more than a slight depression.

Key to the Subgenera of *Orthogeomys*

A Frontal wide and greatly inflated; no interorbital constriction; enamel plate on posterior wall of P4 usually absent, although sometimes having small plate, restricted to lingual end of wall. Subgenus *Orthogeomys*, p. 529

A′ Frontal narrow and not greatly inflated; interorbital region decidedly constricted; enamel plate on posterior wall of P4 always present but short and restricted to lingual end of wall.

  B Anterior margin of mesopterygoid fossa even with plane of posterior wall of M3; postorbital bar weakly developed; anteroposterior occlusal length of M3 equal to, or less than, combined length of M1 and M2. Subgenus *Heterogeomys* . . . . p. 530

  B′ Anterior margin of mesopterygoid fossa decidedly behind plane of posterior wall of M3; postorbital bar strongly developed; anteroposterior occlusal length of M3 more than combined length of M1 and M2. Subgenus *Macrogeomys* . . . . p. 531

Subgenus Orthogeomys Merriam

1895. *Orthogeomys* Merriam, N. Amer. Fauna, 8:172, January 31.

Type.—Geomys scalops Thomas, 1894, from Tehuantepec, Oaxaca, México.

Chronologic range.—Known only from the Recent.

Description.—Skull elongated and narrow (many skulls of nearly uniform breadth throughout), being extreme in dolichocephalic specializations; mandibles long and narrow, rami not spreading laterally, being more nearly parallel-sided than in other subgenera; angular processes short; breadth across zygomata not significantly exceeding breadth across mastoid processes (in many skulls considerably less); interorbital area remarkably broad, lacking deep constriction; frontals between orbits greatly inflated laterally, postorbital prominence inconspicuous; mesopterygoid fossa extending to level of posterior margin of M3; I having sulcus broader than in other subgenera, mostly on inner half of anterior surface but sometimes overlapping mid-line; enamel plate lacking from posterior wall of P4, rarely retaining narrow vestige near lingual border of posterior loph; M3 having distinct heel, bicolumnar pattern with inner re-entrant fold usually minute, occlusal length less than in other subgenera, length less than combined lengths of M1-2; hair generally coarse, sometimes hispid, sparse, in lowland forms, so sparse as to impart appearance of nakedness.

Referred species and subspecies.—Fourteen taxa:

Orthogeomys grandis alleni Nelson and Goldman, 1930. Jour. Mamm., 11:156, May 9. Type from near Acapulco, 2000 ft., Guerrero.

Orthogeomys grandis annexus Nelson and Goldman, 1933. Proc. Biol. Soc. Washington, 46:195, October 26. Type from Tuxtla Gutierrez, 2600 ft., Chiapas.

Orthogeomys grandis carbo Goodwin, 1956. Amer. Mus. Novit., 1757:5, March 8. Type from Excurano, 2500 ft., Cerro de San Pedro, 20 km. W Mixtequilla, Oaxaca.

Orthogeomys grandis felipensis Nelson and Goldman, 1930. Jour. Mamm., 11:157, May 9. Type from Cerro San Felipe, 10 mi. N Oaxaca, Oaxaca.

Orthogeomys grandis huixtlae Villa, 1944. Anal. Inst. Biol. Univ. Nac. México, 15:319. Type from Finca Lubeca, 12 km. NE Huixtla, 850 m., Chiapas.

Orthogeomys grandis grandis (Thomas, 1893). Ann. Mag. Nat. Hist., ser. 6, 12:270, October. Type from Dueñas, Guatemala.

Orthogeomys grandis latifrons Merriam, 1895. N. Amer. Fauna, 8:178, January 31. Type from Guatemala, exact locality unknown.

Orthogeomys grandis nelsoni Merriam, 1895. N. Amer. Fauna, 8:176, January 31. Type from Mt. Zempoaltepec, 8000 ft., Oaxaca.

Orthogeomys grandis pluto Lawrence, 1933. Proc. New England Zool. Club, 13:66, May 8. Type from Cerro Cantoral, north of Tegucigalpa, Honduras.

Orthogeomys grandis scalops (Thomas, 1894). Ann. Mag. Nat. Hist., ser. 6, 13:437, May. Type from Tehuantepec, Oaxaca.

Orthogeomys grandis soconuscensis Villa, 1949. Anal. Inst. Biol. Univ. Nac. México, 19:267, April 8. Type from Finca Experanza, 710 m., 45 km. (by road) NW Huixtla, Chiapas.

Orthogeomys grandis guerrerensis Nelson and Goldman, 1930. Jour. Mamm., 11:158, May 9. Type from El Limón, in valley of Rio de las Balsas approximately 20 mi. NW La Unión, Guerrero.

Orthogeomys cuniculus Elliot, 1905. Proc. Biol. Soc. Washington, 18:234, December 9. Type from Zanatepec, Oaxaca.

Orthogeomys pygacanthus Dickey, 1928. Proc. Biol. Soc. Washington, 41:9, February 1. Type from Cacaguatique, 3500 ft., Dept. San Miguel, El Salvador.

Subgenus Heterogeomys Merriam

1895. *Heterogeomys* Merriam, N. Amer. Fauna, 8:179, January 21.

Type.—*Geomys hispidus* Le Conte, 1852, from near Jalapa, Veracruz.

Chronologic range.—Late Pleistocene, Wisconsin deposits (San Josecito Cave local fauna, Nuevo León) to the Recent.

Description.—Skull dolichocephalic (less so than in the other subgenera); zygomata more widely spreading than in *Orthogeomys;* ramus and angular process short; interorbital area noticeably constricted; frontals between orbits neither exceptionally broad or inflated; mesopterygoid fossa extending to level of posterior margin of M3; I having sulcus on inner third of anterior surface usually narrower than in subgenus *Orthogeomys;* enamel plate on posterior wall of P4 restricted to lingual half of loph; M3 distinctly biprismatic, posterior loph usually circumscribed by shallow inner re-entrant fold and outer deep fold well developed in all members of genus; posterior loph forming conspicuous heel longer than in subgenus *Orthogeomys;* occlusal length equal to or slightly less than combined lengths of M1-2; hair coarse and hispid but never so sparse as to impart appearance of nakedness.

Referred species and subspecies.—Eleven taxa:

- **Orthogeomys onerosus* (Russell, 1960). Univ. Kansas Publ., Mus. Nat. Hist., 9 (21):544, January 14. Type from San Josecito Cave local fauna, Upper Pleistocene, Nuevo León.
- *Orthogeomys hispidus cayoensis* (Burt, 1937). Occ. Papers Mus. Zool., Univ. Michigan, 365:1, December 16. Type from Mountain Pine Ridge, 12 mi. S El Cayo, British Honduras.
- *Orthogeomys hispidus chiapensis* (Nelson and Goldman, 1929). Proc. Bio. Soc. Washington, 42:151, March 30. Type from Tenejapa, 16 mi. NE San Cristobal, Chiapas.
- *Orthogeomys hispidus concavus* (Nelson and Goldman, 1929). Proc. Biol. Soc. Washington, 42:148, March 30. Type from Pinal de Amoles, Queretaro.
- *Orthogeomys hispidus hispidus* (Le Conte, 1852). Proc. Acad. Nat. Sci. Philadelphia, 6:158. Type from near Jalapa, Veracruz.
- *Orthogeomys hispidus latirostris* (Hall and Alvarez, 1961). Anal. Escuela Nac. Ciencias Biol., 10:121, December 20. Type from Hacienda Tamiahua, Cabo Rojo, Veracruz.
- *Orthogeomys hispidus negatus* (Goodwin, 1953). Amer. Mus. Novit., 1620:1, May 4. Type from Gomez Ferias, 1300 ft., about 45 mi. S Ciudad Victoria, 10 km. W Pan American Highway, Tamaulipas.
- *Orthogeomys hispidus tehuantepecus* (Goldman, 1939). Jour. Washington Acad. Sci., 29:174, April 15. Type from mountains 12 mi. NW Santo Domingo and about 60 mi. N Tehuantepec, 1600 ft., Oaxaca.
- *Orthogeomys hispidus torridus* (Merriam, 1895). N. Amer. Fauna, 8:183, January 31. Type from Chichicaxtle, Veracruz.
- *Orthogeomys hispidus yucatanensis* (Nelson and Goldman, 1929). Proc. Biol. Soc. Washington, 42:150, March 30. Type from Campeche, Campeche.
- *Orthogeomys lanius* (Elliot, 1905). Proc. Biol. Soc. Washington, 18:235, December 9. Type from Xuchil, Veracruz.

Subgenus Macrogeomys Merriam

1895. *Macrogeomys* Merriam, N. Amer. Fauna, 8:185, January 31.

Type.—*Geomys heterodus* Peters, 1865, from Costa Rica, exact locality unknown.

Chronologic range.—Known only from the Recent.

Description.—Skull dolichocephalic in varying degree (overlapping subgenera *Orthogeomys* and *Heterogeomys* in this respect); mandibles elongated, not spreading far laterally; angular processes decidedly short; breadth across zygomata in no instance significantly exceeding mastoid breadth; interorbital area strongly constricted; frontals between orbits slightly inflated laterally (especially in forms having more strongly dolichocephalic skulls); postorbital prominence conspicuous; anterior margin of mesopterygoid fossa terminating well behind M3; I having narrow and deep sulcus entirely on inner third of anterior surface; enamel plate on posterior wall of P4 restricted to inner half of loph; M3 bilophodont (outer and inner re-entrant folds each circumscribing a loph), posterior loph remarkably elongated and forming pronounced heel, length of crown more than combined lengths of M1-2; hair wooly in some individuals, harsh in others but seldom hispid, never so sparse as in subgenus *Orthogeomys;* some species having white markings, especially on lumbar region and head.

Referred species and subspecies.—Eleven taxa:

Orthogeomys heterodus cartagoensis (Goodwin, 1943). Amer. Mus. Novit., 1227:2, April 22. Type from Paso Ancho, Province Cartago, Costa Rica.

Orthogeomys heterodus dolichocephalus (Merriam, 1895). N. Amer. Fauna, 8:189, January 31. Type from San José, Costa Rica.

Orthogeomys heterodus heterodus (Peters, 1865). Monatsb. preuss. Acad. Wiss., Berlin, 1865:177. Type from Costa Rica, exact locality unknown.

Orthogeomys cavator nigrescens (Goodwin, 1943). Amer. Mus. Novit., 1227:3, April 22. Type from El Muneco (Río Navarro), 10 mi. S Cartago, 4000 ft., Province Cartago, Costa Rica.

Orthogeomys cavator pansa (Bangs, 1902). Bull. Mus. Comp. Zool., 39:44, April. Type from Bogava (=Bugaba), 600 ft., Chiriquí, Panamá.

Orthogeomys dariensis (Goldman, 1912). Smithsonian Misc. Coll., 60(2):8, September 20. Type from Cana, 2000 ft., mountains of eastern Panamá.

Orthogeomys underwoodi (Osgood, 1931). Field Mus. Nat. Hist., Publ. 295, Zool. Ser., 185:143, Aug. 3. Type from Alto de Jabillo Pirris, between San Geronimo and Pozo Azul, western Costa Rica.

Orthogeomys cherriei carlosensis (Goodwin, 1943). Amer. Mus. Novit., 1227:3, April 22. Type from Cataratos, San Carlos, Alajuela, Costa Rica.

Orthogeomys cherriei cherriei (J. A. Allen, 1893). Bull. Amer. Mus. Nat. Hist., 5:337, December 16. Type from Santa Clara, Costa Rica.

Orthogeomys cherriei costaricensis (Merriam, 1895). N. Amer. Fauna, 8:192, January 31. Type from Pacuare, Costa Rica.

Orthogeomys matagalpae (J. A. Allen, 1910). Bull. Amer. Mus. Nat. Hist., 28:97, April 30. Type from Peña Blanca, Matagalpa, Nicaragua.

Genus Pappogeomys Merriam

1895. *Pappogeomys* Merriam, N. Amer. Fauna, 8:145, January 31.

1895. *Cratogeomys* Merriam, N. Amer. Fauna, 8:150, January 31. Type: *Geomys merriami* Thomas.

1895. *Platygeomys* Merriam, N. Amer. Fauna, 8:162, January 31. Type: *Geomys gymnurus* Merriam; Hooper, Jour. Mamm., 27:397, November 25, 1946.

Type.—*Geomys bulleri* Thomas, 1892, from near Talpa, west slope Sierra de Mascota, 8500 ft. (actually about 5000 ft.), Jalisco.

Chronologic range.—Late Pliocene, from deposits of early Blancan age (Benson local fauna, Arizona) to the Recent. However in the Pleistocene, only late Pleistocene records are known, and *Pappogeomys* has not been found in early (late Blancan) or middle (Irvingtonian) Pleistocene local faunas. Presumably the genus was restricted to México during the Pleistocene until post-Wisconsin time.

Description and discussion.—The size ranges from as little as in the smaller kinds of *Thomomys* to the maximum attained in the subfamily and matched elsewhere perhaps in only a few of the larger subspecies of *Orthogeomys grandis.* Depending on the species and subgenus, the form of the skull varies from generalized to specialized. The generalized skulls are short and not especially narrow; the zygomatic arches are spread laterally so far that the breadth across them exceeds the breadth across the mastoid processes. The most specialized skulls are platycephalic and the breadth across the mastoid processes equals or exceeds the breadth across the zygomatic arches (even so, the zygomatic arches are still relatively wide-spread). In correlation with the great breadth of the posterior part of the cranium, the rami of the mandibles diverge widely posteriolaterally and the angular processes are remarkably elongated. The rostrum is moderately broad in most species, but not nearly so broad and heavy as in *Orthogeomys*.

The single deep, median sulcus on the outer surface of the upper incisor is slightly displaced to the inner side of the tooth. The posterior surface of P4 lacks enamel (small vestige found on lingual end of posterior wall in only two adult individuals—UA 3260 and KU 100442, of the subgenus *Pappogeomys*); the other three plates are fully developed as usual. The p4 is provided with four fully developed enamel plates, in the pattern characteristic of the tribe Geomyini. In the p4 of the late Pliocene species (*P. bensoni*) the re-entrant angles are open (obtuse), a trait that is evidently primitive in the Geomyini.

All three lower molars are single, compressed, elliptical columns with enamel on only the posterior surfaces. M1 and M2 are also elliptical in cross-section and decidedly anteroposteriorly compressed, like the lower molars. Nevertheless, the enamel pattern is variable; enamel plates may be retained completely across both the anterior and posterior walls of M1 and M2 or only the anterior plate may be retained without reduction and the posterior plate may be reduced so that only a vestige is retained on the lingual fourth of the tooth or the posterior plate may be completely lost.

M3 tends to remain at least incompletely bilophodont by reason of retaining a permanent labial re-entrant fold in most species (with exceptions in *Pappogeomys bulleri* and some old adults of *P. castanops*). Primitively the occlusal surface of M3 is subtriangular (subgenus *Pappogeomys*), but in the *castanops* species-group of the advanced subgenus *Cratogeomys*, the posterior loph usually is reduced and the occlusal surface is quadriform or obcordate. Curiously, the trend towards reduction of the posterior loph is reversed in one subspecies (*P. merriami fulvescens*) and, the loph has elongated into a pronounced heel in some specimens, resembling the condition in *Orthogeomys*. The entire range of variation occurs in *P. m. fulvescens*. The subtriangular pattern is retained in the most specialized species of *Cratogeomys* where that pattern is associated with extreme platycephaly in the *gymnurus* species-group. In most species the posterior loph supports two lateral plates, the outer one always bordering the labial re-entrant fold. In *Pappogeomys bulleri* and in the *castanops* species-group, the outer re-entrant fold of M3 tends to be obsolete, and the tooth becomes quadriform or suborbiculate in some individuals and loses the bilophodont pattern that characterizes other species. The lingual enamel plate is displaced to the posterior surface of the tooth, and one or both plates may disappear with advancing age. Consequently, only the anterior enamel plate remains in some adults, and constitutes the maximum degree of reduction of enamel on M3 in the Geomyinae. In many adults of *Pappogeomys bulleri*, the enamel investment of the posterior loph is complete and the two lateral plates are connected, without interruption around the posterior apex of the tooth, evidently representing the retention of a primitive character of the ancestral lineage.

The m3 of *P. bensoni* from the late Pliocene is distinguished by minute lateral inflections suggesting the primitive biprismatic pattern. Also the posterior enamel plates of m1 and m2 are remarkably long, extending around the ends of the tooth. The associated upper incisor was unisulcate as in the modern species, and the basitemporal fossa of the mandible is well developed and deep.

The lower jaw is stout and relatively short. The masseteric ridge is well developed and has an especially thick crest. The basitemporal fossa is deep. In most living species, the pelage is soft and dense, but in one species, *Pappogeomys fumosus*, the hairs are coarse and hispid somewhat as in *Orthogeomys*.

Key to the Subgenera of *Pappogeomys*

A Enamel plates completely developed across posterior walls of M1 and M2, except in one species (*P. alcorni*) having enamel restricted to lingual fourth in M1; sagittal crest lacking owing to impressions of temporal muscles remaining separated (even in old adults); zygomata slender, and without platelike expansion at lateral angle. Subgenus *Pappogeomys*, p. 534

A′ Enamel lacking on posterior walls of M1 and M2; pronounced sagittal crest developed in adults of both sexes by union of temporal impressions at middorsal line; zygomata stout and wide, with lateral angle expanded into broad plate. Subgenus *Cratogeomys* . . . . p. 535

Subgenus **Pappogeomys** Merriam

1895. *Pappogeomys* Merriam, N. Amer. Fauna, 8:145, January 31.

Type.—*Geomys bulleri* Thomas, 1892, from near Talpa, west slope Sierra de Mascota, 8500 ft. (actually about 5000 ft.), Jalisco.

Chronologic range.—Late Pliocene (Benson local fauna, Arizona) to Recent, but no specimens known from Pleistocene.

Description.—Small, approximately same size as small subspecies of *Thomomys umbrinus* but forefeet larger and claws longer; skull of generalized shape, broad, relatively short, smoothly rounded, not especially compressed dorsoventrally; zygomatic breadth great but not exceeding mastoid breadth; zygomata relatively slender for geomyid and lacking platelike expansions at lateral angles; rostrum relatively narrow; sagittal crest lacking, owing to impressions of temporal muscles remaining separated; angular process of mandible not especially elongated; enamel plates extending completely across posterior wall of M1 and M2, except in one species, *P. alcorni*, where posterior plate of M1 remains only on lingual fourth of posterior wall (remainder of plate lacking); with wear, plates sometimes exceptionally thin completely across posterior face of M2 and especially M1 in a few individuals of *P. bulleri* much as Paulson (1961:138-139) describes in extinct *Geomys tobinensis;* one or both plates rarely disappear in final stages of attrition in old individuals resulting in same dental pattern found in *Cratogeomys;* M1 and M2 retaining enamel plate on anterior wall throughout life; M3 usually subtriangular in cross-section but sometimes suborbiculate or ovoid, crown slightly bilophodont owing to shallowness of labial re-entrant angle in modern species; posterior loph of M3 not especially elongated and crown not significantly longer than wide; both lateral enamel plates of M3 usually well developed and approximately equal in length, occasionally plates reduced in length and rarely one or both plates are lost with wear in old individuals; patch of whitish or buffy hairs surrounding nose of most individuals.

The primitive character of the lower dentition, as described in the species account above, suggest that *Cratogeomys* [= *Pappogeomys*] *bensoni* Gidley should be referred to the subgenus *Pappogeomys* rather than *Cratogeomys*. Only the upper dentition would make positive identification possible; however, reference to the subgenus *Pappogeomys* seems to be the best arrangement at this time.

Referred species.—Three (one extinct):

°*Pappogeomys bensoni* (Gidley), 1922. U. S. Geol. Surv. Prof. Papers, 131:123. Type from Benson local fauna (late Pliocene), Cochise County, Arizona.

Pappogeomys alcorni Russell, 1957. Univ. Kansas Publ. Mus. Nat. Hist., 9(11):359. Type from 4 mi. W Mazamitla, Jalisco.

Pappogeomys bulleri Thomas, 1892. Ann. Mag. Nat. Hist., Ser. 6, vol. 10:196, August. Type from "near Talpa," west slope of Sierra Madre de Mascota, Jalisco.

Subgenus Cratogeomys Merriam

1895. *Cratogeomys* Merriam, N. Amer. Fauna, 8:150, January 31.

1895. *Platygeomys* Merriam, N. Amer. Fauna, 8:162, January 31. Type: *Geomys gymnurus* Merriam, 1892.

Type.—*Geomys merriami* Thomas, 1893, from "Southern México," probably in Valley of México.

Chronologic range.—Late Pleistocene, from Wisconsin deposits (San Josecito Cave, Nuevo León, Upper Bercerra, México, and Burnet Cave, New Mexico, local faunas) to the Recent.

Description.—Size medium to large; skull becoming angular and rugose with age, and tending towards platycephaly and dorso-ventral compression; zygomata stout, each bearing platelike expansion at anterolateral angle into which anterior end of jugal becomes morticed; breadth across zygomata great relative to length of skull; rostrum relatively broad; squamosals expanding medially with age eventually growing over lateral parts of parietals, and sometimes also expanding laterally displacing postglenoid notch; sagittal crest well developed in adults of both sexes, but especially high and bladelike in males; lambdoidal crest prominent in all but young animals, having dorsal outline broadly convex posteriorly in most species but strongly sinuous in *gymnurus*-group; enamel plate on posterior wall of P4 absent; enamel plates present only on anterior walls of M1 and M2; M3 variform in occlusal shape (as described in species account), either subtriangular (*gymnurus*-group), quadriform or obcordate (*castanops*-group, with exceptions as noted before); lateral plates of M3 usually present in all species, labial plate approximately as long as lingual plate in *gymnurus*-group (like that in subgenus *Pappogeomys*) or distinctly shorter in *castanops*-group (labial plate scarcely extending beyond border of labial re-entrant fold); one or both lateral plates tending to disappear with wear in *castanops*-group, with lingual plate usually disappearing first; breadth across angular processes clearly more than breadth across zygomatic processes, especially in *gymnurus*-group.

Remarks.—In the species of the *castanops*-group the skulls can be spoken of as generalized and the least platycephalic of the subgenus. Indeed, the species of the *castanops*-group are hardly more specialized in this respect than is the subgenus *Pappogeomys*. In these skulls the breadth across the squamosal processes is less than that across the zygomatic arches, although the two dimensions are almost equal in some examples of *P. merriami* of the *castanops*-group (where squamosal breadth varies from 85 to 98% of zygomatic breadth). In the species having marked platycephalic skulls (*gymnurus* species-group) the breath across the squamosal processes equals or exceeds the breath across the zygomatic arches (squamosal breadth rarely 97 to 99% of zygomatic breadth), except in *P. zinseri* and *P. tylorhinus zodius*.

The variable character of the third upper molar as between species suggests that this tooth is presently undergoing active evolution. The structure of this tooth, although differing between taxa, is remarkably stable in other kinds of Geomyini. The most remarkable modification of M3 in *Cratogeomys* is the obcordate pattern developed in *P. merriami* of the *castanops*-group. The posterior loph and entire tooth is shortened somewhat resembling in shape that of *Thomomys*. Moreover, the posterior loph is twisted labially; consequently, its posterior surface now forms the labial border of the weakly defined posterior loph. Owing to the torsion, the lingual enamel plate has been rotated to the posterior surface of the tooth. Therefore, the tooth is provided with two transverse enamel plates, including the plate on the anterior wall of the tooth. The labial plate is greatly reduced, its total surface being restricted to the small labial inflection. The highly specialized obcordate M3 is not found in the most specialized platycephalic skulls characteristic of the *gymnurus* species-group. Instead the *gymnurus*-group retains the primitive subtriangular pattern without significant modification.

Referred species.—Seven:

castanops species-group

Pappogeomys castanops (Baird, 1852). Report Stanbury's Exp'd. to Great Salt Lake, p. 313, June. Type from "Prairie road to Bent's Fort," near present town of Las Animas, Colorado.

Pappogeomys merriami (Thomas, 1893). Ann. Mag. Nat. Hist., ser. 6, 12:271, October. Type from "southern Mexico," probably Valley of México (see Merriam, 1895:152).

gymnurus species-group

Pappogeomys fumosus (Merriam, 1892). Proc. Biol. Soc. Washington, 7:165, September 29. Type from 3 mi. W Colima, Colima.

Pappogeomys gymnurus (Merriam, 1892). Proc. Biol. Soc. Washington, 7:166, September 29. Type from Zapotlan (Ciudad Guzman), Jalisco.

Pappogeomys neglectus (Merriam, 1902). Proc. Biol. Soc. Washington, 15:68, March 22. Type from Cerro de la Calentura, about 8 mi. NW Pinal de Amoles, Querétaro.

Pappogeomys tylorhinus (Merriam, 1895). N. Amer. Fauna, 8:167, January 31. Type from Tula, Hidalgo.

Pappogeomys zinseri (Goldman, 1939). Jour. Mamm., 20:91, February 15. Type from Lagos, Jalisco.

PHYLOGENY OF THE GEOMYIDAE

The fossil record of the Geomyidae provides a sequence of morphotypes, each representing a stage in the phyletic development of the family. Most of the preserved specimens probably represent the stufenreihe rather than the ahnenreihe, as Simpson (1953:219-220) points out. Even so, the stufenreihe closely approximates the general trend of evolution, and the level of structural organization in the different stages of phyletic development may be ascertained. The actual ancestral series of most lineages probably will remain unknown, but hopefully some of the existing gaps will be filled by future discoveries. From the established record, several clearly defined lineages can be distinguished; in fact the sequence of origin, pattern of evolution, and specializations, of the principal lineages are reasonably well expressed.

Primitive Morphotype

In the earliest known geomyids from the Upper Oligocene and Lower Miocene, the premolars and molars are biprismatic and bilophodont. In rodents, this is itself a specialized pattern, and is thought to have evolved from a more primitive sextituberculate prototype by the union of individual cusps, and probably also cuspules, forming the two transverse enamel lophs. The primitive, common ancestor of the Geomyidae and Heteromyidae with sextituberculate teeth in the early Tertiary is unknown.

As soon as geomyids attained the early bilophodont stage of evolution, the basic morphological structure of the family was established. The family probably first became clearly distinguished from other Geomyoidea at this stage. In the early bilophodont stages of evolution, owing to the relatively deep valley between them, the two columns probably failed to unite in the normal cycle of wear, as they do in all later geomyids. *Griphomys* described by Wilson (1940:93) from the late Eocene of California, has a bilophate pattern in which the anterior and posterior lophs are separated by a persistent transverse valley. The occlusal pattern of *Griphomys* closely resembles a stage through which the ancestors of the early Miocene geomyids must have passed in their pre-Miocene evolution, as Wilson suggests (1949:115-116). Although he (1940:95; 1949:110-118) tentatively referred *Griphomys* to the superfamily Geomyoidea and Simpson (1945:80) went so far as to refer it to the family Geomyidae, with a notation of *incertae sedis,* its exact relationship to the pocket gophers is uncertain. However, the structure of the molariform dentition of *Griphomys* does not exclude it from the phyletic ancestry of the Geomyidae. In subsequent stages of evolution the anterior and posterior columns become united. Thereby part of the valley floor between the transverse prisms was progressively elevated, to the stage where attrition on the occlusal surface would unite the two columns. On the unworn enamel cap of living geomyids the two transverse enamel folds are separated by a shallow but well defined valley, briefly reflecting the ancient ancestral pattern.

Union of the lophs may have been either at the mid-points of the two columns or at the edge of their protomeres. [A protomere is the half of a tooth containing the protocone or protoconid—lingual side of upper tooth and labial side of lower tooth. The paramere is the opposite half of a given tooth—labial side of upper tooth and lingual side in lower tooth. See Miller and Gidley, 1918:434.] Union of the columns at the mid-points would have produced the figure-8 occlusal pattern (or H-pattern), which is characteristic of the early Miocene Geomyinae (*Dikkomys*). Union of the two columns at the protomeres would have produced the U-shaped pattern of the Entoptychinae, which also occurred in the early Miocene and were contemporary with the earliest Geomyinae. Since pre-Miocene geomyids are unknown, the actual phyletic development of the dentition is a matter of speculation. Probably the development of the two divergent lineages, one leading to the Entoptychinae and the other to the subfamily Geomyinae, occurred in the Oligocene (as depicted in Fig. 3). Of the two lineages, the subfamily Geomyinae, in my view, is the more primitive and less specialized. Support for this view is furnished by a reconstruction of the pattern of occlusal wear in *Dikkomys* and *Pliosaccomys*, especially on the first and second molars.

In *Dikkomys*, the anterior and posterior column first unite near their mid-points in the first stages of wear thus producing a figure 8-shaped (H-shaped) occlusal pattern in the premolar and all three molars. Evidently in the first two upper molars, the columns unite closer to their lingual margins than their mid-points, but at any rate both outer and inner re-entrant folds are evident at this stage of wear. With continued attrition on m1 and m2 of *Dikkomys*, the anterior and posterior columns secondarily unite at the edge of their labial margins thus enclosing a fossette of enamel in the labial half of the tooth. The lateral coalescence at the ends of the protomers occurs because of the shallow vertical depth of the labial re-entrant fold, and the fossette itself does not reach the base of the crown and with continued wear it too would disappear, but not until the last stages of wear, at least in *Dikkomys matthewi*. The lingual re-entrant fold is deep, and therefore, persistent through all stages of wear. Although the amount of wear required for its effacement would be great, the occlusal configuration of the first and second lower molars in *Dikkomys* could be eventually ground down to a U-pattern as in the entoptychids. Only one upper molar of *Dikkomys*, the first, has been recovered (see Wood, 1936:23, fig. 32B). Although the tooth is in an early stage of wear, the lingual valley is minute. Less attrition than required in m1 and m2 would progressively reduce the lingual fold until it too would essentially form a U-pattern, perhaps retaining a slight lingual inflection. Hence, the first upper molar becomes a mirror image of the first lower molar, and the second upper molar probably had the same pattern as the first (at least it does so in *Pliosaccomys*). Both of the lateral re-entrant folds of the premolar are deep vertically, and consequently would not disappear with occlusal wear. Therefore, the H-pattern of the premolars is retained throughout life.

The m3 (M3 unknown for *Dikkomys* or *Pliosaccomys*) also has deep lateral folds; hence, it too retains the H-pattern in all stages of attrition, although the isthmus between the two prisms may become wider in the final phases of wear (as it does in *Pliosaccomys*).

In *Pliosaccomys*, the stages of wear are essentially the same as those described for *Dikkomys*, except that the anterior and posterior loph of the first and second molars tend to unite closer to one side of the tooth, lingual side in upper molars and labial in lower. Only a slight inflection of the re-entrant fold is evident on the side of union, and the inflection disappears in the first phases of wear as the columns unite. Concomitant with the lateral shift in the initial point of coalescence of the transverse lophs, the occlusal penetration of the re-entrant fold from the opposite side increases in horizontal depth, and the fold extends medially more than half way across the occlusal surface, thus forming a pattern essentially like that of the entoptychids. The U-pattern in *Pliosaccomys* appears in the initial stages of wear without going through an earlier H-pattern as is the case in its Miocene ancestors of the genus *Dikkomys*, unless the minute inflection is considered as indicative of that stage. The two columns of the premolar and m3 are joined near their mid-points as in *Dikkomys;* therefore, they retain their primitive H-pattern, a feature unique to the Geomyinae.

The evolutionary trend toward an ontogenetically earlier U-pattern in the first two molars in the primitive lineage of the Geomyinae suggests that the U-pattern characteristic of the Entoptychinae was simply an earlier tendency toward the same specialization that occurred later in the subfamily Geomyinae. If so, early entoptychines would have been characterized by an H-pattern in the first stages of attrition, like *Dikkomys*, and later developed union at the edge of the protomeres. However, in the entoptychines, all the molariform dentition, and not merely the first and second molar, became specialized; consequently the U-pattern was produced on the occlusal surfaces of each of the cheek teeth. As in *Pliosaccomys*, the transitional phase, in which the two columns were united at their mid-points, was eventually eliminated from the pattern of wear and only the U-pattern, that now appeared in the initial stages of wear, was retained. In the entoptychines of the early Miocene there is no suggestion of the H-pattern that characterizes the Geomyinae, except in the position of the cusps before wear in the lower molars of *Pleurolicus sulcifrons*, which, according to Wood (1936:6), suggests the H-pattern. In earlier unknown Oligocene stages of evolution, the prisms possibly united first at their mid-points, and the columns may have joined at the side of the tooth only in the terminal stages of wear. The U-pattern of pre-Miocene entoptychines, therefore, may have become the dominant occlusal pattern only in the later stages of phyletic development.

According to the recently expressed views of several paleontologists, the Entoptychinae constitute the primitive lineage of the family and the early Geomyinae constitute a specialized offshoot of the entoptychine ancestral assemblage. The structure of the Entoptychinae, especially of the less advanced genera, closely approximates that of the hypothetical primitive morphotype. But, according to my view, the subfamily Geomyinae constitutes the ancestral assemblage and its structure is essentially that of the primitive morphotype of the family. At any rate the structure of the early geomyines more closely approximates the structure of the ancestral stock than the more divergent entoptychines. Therefore, the genus *Dikkomys* of the early Miocene, the first known geomyine, is considered to be a generalized geomyid, and, although it is a contemporary of the more specialized entoptychid assemblage, is considered to be more closely allied to the ancestral stock.

The entoptychines were the dominant and most highly differentiated geomyids of the early and middle Miocene. Nevertheless, they became extinct in the middle Miocene, and the geomyines of that time survived and later gave rise to the modern pocket gophers. Therefore, the early history of the family Geomyidae is characterized by an early radiation and trend toward specialization, followed by survival of the less specialized Geomyinae and extinction of the more specialized Entoptychinae.

Entoptychid Radiation

The most abundant geomyids of the early and middle Miocene, the Entoptychinae, consisted of at least 24 species (see Wood, 1936:4-25) classified in four genera: *Pleurolicus, Gregorymys, Grangerimus,* and *Entoptychus.* The genera were essentially contemporaneous (see Figure 3). Even so, the subfamily was morphologically varied, pointing to an earlier origin in the Oligocene (actually a part of the John Day Fauna, including *Pleurolicus* may be correlated with late Oligocene Whitneyian age) followed by a relatively rapid radiation including all four genera in the early

Miocene. Two genera, *Pleurolicus* and *Gregorymys,* continued into the Middle Miocene (Hemingfordian). This divergence, specialization, and subsequent radiation suggest that the entoptychines evolved into a new major adaptive zone, in the sense described by Simpson (1945:199-206).

The radiation is correlated geographically and temporally with the southward retreat of the Neotropical flora of the Tertiary from the western United States and southward movement of the Arctic flora of the Tertiary (see Axlerod, 1950; Berry, 1937:31-46; Chaney, 1947:139-148; and Kendeigh, 1961:280-283). In the early Tertiary the Neotropical-tertiary geoflora occured northward to at least 49° latitude in western North America, and the boreal Arctic-tertiary flora was restricted to a circumpolar zone. The southward and eastward shift of the Neotropical-tertiary flora, associated with the drying and chilling of the continent, began in the middle or late Oligocene and was concurrent with the divergence and radiation of the Entoptychinae. Beginning in late Oligocene and continuing at least into middle Miocene, most of the region in which the entoptychines occurred was occupied by the Arcto-tertiary geoflora of which the temperate forest division contributed the dominate plant associations. The maples, chestnuts, dogwoods, beeches, walnuts, oaks, elms, birches, and sycamores of that flora were the forerunners of today's eastern deciduous forest. It is my view that the entoptychines became adapted to the conditions of this paleoecological environment and radiated rapidly in the Arikareean when the major change occurred in climax vegetation. The ancestral stock of the Geomyinae was not so successful in the Arcto-tertiary climax, and most of it probably was displaced southward along with the tropical flora.

The skeleton in the entoptychines is not so strongly fossorial as in the modern geomyids (Wilson, 1949:117), and these early geomyids probably were semi-fossorial with somewhat the same burrowing habits as those of the living mountain beaver (*Aplodontia*). Inasmuch as the morphology and taxonomy of the entoptychines were discussed in detail by Cope (1884) and reviewed later by Wood (*loc. cit.*), there is no need to recount the details here. According to Wood (*op. cit.,* 27-28), *Pleurolicus* occupied a central position in the entoptychid radiation and perhaps appeared slightly earlier than the other genera. Wilson (1949) suggested that the lower part of the John Day may actually be Upper Oligocene rather than Lower Miocene, and this arrangement is followed here. Also, *Pleurolicus* is less specialized than the other genera and occurs in deposits of both the Great Plains and the Pacific Coast. *Gregorymys,* also little specialized, occurred only on the Great Plains. The more specialized genera, *Grangerimus* and *Entoptycus,* evidently appeared somewhat later than *Pleurolicus* and evolved from it. Except for a record from southern Texas reported recently by Hibbard and Wilson (1950:621-623) and the new species described by MacDonald (1963:182) from the Sharps Formation of South Dakota (early Arikareean), *Grangerimus* is known only from the Pacific coast. *Entoptycus* was restricted to the Pacific Coast (John Day fauna).

Entoptycus is the most specialized of the known genera; it has pronounced fossorial adaptations, especially in the skull. Its molariform teeth are rootless and ever-growing as in the modern geomyines. Moreover, the continuous enamel bands on only moderately worn teeth become separated in the final stages of wear into anterior and posterior enamel plates by tracts of dentine that extend toward the crown on the sides of each tooth. This extension was made possible by the union of the two columns at both the lingual and labial margins of the tooth forming an O-pattern, and the crown is esssentially monoprismatic save for the isolated enamel fossette in the center of the tooth. The fossette is all that remains of the lateral re-entrant fold that characterized the preceeding U-pattern of the earlier stages of wear. Late in the sequence of wear, the anterior enamel plate is lost in the lower molars and the posterior plate in the upper molars. The U-pattern characterizes the final stages of attrition in the other genera of the Entoptychinae; none developed the dental specializations seen in *Entoptycus.* Rootless, ever-growing cheek teeth, discontinuous enamel patterns, and monoprismatic molars were not evolved in the subfamily Geomyinae until the late Pliocene.

Phyletic Trends in Subfamily Geomyinae

The subfamily Geomyinae is made up of three groups, recognized taxonomically for the first time in this account as tribes—Dikkomyini, Thomomyini, and Geomyini (for full discussion of clasification, see previous account). The phylogeny proposed by me is illustrated in Figure 3. The tribe Dikkomyini is characterized by generalized and primitive features that together form the basic structural foundation of the subfamily. Evolution within the Dikkomyini resulted in the acquisition and perfection of fossorial adaptations. The Thomomyini and Geomyini are considerably more specialized than the ancestral Dikkomyini from which they evolved.

The Geomyini are clearly more specialized than the Thomomyini, suggesting closer affinity between the Thomomyini and the Dikkomyini than between the Geomyini and the Dikkomyini. The specializations in the dentition and the associated changes in the skull of the Thomomyini and Geomyini permit more efficient mastication of fibrous vegetation. Along with these specializations, fossorial adaptations inherited from the Dikkomyini are retained without noteworthy modification.

Dikkomys, the earliest known genus of the tribe Dikkomyini, can be taken as a starting point of evolution for the subfamily Geomyinae. The Pliocene genus *Pliosaccomys* is the only other known geomyine having primitive features closely resembling those of *Dikkomys.* The relatively close but previously unrecognized relationship between *Dikkomys* and *Pliosaccomys* can be understood when patterns of wear on the occlusal surfaces of the cheek teeth are taken into account. It appears that *Pliosaccomys* descended from *Dikkomys*-like stock, if not *Dikkomys* itself. Although *Dikkomys* is towards the beginning of this phyletic sequence and *Pliosaccomys* towards the end of the sequence, the primitive features shared by the two provide a generalized morphotype for the subfamily Geomyinae.

In the molariform dentition, an almost complete series of stages of wear in *Pliosaccomys* has been preserved, and those of *Dikkomys* can be reconstructed with reasonable accuracy from those that are known (see Fig. 4):

(1) In the initial stage of wear in *Dikkomys* the anterior and posterior columns are separated by an intervening valley (Fig. 4A), and the occlusal surface of each column bears a loph of dentine surrounded by a ring of enamel: protoloph on the anterior column and metaloph on the posterior column of the upper teeth (protolophid and hypolophid in corresponding positions in the lower teeth). Actually this stage is not preserved in the known material of *Dikkomys,* but does occur in both geomyines and entoptychines in all stages of evolution, and it must have also occurred in *Dikkomys* in order for the next two stages, which are preserved, to have developed.

(2) The occlusal surfaces are ground down to a level where the enamel loops of the two columns join at their mid-points, thus forming an H-shaped pattern (Fig. 4B), or more exactly a pattern resembling a figure 8. Probably this was the primitive pattern in the final stage of wear in the geomyid ancestor of the Oligocene.

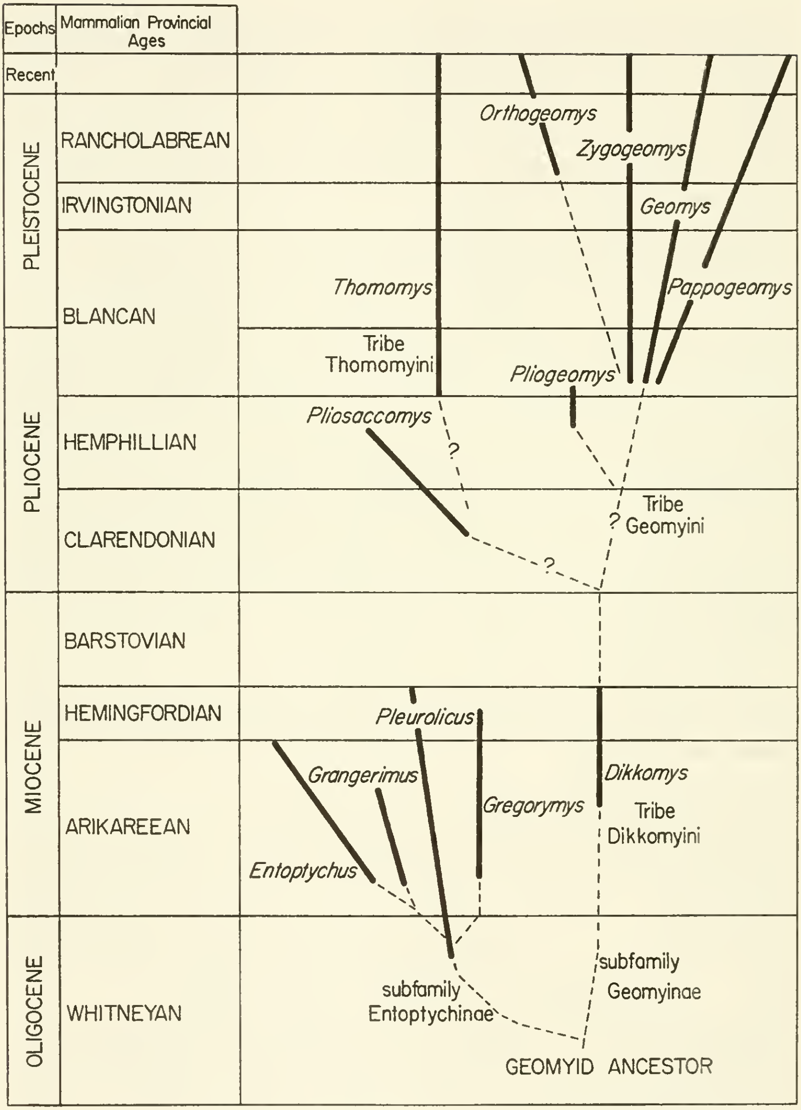


FIG. 3. Diagram depicting geologic range and probable phyletic relationships of the family Geomyidae. Dashed lines represent parts of lineages that are not represented by fossil records, and solid lines represent parts of lineages verified by actual specimens. Question marks indicate uncertainty of suggested ancestry of known taxa. The relationships within the subfamily Entoptychinae are modified after Wood (1936), and the temporal range of the Miocene geomyids have been adjusted to agree with current stratigraphic correlations. Hence, *Pleurolicus, Gregorymys* and *Dikkomys* are illustrated as ranging into the Hemingfordian, rather than being confined to the Arikareean (see MacDonald, 1963, and Black, 1961).

(3) In the pre-final stage of wear, the anterior and posterior lophs of the first and second molars unite secondarily at the edge of their protomers (labial side in the lower and lingual in the upper), thus enclosing an isolated enamel fossette (Fig. 4C). Lateral union occurs in the lower teeth because the vertical depth of the labial re-entrant angle is less than the depth of the lingual re-entrant fold. In the upper teeth the reverse is true. The re-entrant angle on one side of the premolar is as deep vertically as the angle on the other side of that tooth, and both reach the base of the crown; therefore, they do not disappear at any stage of attrition. The same pertains in the third lower molar.

(4) In the final stage of wear (Fig. 4D), the enamel fossette disappears as a result of continued attrition on the occlusal surface in the upper series. The fossette may vary somewhat in vertical depth in m1 and m2, but the amount of wear required for its effacement would be greater than in the upper teeth. Therefore, upon wear, the U-pattern would become characteristic of the final stage in M1 (and probably also M2), but the modified H-pattern described in Fig. 4C would prevail in m1 and m2. Perhaps, in extremely worn teeth, the labial fossette of m1 and m2 would disappear. If this advanced stage of effacement is obtained, then the two columns would be united across the entire surface of their protomeres from the center of the crown to its labial edge, and the occlusal pattern would be in the shape of a U.

The occlusal pattern, at least in M1 and M2, in the final stages of wear in *Dikkomys* resembles that in the subfamily Entoptychinae, but the U-pattern develops on only the first and probably the second molar in *Dikkomys* and not on all of the cheek teeth as it does in the entoptychines. Judging from the material that has been described, the U-pattern did not develop in the lower teeth of *Dikkomys* until the Hemingfordian (*D. woodi*), upper Rosebud, and specimens of *D. matthewi* from the earlier Arikareean, lower Harrison, suggest that the modified H-pattern, with secondary coalescence at the edge of the protomeres, persisted throughout life, without developing the U-pattern in the final stages of wear.

Essentially the same patterns of wear characterize the genus *Pliosaccomys,* except that the earlier stages were telescoped and the second stage was omitted while another (final) stage was added. The stages are reconstructed in sequence in figure 4, and all are based on preserved dentitions, as follows:

(1) The first phases of wear produced the pattern (Fig. 4E and I) described for *Dikkomys* in the previous account (Fig 4A).

(2) A small additional amount of wear produced the 2nd stage (Fig. 4F and J) characterized by a U-pattern, formed by union of the anterior and posterior columns at the edge of the protomeres of the first and second molars, both above and below, without first forming an H-shaped pattern. Union at the mid-points thus was omitted from the sequence of wear in these two teeth. In the premolars and third molars the primitive H-pattern did form, as in *Dikkomys.* The pattern of wear in the first two molars is the same as in the entoptychines of the early Miocene. The trend of evolution through which the *Pliosaccomys* lineage passed must have featured a progressively earlier union at the edge of the tooth until the lateral coalescence occurred simultaneously with the median union. At that stage, emphasis was shifted to the union at the edge of the tooth, and eventually the teeth failed to unit at their mid-points and the U-pattern developed directly. Therefore, the horizontally deep re-entrant fold that separates the two lophs of the U-pattern is equivalent to one fold plus the apex of the opposite fold.

(3) The horizontal re-entrant fold of the U-pattern was remarkably shallow vertically and disappeared with little additional wear. Thus the two parts of M1, and also of M2, are united into a single column except for a slight inflection on the labial side and this is true also of m1 and m2 except for a slight inflection on the lingual side (Fig. 4G and K). The inflection appears to have persisted in the upper teeth (Fig. 4H), but evidently with slight wear, disappeared in the lower teeth (Fig. 4L). The final monocolumnar pattern was attained early ontogenetically, evidently before the permanent premolar had fully erupted; hence, the earlier stages occurred only in transition, persisted for only a brief interval in the teeth of juveniles, and the final stage developed in the young animal and lasted throughout the rest of its life in *Pliosaccomys.* In *Dikkomys* the two columns never united into a single column, and a bilophodont occlusal pattern persisted throughout life.

The early phyletic development of the subfamily Geomyinae took place in the tribe Dikkomyini from the early Miocene into the early Pliocene. Compared with the rapid evolution of the specializations that distinguish the Entoptychinae, the structural changes in the early Geomyinae occurred at a remarkably slow rate. In fact the lineage changed but little from *Dikkomys* to *Pliosaccomys,* in parts of the animal that can be compared, as illustrated by the low-crowned and rooted cheek teeth, the continuous enamel bands, the lack of grooving of the upper incisor, the retention of the primitive H-pattern, both above and below, in the premolar and third lower molar, and the ridges and fossae of the mandible to which the muscles of mastication attach. The only major changes detected in the know fragments are in the pattern of wear and the final configuration of the first and second molars, as described above. The unification of the two lophs in each of these two teeth into a single column was a significant step in the evolution of the Geomyinae, and is a stage between the primitive bilophodont pattern of the early and middle Miocene geomyines having continuously bicolumnar teeth and the monolophodont pattern in the modern pocket gophers of both lineages in which these teeth consist of a single column in all but the initial stages of wear. The monocolumnar structure of the first and second molars in the final stages of wear, therefore, is closer to that in the lineage of *Thomomys* than it is to that of *Dikkomys.* Other specializations in the dentition of *Pliosaccomys,* especially in m1 and m2 where the H-pattern has been completely eliminated from the sequence of wear, are too far advanced for *Pliosaccomys* to have given rise to the tribe Geomyini. The teeth in the immediate ancestor of the Geomyini must have been less specialized in m1 and m2, perhaps about as in *Dikkomys.* In the m1 and m2 of the tribe Geomyini, the H-pattern is formed in the initial stages of wear; therefore, in the early Pliocene ancestor, presently unknown in the fossil record, the H-pattern probably was present. Even so, the ancestor of the Geomyini and that of *Pliosaccomys* probably were closely allied otherwise, and both probably had attained the highly specialized fossorial adaptations characterizing all modern pocket gophers, before the divergence of *Pliosaccomys* and the Geomyini took place.

The evidence points to a major divergence of the geomyines that lived in the latest Miocene or the early Pliocene (probably the latter) and that gave rise to the two modern lineages, Thomomyini and Geomyini (see Fig. 3). One, the most primitive of the two, gave rise to the Thomomyini lineage that eventually evolved into *Thomomys. Pliosaccomys* is closely allied to the ancestry of this lineage, although it is probably not the actual ancestor, as mentioned previously. Aside from the aforementioned specializations of the first and second molars, the features of the Thomomyini are less advanced than in the other specialized lineage (tribe Geomyini). Primitive traits retained in the tribe Thomomyini (and also characteristic of the ancestral tribe Dikkomyini) are: (1) Small size, in general no larger than the ancestral morphotype; (2) lack of grooving on the upper incisor (although a slight

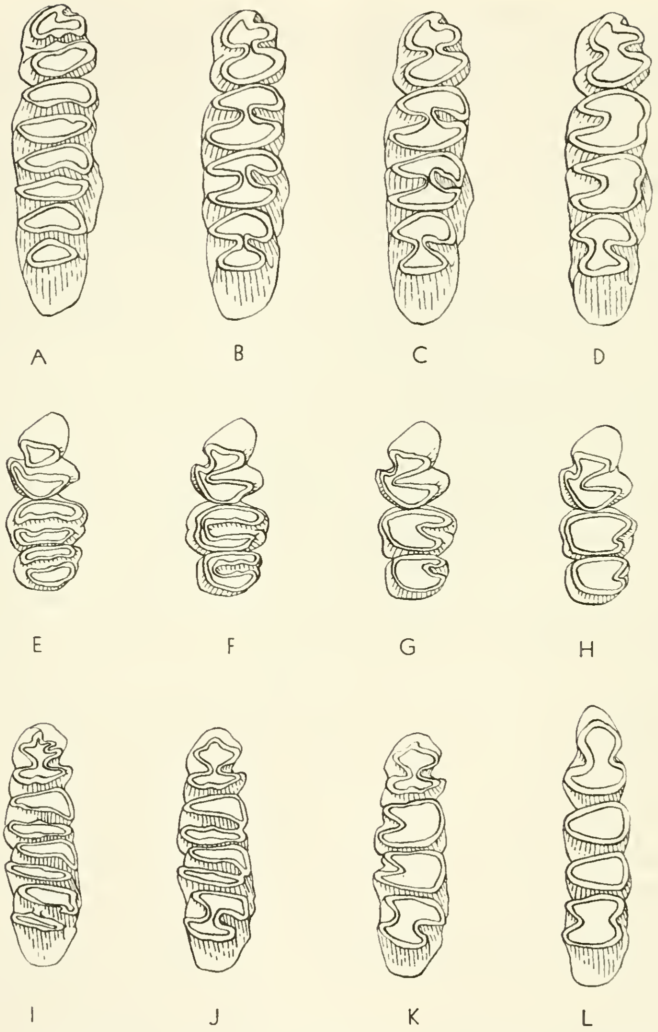


FIG. 4. Drawings of the molariform dentitions of *Dikkomys* and *Pliosaccomys* (Tribe Dikkomyini) depicting the patterns of wear on the occlusal surfaces. Ontogenetically, the stages of wear are arranged from left to right in each row. Stages not represented by actual specimens have been carefully reconstructed from information provided by known stages in the sequence of wear and the dentitions of other geomyines. × 5.

A—D. *Dikkomys woodi*, right lower tooth-row, including p4—m3. Patterns based on No. P26284 (FMNH) from Upper Rosebud (Middle Miocene), Shannon Co., South Dakota (B above).

E—H. *Pliosaccomys dubius*, left upper tooth-row, including P4—M2 (M3 unknown). Patterns based on Nos. 1798 and 1799 (LAM) from Smiths Valley (Middle Pliocene), Lyon Co., Nevada.

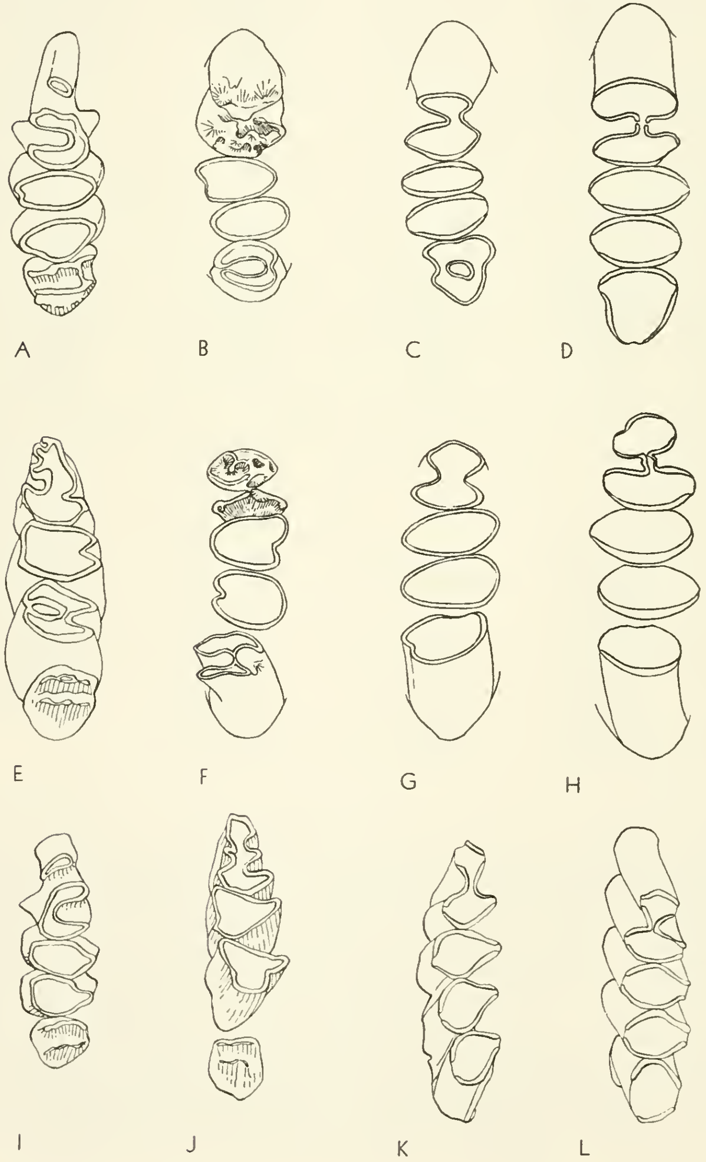
I—L. *Pliosaccomys dubius*, right lower tooth-row, including p4—m3. Patterns based on Nos. 1796 (holotype), 1804, and 1806 (LAM) from Smiths Valley (Middle Pliocene), Lyon Co., Nevada.

rudimentary groove is developed rarely in some living species); (3) retention of anterior and posterior enamel plates in lower and upper cheek teeth; (4) premolars having widely open re-entrant folds; (5) smooth and generalized skull lacking marked angularity, regosity or cresting (neither the sagittal nor the lambdoidal crest are ordinarily well developed except in *Thomomys bulbivorous*); (6) forefoot small, less modified for digging than in the Geomyini.

The lineage of the Thomomyini is essentially rectilinear and without the major branching seen in the tribe Geomyini. The one genus, *Thomomys,* appears first in the Upper Pliocene (early Blancan time), and the specializations characterizing the lineage had already developed by that time. Evidently, the early stages of divergence from the ancestral stock resulted in the development of rootless, ever-growing, more hypsodont cheek teeth, simplification of M3, and enlargement of the masseteric ridge on the mandible. The enamel investment on the sides of the molariform teeth is interrupted owing to intrusion of tracts of dentine on the sides of each column. Even so, complete anterior and posterior plates are retained on all of the cheek teeth (Fig. 5, K and L) and there is no trend toward additional loss of enamel as in the Geomyini. The enamel on the sides of the column has little functional value, and its elimination probably reduces friction during the anteroposterior movements of the lower jaw, thereby increasing the efficiency of the cutting blades on the anterior and posterior wall of the tooth. The simplification of M3 was achieved by union of the two columns of the primitive pattern into a single column and obliteration of both the labial and lingual re-entrant folds in the first stages of wear. The adult tooth (see Fig. 5L) is without trace of the bilophate pattern and is not elongated; therefore, its structure is essentially the same as that of the first and second upper molars.

In the Thomomyini, the two lophs of the unworn molars unite entirely across the width of their surfaces with the first traces of wear (see Fig. 5, I and J), owing to the shallow and uniform depth of the transverse valley. In the molars, the final pattern is acquired, therefore, before the deciduous premolar has been replaced by the permanent tooth. A relatively shallow re-entrant inflection between the ends of the parameres sometimes is retained, although it also will disappear with slight additional wear. Therefore, both lophs tend to unite completely with the first stages of wear in the Thomomyini, thus omitting both U and H patterns from the sequence of wear. This is the highest degree of specialization attained in the Geomyidae in regard to the patterns of wear, since a sequence of bilophodont patterns appear in both the Dikkomyini and Geomyini before the monoprismatic pattern is developed.

Relationship of the Geomyini with the ancestral Dikkomyini is most clearly demonstrated in the sequence of wear on the occlusal surfaces of the molars. As in all geomyids, the upper part of the



crown is biprismatic in the newly erupted tooth, and the two columns are separated by an intervening valley. With slight attrition on the unworn enamel cap, the weakly developed cusps merge and form a transverse enamel loop on each of the two columns (see third molar in Fig. 5, A and E), each loop enclosing a core of dentine that had become exposed. The valley between the two columns is shallow, and upon further wear of the tooth, the two loops unite. The two columns become joined at different points in the upper and lower molars depending on the varying depth of the valley in different teeth. Therefore, upper and lower molars develop distinctly different occlusal configurations.

In the lower molars, the pattern characteristic of *Dikkomys* (Fig. 4C) is preserved without significant modification, as illustrated in an immature specimen of *Geomys* (see Fig. 5E). The H-pattern and modified H-pattern are developed in the same sequence of wear in the Geomyini. A juvenal female (not illustrated), KU 2931, provides an example of the intermediate H-pattern. In this specimen, the protolophid and hypolophid of the left m2 are united only at their mid-points, indicating that the pattern of wear occurs in the same sequence in the Geomyini as it did in the Miocene genus *Dikkomys*. After the two columns have become united at their mid-points, a secondary union is formed at the edge of their

FIG. 5. Drawings of molariform dentitions representative of the tribes Geomyini and Thomomyini depicting patterns of wear on the occlusal surface. A—D represent, in ontogenetic sequence from left to right, upper tooth-rows of the tribe Geomyini. E—H represent, in the same sequence of stages, lower tooth-rows of the tribe Geomyini. I—L represents both upper and lower tooth-rows of both pre-final and final stages of wear in the tribe Thomomyini. All × 5.

A and E. *Geomys bursarius majusculus*, No. 2948 (KU), Douglas Co., Kansas. Right upper (A) including DP4—M3; lower left (E) including dp4—m3.

B and F. *Pappogeomys bulleri burti*, No. 100444 (KU), 10 mi. NNW Barra de Navidad, Jalisco. Right upper (B) including P4—M3; right lower (F) including p4—m3 (both P4 and p4 with unworn enamel caps).

C and G. *Pappogeomys bulleri albinasus*, No. 31044 (KU), 10 mi. S and 8 mi. W Guadalajara, Jalisco. Right upper (C) including P4—M3; right lower (G) including p4—m3.

D and H. *Pappageomys bulleri albinasus*, No. 31002 (KU), W side La Venta, 13 mi. W and 4 mi. N Guadalajara, Jalisco. Right upper (D) including P4—M3; right lower (H) including p4—m3.

I and J. *Thomomys talpoides bridgeri*, No. 6865 (KU), 2 mi. up Mink Creek, Pocatella, Bannock Co., Idaho. Left upper (I), DP4—M3; left lower (J), dp4—m3.

K and L. *Thomomys talpoides fossor*, No. 13205 (KU), Wasson Ranch, 3 mi. E Creede, Mineral Co., Colorado. Right lower (K), p4—m3; left upper (L), P4—M3.

protomeres, thus enclosing the enamel fossette as illustrated in Figure 5E (this is the modified H-pattern mentioned above). However, the fossette itself is shallow and soon disappears with slight wear. At this stage, the occlusal configuration would be in a U-pattern (m1 in Fig. 5E). The lingual re-entrant fold is also shallow in vertical depth; therefore, it is obliterated by wear following the eradication of the labial fossette. Consequently, the two columns are united into one. In m3 (see Figs. 5E, F, and G), the two columns merge by progressive lateral expansion of the medial isthmus.

In the first and second upper molars, the two columns unite across the entire surface of their protomeres from near the lingual edge of the crown to near its center. A minute inner inflection may be temporarily retained in some teeth. At this stage (see Fig. 5B), the parameres are still separated by the labial fissure, and the occlusal pattern is in the shape of a U, resembling, but not exactly duplicating, the pre-final pattern of M1 and M2 in the genus *Pliosaccomys* (see Fig. 4H). The labial fissure is shallow, and, with further wear, the inflection is worn away and the parameres also unite, thereby forming a monoprimatic crown in the final stage. In M3, the two lophs first become united near the edge of their protomeres (see Fig. 5B), therefore forming a U-pattern similar to that developed in M1 and M2 of *Pliosaccomys.* The connection of the two lophs is not directly at the end of the protomere; consequently a shallow lingual inflection remains. The lingual edge of the valley is also shallow, and, with continued wear a second union of the two lophs takes place near the ends of their parameres, and the deeper, interior part of the valley remains as an isolated enamel fossette (see Fig. 5C). The two primary lophs of the tooth are now joined near both sides, having shallow lingual and labial re-entrant angles on the sides and the enamel island in the center. With continued effacement of the occlusal surface, the fossette will be eradicated, and the pattern of the occlusal surface will become the partially biprismatic pattern of the final stages (adult) of wear (see Fig. 5D). M3's of *Dikkomys* and *Pliosaccomys* are not known; however, it seems reasonable to assume that the pattern of wear in the M3 of Dikkomyini was not essentially different from that of the Geomyini, except that it is likely that the U-pattern of the second stage of wear in the Geomyini was probably the final stage in the genus *Dikkomys.*

Judging from the pre-final stages of wear, the dentition of the

Geomyini provides a curious combination of patterns that resemble in part the Miocene genus *Dikkomys* and in part the early and middle Pliocene genus *Pliosaccomys.* There is no significant variation in the premolars or third molars (at least in the lower teeth) of the Geomyinae from the early Miocene to late Pliocene; therefore, deviations of major significance are in the character of the first and second molars. In the Geomyini, the patterns of wear of m1 and m2 are the same as those of *Dikkomys,* and are distinctly different from those of *Pliosaccomys* where the two columns first unite at the edge of their protomeres to form a U-pattern, rather than at their mid-points to form an H-pattern. Even though the intermediate stages of ontogeny in m1 and m2 of *Pliosaccomys* and the Geomyini are entirely different, the bicolumnar crowns of both eventually unite, upon wear, into a single column. On the other hand, the patterns of M1 and M2 in the Geomyini most closely resemble those of *Pliosaccomys,* rather than *Dikkomys.* In this regard it should be pointed out that the upper molars of *Dikkomys* are presently represented by only one tooth, an M1 in an early stage of wear. As described already, the patterns of M1-2 evidently would be mirror images of m1-2 in corresponding stages of wear. However, the initial union of the two columns, in the M1 that is known, is somewhat to the lingual side of center and the relatively small lingual valley does not reach the base of the crown, indicating, that eventually with wear, the two columns of *Dikkomys* might have become united across the entire surface of their protomeres as in *Pliosaccomys.* Even so, the two columns of M1 do initially join closer to their mid-points than they do in *Pliosaccomys,* and, if they did actually unite across their protomeres, the union would have occurred with subsequent wear. That is, the first occlusal pattern would be H-shaped (but with the connection closer to the lingual than the labial side), as in m1 and m2, and it would become U-shaped only after additional wear. This sequence of patterns of M1 and M2, as already pointed out, does not pertain in *Pliosaccomys* or the Geomyini, since the U-pattern is formed with the first union of the two columns at the edge of their protomeres, and the primitive H-pattern is never developed, unless one counts the slight lingual inflection, that occasionally is formed just after the two columns unite, as being indicative of the primitive pattern. As in the lower teeth, the bicolumnar crowns of early ontogeny in both *Pliosaccomys* and the Geomyini become eventually united, with wear, into a single column.

Based upon the foregoing evidence, it would seem likely that the Geomyini evolved from an early Pliocene (perhaps late Miocene) Dikkomyini ancestor that had evolved the specializations of M1 and M2 that characterize its relative, *Pliosaccomys,* but had not also evolved the specializations of m1 and m2 that distinguish *Pliosaccomys.* Therefore, the ancestor of the Geomyini differed from the *Pliosaccomys*-Thomomyini lineage in its retention, unmodified, of the primitive patterns in m1 and m2 that characterized the earliest known Geomyines (*Dikkomys*). The same patterns are preserved in m1 and m2 of its modern descendents, the living Geomyini. In the *Pliosaccomys*-Thomomyini lineage the pattern of m1 and m2 are entirely different, as described above.

The earliest record of the Geomyini is the extinct genus *Pliogeomys* (see Fig. 6) in the latest Hemphillian (middle Pliocene) and earliest Blancan (late Pliocene). *Pliogeomys* is more primitive than any modern genus of the Geomyini, seems to have been a late survivor of the primitive stock, but was itself probably a collateral lineage and not on the direct line of descent. The cheek teeth in *Pliogeomys* are rooted and less hypsodont than in the late Pliocene examples of the modern genera, and the anterior enamel plate of the lower molars shows no indication of reduction, as would be expected if *Pliogeomys* were in the direct line of evolution. Separation of *Pliogeomys* from the main stem of the Geomyini probably occurred after several specializations had already been achieved by the Geomyini. Two inheritances might have been grooving on the upper incisors and some reduction in amount of enamel on the sides of the cheek teeth. The dentine tracts on the sides of the cheek teeth of *Pliogeomys* are narrow (see Fig. 7A) and barely separate the enamel blades and there is no discernible reduction in the anterior enamel blades on its lower molars. Those blades evidently were lost in the main lineage before the Pleistocene radiation of the living genera took place. *Pliogeomys* is in an intermediate stage in evolution, and was not so advanced as was the main lineage at the time *Pliogeomys* died out. Its structure does provide clues as to phyletic development that took place in the main lineage.

Specialized trends in the early phylogeny of the Geomyini included: development of rootless, ever-growing cheek teeth and an increase in hypsodonty; loss of the bicolumnar structure of the first and second molars, and, consequently, the formation of a single elliptical column in the final stage of wear; interruption of the enamel investment of the molariform teeth and formation of anterior and posterior enamel plates; and enlargement of the masseteric ridge and fossa. Each of these trends occurred independently in the Thomomyini, and each is an example of parallelism in the phyletic evolution of the two lineages. Three additional specializations lacking in the Thomomyini are the grooving on upper incisors, loss of anterior enamel plate in lower molars, and development of a basitemporal fossa on the mandible. Evidently, two grooves evolved in the ancestral incisors in the same bisulcate pattern preserved in *Pliogeomys, Zygogeomys* and *Geomys.* The innermost groove is weakly developed in *Pliogeomys,* suggesting that this character was in an intermediate stage of evolution in the ancestral lineage at the time that *Pliogeomys* split off. Numerous other specializations in the Geomyini appeared later, but evolved in the different genera that diverged from the ancestral lineage and are discussed separately in the next account. Only two of the major features characterizing the Dikkomyini are retained in the Geomyini: the H-pattern on the occlusal surface of the m1 and m2 developed during the initial stages of wear, and the bicolumnar pattern of M3. Adaptive radiation produced the living genera of the Geomyini in the late Pliocene and early Pleistocene (see Fig. 6) and subsequent specialization of the ancestral morphology followed.

Parallelism in the molars of later geomyines and the Entoptychinae is illustrated by the lateral interruption of the enamel investment and loss of enamel plates and by the omission of the H-pattern stage in the first and second molars (in *Pliosaccomys*). Resemblance of denitions in certain stages of wear in *Pliosaccomys* and in entoptychines led some investigators, for instance, Hibbard (1953:357), to suggest that *Pliosaccomys* descended from one of the less specialized entoptychines, possibly *Grangerimus* but probably *Gregorymys.* Actually, the highly specialized upper and lower premolars and third molars of the entoptychines rule them out as ancestors of the later geomyines. The evolution of entoptychine-like features in *Pliosaccomys* is regarded as an example of iteration, a pattern of parallelism (see Simpson, 1953:248-253) where an allochronic and independent lineage undergoes the same evolutionary trend that phyletically characterized an earlier lineage, usually after the latter has become extinct. In this case, the lineage giving rise to *Pliosaccomys* passed through the same phyletic stages in its evolution in the early Pliocene (and possibly the late Miocene) as did the entoptychines in the late Oligocene and early Miocene.

Another parallelism by iteration, occurring in the middle and late Pliocene in both the Thomomyini and Geomyini, is the loss of enamel from the lateral surfaces of the cheek teeth, and, in the Geomyini only, the eventual loss of the anterior plate in the lower teeth and the posterior plate in the upper teeth. Both features were evolved more than an epoch earlier in the specialized entoptychid genus *Entoptychus* of the lower Miocene. In *Entoptychus,* only the posterior plate of the lower molars and the anterior plate of the upper molars remained in the final stages of attrition, although a central enamel fossette, a remnant of the re-entrant fold, remained throughout life. Iteration is also expressed in the subfamily Geomyinae by the development of grooving on the upper incisor and the formation of the basitemporal fossa. A shallow but distinct basitemporal fossa occurs between the coronoid process and the third lower molar in the genus *Entoptychus* and a sulcated upper incisor, a single shallow groove usually near the median border of the tooth, is found in the genus *Gregorymys* of the subfamily Entoptychinae. Both features are regarded as advanced specializations in the tribe Geomyini, even though each was evolved in the entoptychines of the Lower Miocene.

The postcranial skeleton of living genera of pocket gophers, as befits animals that spend most of their life within underground burrows, are highly specialized for a fossorial life. Elements of the postcranial skeleton recovered from Lower Miocene deposits indicate that the entoptychines were only semi-fossorial (see Cope, 1884:857; Wood, 1936:4-5; Wilson, 1949:117-118). One of the basic trends of the entoptychines was towards greater fossorial adaptation; the skeleton of *Entoptychus* shows a greater degree of fossorial adaptation than earlier genera of the subfamily. There is no reason to suppose that the geomyine genus *Dikkomys,* which lived at the same times as the entoptychines, had acquired any more advanced fossorial adaptations than had the entoptychines.

The most pronounced fossorial adaptations seem to have evolved only in the ancestral lineage of the modern geomyines, probably in the latter part of the Miocene and in the early Pliocene, before the modern Thomomyini and Geomyini diverged. Extreme fossorial adaptations in herbivorous rodents, such as those characteristic of the modern pocket gophers and their immediate ancestors, are thought to have evolved only in response to pronounced arid conditions. The Entoptychinae and evidently the early geomyines lived in environments that were either tropical or temperate, and under conditions more mesic than I would consider necessary to bring about selection pressure resulting in fossorial specializations. In late Oligocene and early Miocene, according to Axelroad (1958: 433-509), arid conditions did not exist in the United States, and the only xerophytic environments in North America occurred on the Central Plateau of México. Moreover (Axelroad, *loc. cit.*), arid conditions did not develop in the western United States until the early Pliocene. Geomyids evidently became extinct in this region at the close of the Middle Miocene, and none appear in fossil deposits in the western United States until the latest Lower Pliocene (Clarendonian). The reappearance of geomyids, *Pliosaccomys,* in the western United States coincides with a trend toward aridity and the northward movement of the Madro-tertiary geoflora into the Great Basin and Great Plains from its place of origin on the Central Plateau of México (Axelroad, *loc. cit.*). Later, in the middle and later Pliocene, the Madro-tertiary geoflora gave rise to the modern xerophytic plants that now characterize the desert vegetation of North America.

The Madro-tertiary climax does not appear as a major flora until the Miocene, but probably originated earlier. According to Axelroad (*loc. cit.*), this xerophytic flora evolved from elements of the Neotropical-tertiary geoflora that became adapted to arid conditions that developed in the rain shadow of the high mountains flanking the Central Plateau of México. Originally, the Madro-tertiary flora consisted of small trees, shrubs, and grasses. Although some elements of this flora moved northward in the late Miocene, the major part of it remained in México until the early Pliocene. In the western United States, mountain formation increased in intensity in the Pliocene and continued on into the early Pleistocene. As the mountains became more elevated, especially the Sierra Nevada and Cascade ranges, they blocked the prevailing winds from the Pacific Ocean and extensive aridity developed on their leeward side. As xeric conditions became widespread, the Madro-tertiary flora successfully occupied the drier regions of southern California, the Great Basin, and the western parts of the Great Plains.

While the Entoptychinae probably evolved in response to the Arcto-tertiary flora, the late Tertiary geomyines probably evolved in response to the Madro-tertiary geoflora on the Central Plateau of México. Some of these early geomyines, especially ancestors of the modern lineages, probably were pushed southward by competition with the more specialized entoptychines. Most geomyines were pushed out of the northern area of distribution, except for *Dikkomys* that survived in association with the entoptychids throughout the early and middle Miocene. During this time, and probably continuing on into the late Miocene, the geomyines occurring to the south in México became adapted to the arid environments of the Madro-tertiary geoflora.

Of course, information is lacking about climates in several parts of the late Miocene and early Pliocene. When such information becomes available it conceivably could modify the hypothesis outlined immediately above.

The principal trend of evolution in these semi-fossorial rodents was toward more complete fossorial adaptation, and the pronounced fossorial features characteristic of the modern pocket gophers were perfected. This trend continued in response to the intense selection pressures in this arid environment. The principal structural characters effected were in the post-cranial anatomy, especially in the skeletal and muscular systems. Consequently, it is not surprising that in skull and dentition, *Pliosaccomys* differs but little from *Dikkomys.* Therefore, most of the basic structural specializations so far developed for subterranean existence probably had evolved by the time geomyines moved back north in the early Pliocene. Both modern lineages, the tribes Thomomyini and Geomyini, have essentially the same fossorial features, and it seems unlikely that these features were acquired independently in the relatively short period of time available to them after their divergence; probably they were inherited from a common ancestor. These probabilities indicate that the evolution of the fossorial specialization was in the later phyletic development of the tribe Dikkomyini.

Plio-Pleistocene radiation of Geomyini

Unlike the lineage of the Thomomyini that remained essentially rectilinear through out its history, the Geomyini in the late Pliocene and the early Pleistocene underwent adaptive radiation in a degree comparable to the earlier radiation of the Entoptychinae, and all of the later history of the tribe is dominated by the radiation—the resulting structural diversity. At least four lineages were produced by the Plio-Pleistocene radiation (see Fig. 6); each originated at essentially the same time (late Pliocene) presumably from the same ancestral stock. Each of these lineages within the Geomyini has given rise to one of the four modern genera: *Zygogeomys, Geomys, Orthogeomys,* and *Pappogeomys.*

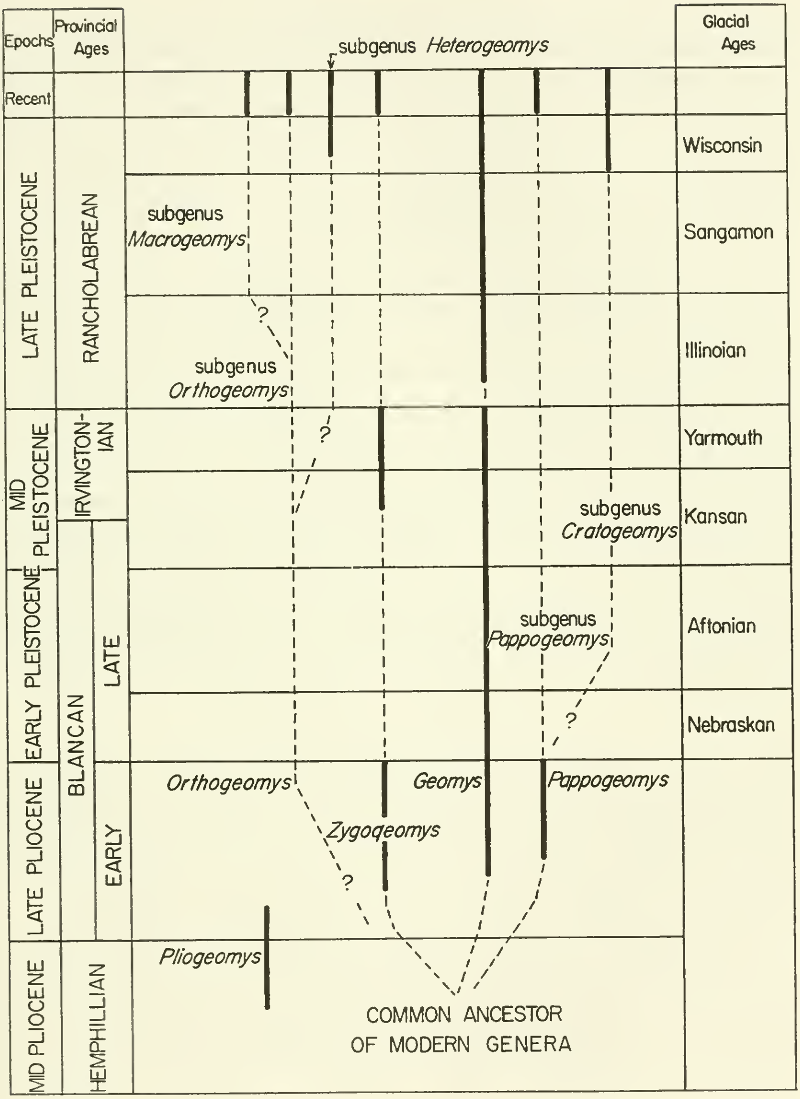


FIG. 6. Plio-Pleistocene radiation of the Tribe Geomyini.

Morphotype

The immediate, unknown, ancestor probably lived on the Central Plateau of México. After the radiation began the ancestors of *Geomys* and *Zygogeomys* extended their ranges northward.

Features of the hypothetical morphotype, that would permit derivation of the modern genera would include the following: (1) Skull generalized, neither excessively long and narrow or short and broad; (2) skull smoothly rounded, without pronounced angularity, rugosity or cresting (sagittal crest probably lacking, even in old individuals); (3) zygomata slender, without lateral platelike expansions; (4) rostrum moderately broad; (5) upper incisors bisulcate, two grooves in pattern found in *Pliogeomys*, *Zygogeomys* and *Geomys;* (6) lateral re-entrant angles of premolars obtuse; (7) p4 having four enamel plates (one on anterior wall, one on posterior wall, and two lateral plates) and lower molars having one enamel plate on the posterior wall of tooth (anterior plate is lacking); (8) P4 having four enamel plates, in same pattern as described for p4, M1 having two enamel plates (one anterior and one posterior), M2 same as M1, M3 having three plates (one anterior, two lateral on sides of posterior loph, none posterior); (9) M3 subtriangular in cross-section, distinctly bicolumnar, two columns marked by shallow re-entrant folds and connected by broad isthmus; (10) masseteric ridge large, forming high crest bordering masseteric fossa; (11) basitemporal fossa shallow; (12) angular process of mandible short, its lateral projection barely exceeding that of zygomatic arch.

Specializations in Genera

In relation to the primitive morphotype, increase in size, simplification of dentition, and changes in shape of skull are regarded as specializations. Considerable parallelism between the four lineages is seen. But each lineage is distinguished by a combination of specialized features, and three by a few unique specializations.

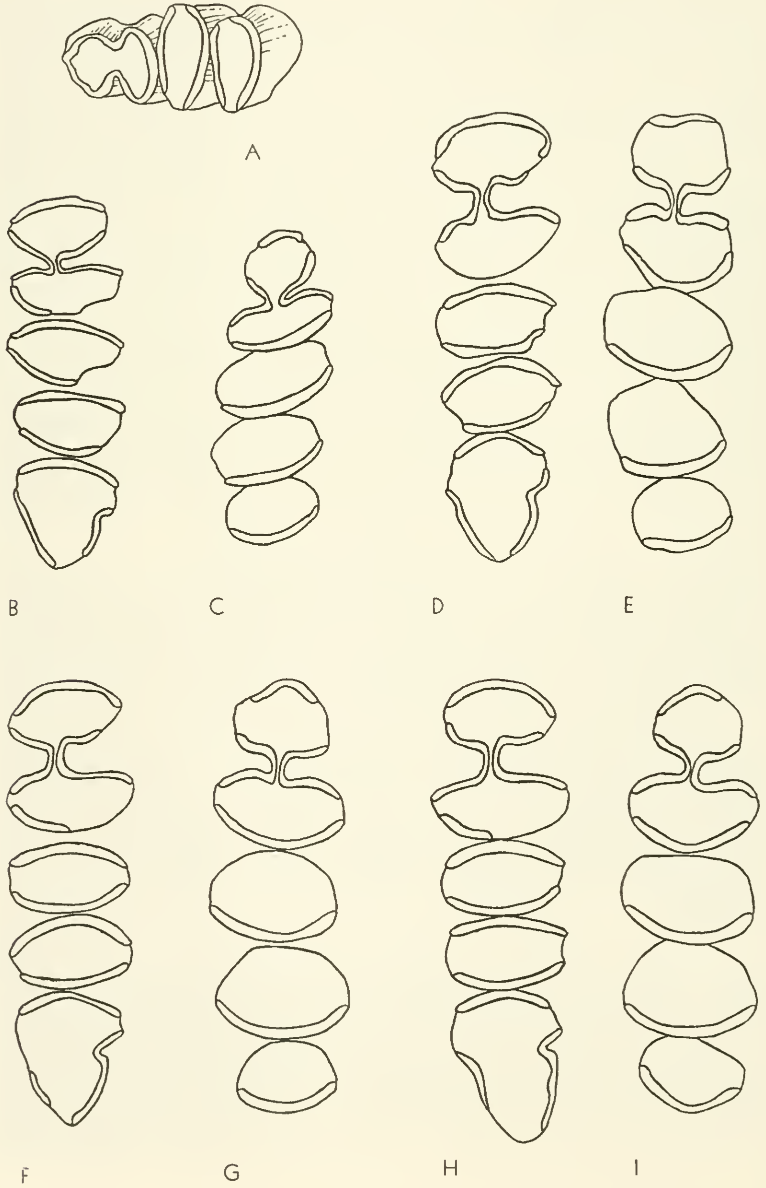
Among trends resulting in simplification of the dentition, reduction of enamel on the posterior wall of the upper check teeth has occurred in various degrees in all lineages of the Geomyini even to loss of all enamel on the posterior wall of the premolars and molars in two genera. Loss of some enamel is more common on P4 than on M1-2, and has occurred in all genera (see Figs. 7 and 9.)

In evolutionary sequence loss of enamel from M1 and M2 usually occurs after, but never preceeding, the reduction of enamel on P4. Loss of enamel plates from the posterior face of M1 and M2 is associated with the evolution of an efficient antero-transverse shearing action of the teeth.

On the anterior wall of those teeth no reduction of the cutting blade has been observed; a complete anterior plate is retained in all living Geomyini.

Presence of both the posterior and anterior plates decreases the efficiency of transverse shearing, by providing two upper plates (anterior plate of one tooth and posterior plate of the preceding tooth) over which the lower cutting blade *simultaneously* must pass with each movement. The advantages of shearing over the more common mechanics of planing are largely lost unless the posterior plates are eliminated. Also, none of the living Geomyini have retained a definitive posterior enamel plate on M3, the last upper molar; but two well-developed lateral plates, that extend almost all of the way back to the posterior apex of M3, have been retained, and, together function as a posterior plate. Loss of either or both of the lateral plates of M3 is rare, and occurs only in old individuals. Their loss in the final stages of wear may represent the beginning of a new trend in those species where it occurs (the *castanops*-group of the subgenus *Cratogeomys*). In any case, reduction of enamel takes place by transverse shortening of the plate through the complete loss of enamel on one end, the diminution beginning first on the labial end and proceeding by progressive atrophy to the lingual end of the plate. Evidently, when enamel has been eliminated from the labial end of a plate, the rate of loss decreases markedly, and the last stages of evolution, terminating in complete loss of an enamel plate, occurs more slowly. Evolution may be arrested before complete loss has occurred, and that part of the enamel that remains forms a short, vestigial plate restricted to the lingual one-fourth or one-third of the wall. The enamel pattern of the lower dentition is the same in all of the diverging lineages, with no evidence of additional loss of enamel from that which had already occurred in their common ancestor (see Figs. 7 and 9). Reduction and loss of enamel plates began and was terminated in the lower dentition before reduction began in the upper dentition.

Other dental specializations have occurred in the shape of the third upper molar and in the pattern of grooving in the upper incisor. Unlike M3 of the Thomomyini, that of the Geomyini differs in shape from M2, and its enamel investment differs from that of M2. Primitively, M3 was probably subtriangular in cross-section, and the posterior loph evidently projected posteriorly as a short, rudimentary heel that formed the apex of the triangle. Other shapes of M3 are considered to be specializations that have been derived from the primitive form. In addition to the primitive subtriangular pattern, the M3 of living Geomyini may be suborbicular, quadriform, elongate, or obcordate in shape. Usually each lineage is



characterized by only one pattern, but in one genus (*Pappogeomys*) all patterns occur. Of the different forms, the elongate and obcordate seem to be the most highly specialized deviations from the triangular-shaped tooth. The bicolumnar pattern is accentuated in the elongate type (Fig. 7D, F, H) by deep lateral re-entrant folds, on both the lingual and labial sides, and by the elongation of the posterior loph into a pronounced heel. Teeth having this pattern have been illustrated by Merriam (1895:76-82) in Figures 27 (6 and 7), 28 (c and d), 34 (7 through 15), and 35 (8).

The subcordate form is characterized by pronounced anteroposterior compression, and retention of a distinct labial re-entrant fold. The posterior loph apparently has been rotated in such a way that what was previously its posterior border now lies on the outer margin of the tooth; therefore, the axis of the posterior loph is strongly oblique in relation to the anteroposterior bearing of the maxillary tooth-row, and the median enamel plate also has been rotated and so lies transversely across the posterior wall of the tooth. Owing to the rotation of the posterior loph, the apex of the obcordate tooth is at its lingual side. The subcordate type is illustrated by Merriam (*loc. cit.*) in Figures 27 (3 and 4), 28 (a and b), 34 (3 and 4), and 35 (5, 6, and 7). The suborbicular and quadriform types are less specialized than the two described above. Both are characterized by reduction, often obliteration, of the bicolumnar pattern of the subtriangular ancestral form, especially marked by the decrease in depth of the lateral re-entrant folds and the decrease in length of the posterior projection of the posterior loph. With these

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FIG. 7. Molariform dentitions of the Tribe Geomyini. Drawings illustrating enamel patterns characteristic of *Pliogeomys*, *Zygogeomys*, and the subgenera of *Orthogeomys* (*Orthogeomys*, *Heterogeomys* and *Macrogeomys*). × 5.

A. *Pliogeomys buisi*, No. 29157 (UMMP), holotype, Buis Ranch (Upper Middle Pliocene), Beaver Co., Oklahoma. Right lower, p4—m2 (m3 unknown).

B and C. *Zygogeomys trichopus trichopus*, adult female, No. 51971 (FMNH), Mt. Tancítaro, 10,500 ft., Michoacán. Left upper (B), P4—M3; right lower (C), p4—m3.

D and E. Subgenus *Orthogeomys*. *Orthogeomys grandis guerrerensis*, adult female, No. 39807 (KU), ½ mi. E La Mira, 300 ft., Michoacán. Left upper (D), P4—M3; right lower (E), p4—m3.

F and G. Subgenus *Heterogeomys*. *Orthogeomys hispidus hispidus*, adult female, No. 23975 (KU), 4 km. W Tlapacoyan, 700 ft., Veracruz. Left upper (F), P4—M3; right lower (G), p4—m3.

H and I. Subgenus *Macrogeomys*. *Orthogeomys heterodus cartagoensis*, adult female, No. 60664 (KU), Rancho Redando, Volcán Lrozá, Prov. San José, Costa Rica. Left upper (H), P4—M3; right lower (I), p4—m3.

changes, the tooth becomes essentially monocolumnar, its occlusal surface oval in outline in one and squarish in shape in the other. Occlusal views of the suborbicular form are presented by Merriam (*loc. cit.*) in Figure 33 (1, 5, 6, 7, 11, and 12) and the quadriform tooth is depicted in Figure 29. Grooved upper incisors are characteristic of the living Geomyini, but variation occurs in the number of grooves, and, if only one groove is present, its position on the anterior face of the tooth varies. Except for the previously mentioned (p. 480) abnormal tooth having three grooves, incisors with no more than two grooves are found in these pocket gophers, and this number of grooves is taken to be primitive. Loss of one or the other of the two grooves of the bisulcate pattern, therefore, is regarded as specialization. However, complete loss of both grooves never occurs in the Geomyini. Each of the four major lineages is characterized by one of the three patterns of grooving, and the particular groove-pattern is remarkably stable in each group.

Shape of skull varies from dolichocephalic to platycephalic. The morphology of each has been described in foregoing accounts. The dolichocephalic skull is highly specialized for planing, a grinding action of the teeth; whereas, the platycephalic skull is highly specialized for shearing, a slicing action of the teeth. Of course, concomitant specializations of the dentition, as described above, are closely associated with both specialized trends in the skull. Most kinds of living Geomyini have generalized skulls that show no tendency toward either of the specialized conditions.

Increase in size of body and skull is seen in most Pleistocene lineages of the Geomyini. Judging from the smallness of the skull in late Pliocene species, representing the base of three of these lineages, the ancestral species of the living assemblage were no larger than the living species of the subgenus *Pappogeomys* or the smaller subspecies of *Geomys bursarius.* The recorded range of variation in condylobasal length is 36.1 to 45.5 in *Pappogeomys bulleri,* including both adult males and females. Probably the skulls of the ancestral species were not significantly larger. Maximum dimensions of males in living species are 74.5 (subgenus *Cratogeomys*) and 75.0 (subgenus *Orthogeomys*). These are more than twice the minima observed in *Pappogeomys bulleri.*

Zygogeomys

This is the least specialized and most primitive of the four lineages, has a generalized type of skull, two grooves on the anterior face of each upper incisor, an enamel plate on the posterior wall of

P4, open or divergent lateral re-entrant angles on the premolars, and a bicolumnar and elongated M3. All of these features are primitive and essentially as in the ancestral morphotype. No other modern genus retains so much of the primitive structure. Phyletic trends in *Zygogeomys* are not well documented in the fossil record; and only a few fossils are known and they are fragmentary as discussed before. The genus is represented in the late Pliocene (*Z. minor*), middle Pleistocene (*Z. persimilis*), and Recent (*Z. trichopus*). The living species is a relict population in the mountains of Central México. Judging from the known material, the phyletic trends in the genus have been increase in size, reduction of enamel on the posterior face of P4 (occurring only in the living species) where a short enamel plate is retained on the lingual side of the tooth (see Fig. 7B), loss of the outer fourth of the enamel blade on the posterior wall of M1 and M2 (also occurring only in the living species), development of a more pronounced heel on the M3 by progressive elongation of the posterior loph, reduction in size of the jugal and its displacement ventrally, which allows the maxillary and squamosal bones to meet along the dorsal border of the zygomatic arch. The last specialization is seen in at least one taxon of *Orthogeomys* (*Orthogeomys cherriei costaricensis*). In my opinion, too much weight has been given to this feature in past classifications. Reduction of enamel in the upper dentition evidently occurred in the late Pleistocene, since the posterior plates on the upper cheek teeth were complete in specimens from the middle Pleistocene (*Z. persimilis*).

Geomys

Geomys, slightly more specialized than *Zygogeomys,* must also be regarded as one of the most primitive of the living genera. Primitive features that have been retained are the generalized type of skull, the bisulcate pattern of grooves on the upper incisor, and the retention of enamel plates on both the anterior and posterior walls of M1 and M2 (see Fig. 9A). All of these primitive features are shared with *Zygogeomys.* In addition, three other trends, or specializations, in evolution characterize the phyletic development of *Geomys.* One major trend is toward loss of the enamel plate from the posterior wall of P4. No trace of enamel remains on the posterior wall of this tooth in late Pleistocene or Recent species of *Geomys,* and at least one of the earlier species (*quinni*) was also characterized by loss of this enamel plate. Secondly, M3 retains only a vestige of the primitive bicolumnar pattern after the initial stages of wear. In most Recent specimens, especially of the species

G. bursarius, the lateral re-entrant fold and the heel of M3 are small, and the re-entrant inflection is hardly evident. The lateral fold is more frequently well-developed in Irvingtonian species than in living species (White and Downs, 1961:13), illustrating progressive loss of the bicolumnar pattern in Pleistocene evolution. A third trend involves the modification of the lateral folds of the premolars. Primitively the angles of these folds are broadly open or divergently V-shaped, and some of the earliest species of *Geomys,* for example *G. quinni,* have retained this feature throughout life. Nevertheless, the main trend is toward progressive compression of the folds resulting in their walls being more nearly perpendicular, and parallel, to the long axis of the tooth. Obtuse re-entrant angles persist in premolars of young individuals of Irvingtonian species, but the adults are characterized by well-compressed folds, as in Recent species.

Remains of *Geomys* are abundant, especially from Pleistocene deposits of the Great Plains, but in most instances specific assignment is difficult or impossible since only isolated teeth or fragments of skulls have been preserved. Estimates of phyletic relationships of the known species of *Geomys* are depicted in Figure 8; those estimates are useful in discussing the phyletic development of the genus. One of the earliest known species, *Geomys quinni,* ranges from Upper Pliocene to the later stages of the Lower Pleistocene (Aftonian interglacial deposits). The dentition of *G. quinni* is essentially the same as in the living species except that open lateral re-entrant angles are retained in the premolars. *Geomys paenebursarius,* also of the early Pleistocene, is a smaller species and seems to be more directly in the line of evolution of the modern species. As yet unnamed smaller species of *Geomys* from the Rexroad fauna (late Pliocene) and Saunders fauna (latest Aftonian) may also be on the main line of evolution. Surprisingly, *Geomys tobinensis* and *Geomys garbanii* of later Irvingtonian provincial age are less specialized than either *Geomys quinni* or *Geomys paenebursarius.* It is likely that *G. tobinensis* and the unnamed species from the Dixon are closer to the main line of descent than *G. paenebursarius* suggesting that the direct ancestral lineage of the living species of *Geomys* was more conservative and less specialized than *Geomys paenebursarius* of the Lower Pleistocene. *Geomys quinni* and *G. paenebursarius* seem to have acquired specialized dental features in the early Pleistocene. *Geomys quinni* was successful on the Great Plains, and persisted into the late Blancan. The main line may be represented in the early Pleistocene by

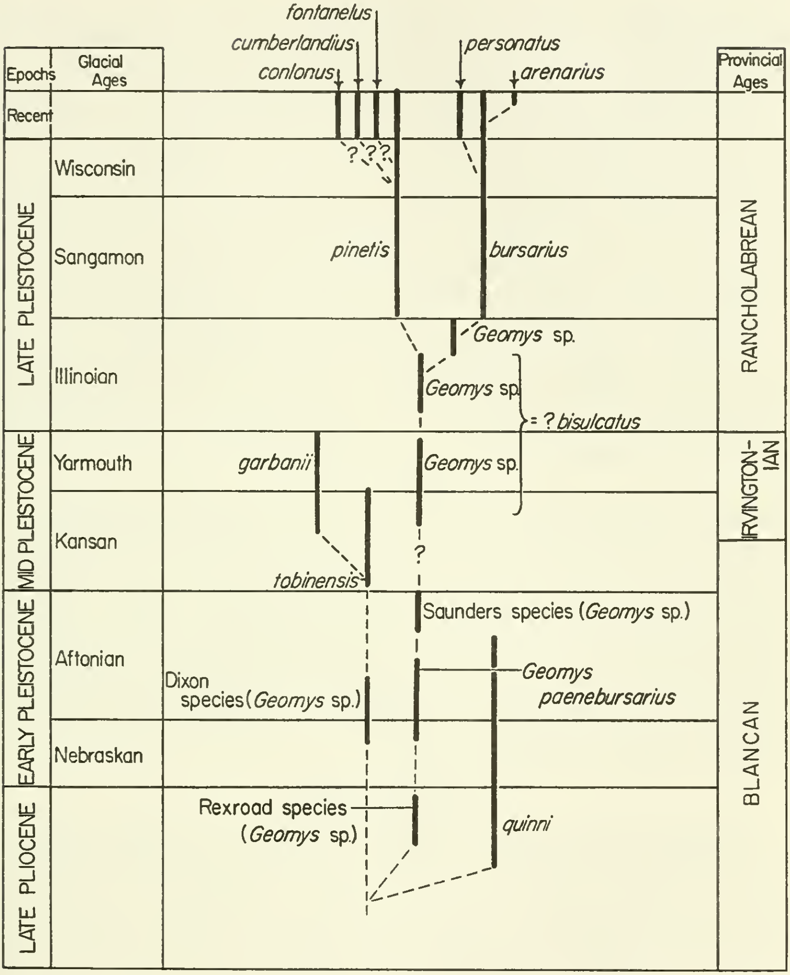


FIG. 8. Tentative arrangement of species of the genus *Geomys*, depicting phylogenetic trends and probable relationships within the genus.

Geomys paenebursarius from the Hancock formation of the Texas Trans-Pecos. The structure of *G. paenebursarius* indicates that it is in or close to the main line of descent, and probably evolved from one of the more primitive late Pliocene species of *Geomys* from the Rexroad fauna.

Isolated teeth, to which the name *Geomys bisulcatus* probably applies, from Illinoian deposits on the Great Plains, show that the dentition characteristic of the living *Geomys* had been developed by that time. Actually, the Illinoian material is too fragmentary to show clearly its taxonomic or phyletic affinities with the species of the later Pleistocene. Even so, the two main stocks of living *Geomys, G. bursarius* and *G. pinetis,* had certainly been differentiated by Sangamon time. The other living species evidently evolved from one or the other of these two stocks in a period of isolation from the main population, probably in either the Wisconsin or post-Wisconsin. For example, *Geomys arenarius* clearly differentiated from populations of *Geomys bursarius* that were isolated by the eastward retreat of the main population from the southwestern United States as that region became more arid in the post-Wisconsin.

In review, it seems that the Recent species, represented basically by *bursarius* and *pinetis,* evolved from Illinoian species (*Geomys bisulcatus?*), which descended in turn from the more primitive species of the early Pleistocene, possibly *Geomys paenebursarius* or possibly from descendants of the Saunders species. Actually the Saunders species may prove to be *Geomys paenebursarius.* At any rate, three trends that took place during the Pleistocene stage of evolution, in the direction of the modern species, were an increase in size, progressive loss of the posterior enamel plate on P4, and a decrease in the vertical depth of the enamel cap as a result of which the dentine is reached in the initial phases of attrition on the tooth of a juvenile. *Geomys garbanii,* occurring at the periphery of the range of the genus, is regarded as a sterile offshoot of the primitive *tobinensis*-line of evolution.

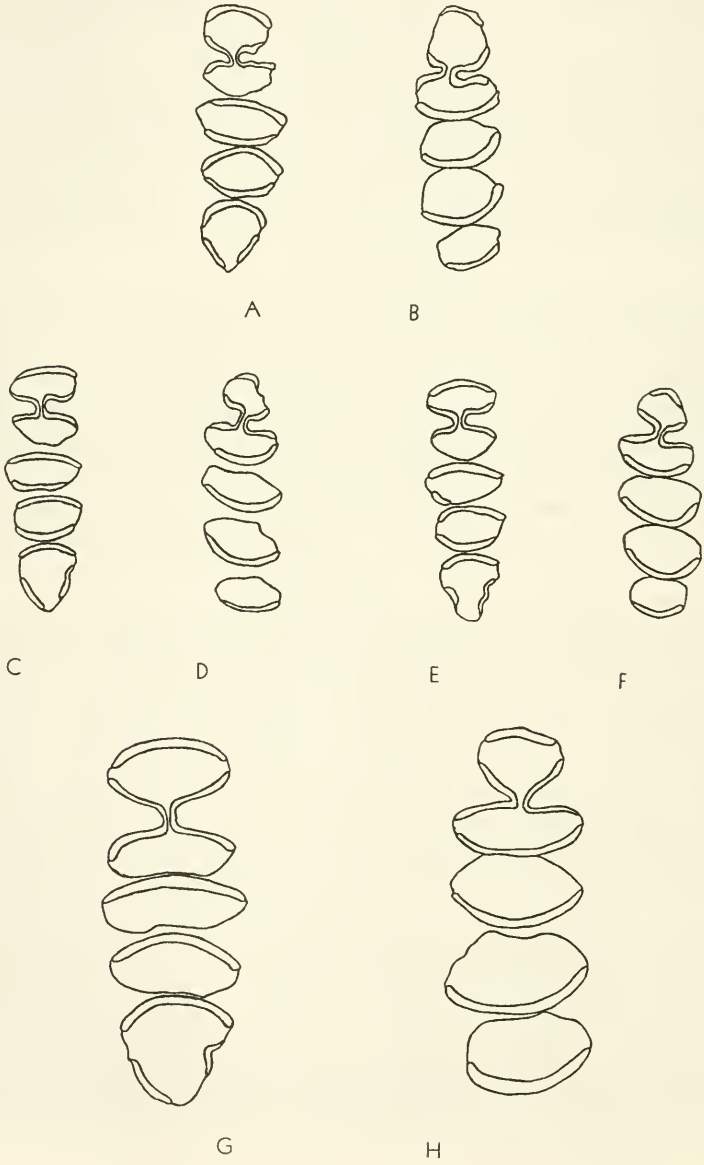
Orthogeomys

This is one of the more specialized genera of the Geomyini. Save for one record in the late Pleistocene (*Orthogeomys onerosus*), there is no fossil history of the genus upon which to reconstruct its phylogeny; therefore, its phyletic development must be estimated by comparing it and the primitive morphotype of the tribe. Results of that comparison suggest that *Orthogeomys* has closer affinities with *Zygogeomys* than with any of the other genera, and that *Orthogeomys* may have originated in an early dichotomy of primitive *Zygogeomys* stock instead of descending from the ancestral stock of the tribe. Except for the unisulcate incisors and the longer posterior loph on the third upper molars, the teeth of the two genera do not differ significantly. As in *Zygogeomys,* the enamel blade on the posterior wall of P4 has been reduced to a short plate restricted to the lingual third of the tooth (see Fig. 7F and H). In *Orthogeomys,* the trend in reduction of enamel is carried to its extreme only in the subgenus *Orthogeomys,* where this plate has been completely lost in most taxa (see Fig. 7D). The most significant trends in *Orthogeomys,* and the principal basis for recognizing the genus, are the dolicocephalic specializations of the skull, as described elsewhere, and the adaptive traits that have equipped the genus for living in tropical environments. The dolichocephalic features are more sharply defined in the subgenera *Orthogeomys* and *Macrogeomys,* and are less developed in the subgenus *Heterogeomys.* Aside from the general dolichocephalic specializations, trends in *Orthogeomys* include: Increase in size; loss of the median one of the two grooves on the anterior face of the upper incisor in the ancestral stock; increase in the anteroposterior length of each of the cheek teeth, as well as the aforementioned elongation of the posterior loph of M3; compression of the lateral angles of the premolars; and the remarkable increase in the size of the rostrum.

Pappogeomys

The genus *Pappogeomys,* as it is conceived of in this study, is comprised of two subgenera; one, *Pappogeomys,* is generalized and primitive, and the other, *Cratogeomys,* is specialized, and includes the most highly specialized of the modern pocket gophers. The subgenus *Pappogeomys* is regarded as the ancestral lineage, and the subgenus *Cratogeomys* is regarded as an early offshoot, probably in the early Pleistocene, that became progressively more specialized in the course of its subsequent evolution. In the same period of time, the subgenus *Pappogeomys* changed little. It is known only from late Pliocene fragments and from the living species. The ancestral morphotype is preserved in *Pappogeomys.* Primitive characters are: (1) Small size; (2) skull generalized and smoothly rounded; (3) temporal ridges separate (not uniting into a sagittal crest); (4) enamel plates retained on both anterior and posterior walls of M1 and M2; (5) M3 bilophate, its posterior loph short. Basic specializations are few and include loss of the inner groove from the anterior face of the upper incisor; anteroposterior compression of the lateral re-entrant folds of the premolars; and loss of enamel from the posterior wall of P4. All three features have been perpetuated in the advanced subgenus *Cratogeomys,* suggesting that they were already developed in the early evolution of the subgenus *Pappogeomys* before *Cratogeomys* diverged. Agreement with *Geomys* is demonstrated by the lack of enamel on the posterior wall of P4 (see Fig. 9) and by retention of the posterior enamel plate on M1 and M2. In *Pappogeomys* (*Pappogeomys*) *alcorni* the enamel from the posterior face of M1 has been lost from all but the lingual fourth or so of the posterior wall (Fig. 9E). Reduction of enamel in M1 provides an example of parallelism with the more advanced subgenus *Cratogeomys*, discussed below.

There is no record as yet of the early evolution of the subgenus *Cratogeomys*. The features that characterize the subgenus were



already well developed in the first known fossils which are from Wisconsin deposits of the late Pleistocene. *Cratogeomys* is not a homogenous assemblage; instead it is composed of two groups of living species, the generalized *castanops* group and the specialized *gymnurus* group. The *castanops* group may be survivors of the ancestral lineage that diverged in two different stages in the phyletic development of the main line. Even so, the *castanops* group has acquired its peculiar specializations. Indeed, *P. merriami* of the *castanops* group differs from the hypothetical stem more than does *P. castanops.* Judging from the structure of the living species of the subgenus *Cratogeomys* and from the primitive subgenus *Pappogeomys,* the subgenus *Cratogeomys* featured five major trends: (1) Increase in size; (2) formation of sagittal crest by union of the temporal impressions; (3) increase in rugosity and angularity of the skull; (4) progressive development of platycephalic specializations, including the elongation of the angular process of the mandible; (5) complete loss of enamel plates from the posterior wall of M1 and M2. Each trend is thought to be adaptive.

Loss of enamel is a trend common to all living genera of the tribe Geomyini, but the greatest loss has occurred in *Cratogeomys.* It has lost the plates on the posterior walls of M1 and M2 (Fig. 9G). If the lateral plates of M3 are considered as one functional plate and the lateral plates on either side of P4 together as two transverse plates, then, the transverse cutting blades in *Cratogeomys* number seven in the upper and seven in the lower cheek-teeth compared with 10 in the upper and seven in the lower in the primitive morphotype. Indeed, in some species of the subgenus, one or both of the lateral plates on M3 is also lost, usually in old age, resulting in even greater reduction of enamel. Loss of enamel from the posterior

FIG. 9. Molariform dentitions of the Tribe Geomyini. Drawings illustrating enamel patterns characteristic of *Geomys* and *Pappogeomys* (including the subgenera *Pappogeomys* and *Cratogeomys*). × 5.

A and B. *Geomys bursarius bursarius,* adult female, No. 46275 (KU), Elk River, Sherborne Co., Minnesota. Left upper (A), P4—M3; right lower (B), p4—m3.

C and D. Subgenus *Pappogeomys. Pappogeomys bulleri albinasus,* adult female, No. 31002 (KU), W side La Venta, 13 mi. W and 4 mi. N Guadalajara, Jalisco. Left upper (C), P4—M3; right lower (D), p4—m3.

E and F. Subgenus *Pappogeomys. Pappogeomys alcorni,* adult female, No. 31051 (KU), holotype, 4 mi. W Mazamitla, 6600 ft., Jalisco. Left upper (E), P4—M3; right lower (F), p4—m3.

G and H. Subgenus *Cratogeomys. Pappogeomys gymnurus tellus,* adult female, No. 31051 (KU), 1 mi. NE Tala, 4400 ft., Jalisco. Left upper (G), P4—M3; right lower (H), p4—m3.

walls of the upper molars may be associated with changes in the mechanics of mastication from anteroposterior planing to anterotransverse shearing, as discussed elsewhere. Merriam (1895:95-96) argues convincingly that the posterior cutting blades of the upper molars would hinder efficient shearing action of the teeth; hence, selection would favor their reduction and eventual loss. Changes in the shape of the skull also seem to be correlated with the shift from a planing to a shearing type of mastication. More efficient shearing action, which depends upon lateral movement of the jaw, can be developed if the functional muscles insert farther laterally than is possible in the generalized type of skull. Therefore, platycephalic specializations involved lateral expansion of the braincase and mandible. Pronounced lateral expansion has been developed only in the *gymnurus* group of species, suggesting that the dental specializations evolved earlier in the evolution of the subgenus than did the platycephalic specializations of the skull, and that the *castanops* group separated from the *gymnurus* group before the common ancestor had developed the more extreme trends in platycephaly. It is interesting to note that the subtriangular M3 (Fig. 9G) postulated for the ancestral morphotype and that characterizes the subgenus *Pappogeomys* is retained also in the *gymnurus* group.

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CONTENTS

INTRODUCTION

Attempts to identify pocket gophers in the research collection of the Agricultural and Mechanical College of Texas in the period 1948-1950 aroused my interest in the systematics of those mammals, especially members of the subgenus *Cratogeomys.* This interest was maintained in the course of graduate study at the University of Kansas in the period 1951-1956. In 1952 I decided (1) to learn how many kinds of pocket gophers there were in the genus *Cratogeomys* (= subgenus *Cratogeomys* of the following account) and what the geographic distribution was of each kind, and (2) to investigate the intergeneric relationships of the nine or so Recent genera of pocket gophers recognized at that time.

By 1955 these interests had led me to begin a study of the fossil—as well as the Recent—representatives of all subfamilies, tribes, genera, and subgenera of the family Geomyidae. The classification down through the subgeneric level arrived at as a result of that study is presented in a preceding paper (Russell, 1968: 473-579). It extended, or more precisely, expanded, so far as my concept is concerned, the limits of the taxon, *Cratogeomys,* that had aroused my curiosity, initially. The following account is a taxonomic revision of all subspecies, species, and subgenera of that taxon, which, in conformance with the law of priority, bears the generic name *Pappogeomys.*

MATERIALS, ACKNOWLEDGMENTS, AND METHODS

At a late stage in the preparation of this manuscript a total of 1557 specimens of the genus *Pappogeomys* had been examined. Most of these were conventional stuffed study-skins, each accompanied by the corresponding skull and lower jaws and an attached label bearing the customary data as to date and place of capture, sex, four external measurements, and name of collector. Some complete skeletons, skulls unaccompanied by skins, and entire animals preserved in alcohol are included.

Bound volumes of collectors' field notes in the University of Kansas Museum of Natural History yielded additional data.

For initial encouragement in studying mammals, including pocket gophers, I am indebted to Professors Walter P. Taylor and William B. Davis. I am especially grateful to Professor E. Raymond Hall for his advice, encouragement, and help with many aspects of this study. Not only did he make available to me the facilities of the Museum of Natural History of the University of Kansas, but he aided my progress in other ways including critical assistance with the manuscript, especially at a time when I was discouraged. Of others at the Museum, Dr. Rollin H. Baker deserves special mention; his assistance and advice were greatly appreciated.

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ingen made, or assisted with, each of the figures. For clerical assistance I thank Miss Mary Alice Crivello, Toni Ward, and my wife, Danna Barton Russell.

Of course I am appreciative of the work of the late Dr. C. Hart Merriam, Mr. Edward A. Goldman, and other mammalogists who have written on the classification of pocket gophers (see Literature Cited), as I am also to the collectors of specimens; without their contributions it would not have been feasible for me or anyone else to contribute much at this time to our understanding of the relationships of the several kinds of geomyids here assigned to the genus *Pappogeomys*. Likewise, I acknowledge with gratitude some financial assistance from the contract NR 160-187 between the Office of Naval Research, United States Department of the Navy, and the University of Kansas, assistance from the National Science Foundation (G 7), the Watkins Fund of the Kansas University Endowment Association, and a grant in 1966 from the Computation Center of the University of Kansas at Lawrence.

Methods of study included initially finding the largest series from each of several localities and in each series separating the sexes and then arranging each sex from youngest to oldest, in order to learn the degree of secondary sexual variation and the degree of variation ascribable to increasing, ontogenetic age.

Males of the subgenus *Cratogeomys* average 7 to 10 per cent more than females in linear measurements of the skull (4 to 5%) in subgenus *Pappogeomys*), about 7 per cent more in length of head and body (2% in subgenus *Pappogeomys*), about 2 per cent more in length of tail (6% in subgenus *Pappogeomys*), and 2 per cent in length of hind foot (no secondary sexual difference detected in length of hind foot in subgenus *Pappogeomys*). See Figure 1 and Table 1 for a sample of the data on secondary sexual variation.

For convenience, five categories of age were recognized in the genus *Pappogeomys*. Many cranial features reflecting stages of ontogenetic growth in the skull made it easy to recognize the categories. Some of the cranial features of each age-category that were relied on are as follows:

Juvenile.—Subgenera *Cratogeomys* and *Pappogeomys:* Deciduous premolar present; impression of temporal muscle on braincase absent.

Young.—Subgenera *Cratogeomys* and *Pappogeomys:* Deciduous premolar absent (permanent premolar functional); impression of temporal muscle on braincase; supraoccipital not fused with exoccipitals.

Subadult.—Subgenus *Cratogeomys:* Supraoccipital fused with exoccipitals; temporal ridges not touching one another. Subgenus *Pappogeomys:* Temporal ridge at junction of frontal and parietal bones less than one-tenth of a millimeter high; median (anteroposterior) ridge on basioccipital not higher anteriorly than posteriorly.

Adult.—Subgenus *Cratogeomys:* Temporal ridges touching one another or forming sagittal crest. Subgenus *Pappogeomys:* Temporal ridge at junction of frontal and parietal bones more than one-tenth of a millimeter high; median (anteroposterior) ridge on basioccipital higher anteriorly than posteriorly.

Old.—For taxonomic use, not separated from adult. In subgenus *Cratogeomys* an occasional female showing great angularity at many places on the skull, and an occasional male showing similar angularity and an exceptionally high, bladelike sagittal crest that extends far posteriorly are recognized as old. In subgenus *Pappogeomys* an occasional female and an occasional male showing exceptionally high ridging on the skull and absence of sutures on the dorsal surface of the skull, except those bounding the nasals and that separating the frontals from the parietals, are recognized as old.

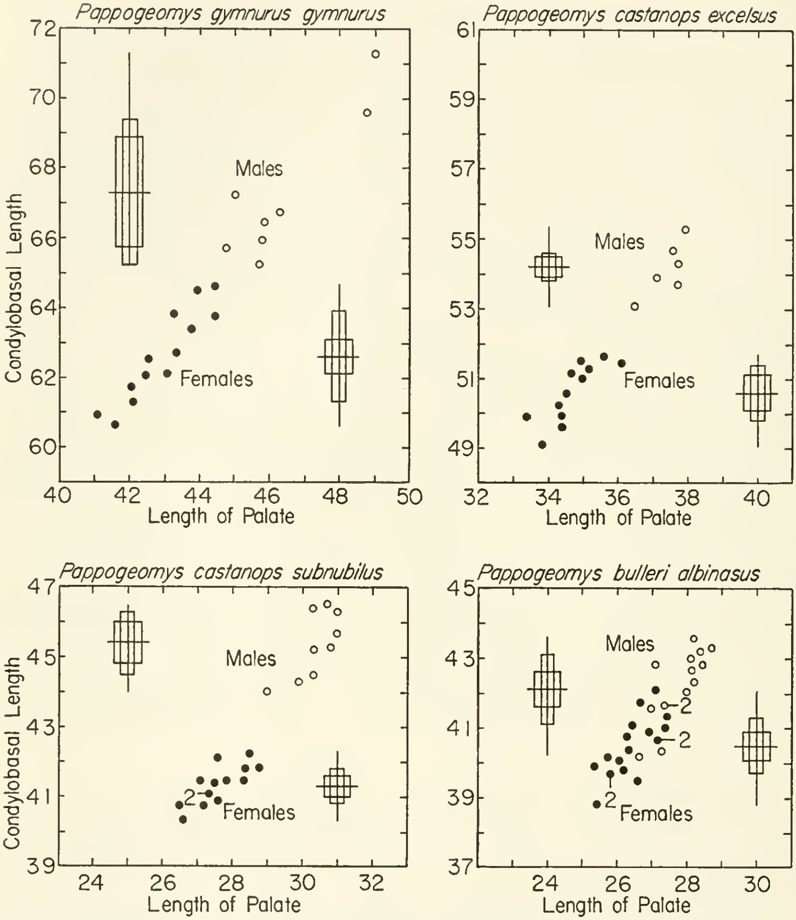

FIG. 1. Secondary sexual variation in adults and old individuals of four taxa. Dicean squares relate to the condylobasal length and show extremes, one standard deviation from the mean, two standard errors from the mean, and the mean.

Specimens of each taxon are from one restricted part of the geographic range of the taxon. Precise localities, together with number of specimens from each, are as follows:

P. g. gymnurus (Jalisco, 21), Ciudad Guzman, 8; Las Canoas, 13.

P. c. excelsus (Coahuila, 18), Acatita, 7; Nuevo Mundo, 1; San Pedro, 2; 1 mi. SW San Pedro, 1; 2 m. E Torrejon, 7.

P. c. subnubilus (Coahuila, Zacetacas, and Nuevo León, 23), Carneros, 1; 1 mi. S. Carneros, 1; 2 mi. W San Miguel, 1; 1 mi. N Agua Nueva, 1; 8 mi. N La Ventura, 3; La Ventura, 5; 3 mi. N Lulú, 4; 15 mi. S Concepción del Oro, 3; 7 mi. NW Providencia, 1; 5 mi. W Ascención, 1; 1 mi. W Doctor Arroyo, 2.

P. b. albinasus (Jalísco, 32), 2 mi. N, ½ mi. W Guadalajara, 11; 4 mi. W Guadalajara, 8; Ciudad Granja in Guadalajara, 2; 8 mi. W and 10 mi. S Guadalajara, 11.

Table 1.—Variation in Cranial Measurements. Specimens are adults and old.

Name of measurement	Mean	Minimum	Maximum	Coefficient of variation	Mean	Minimum	Maximum	Coefficient of variation
Pappogeomys (Cratogeomys) gymnurus gymnurus (see Fig. 1 for localities)								
	13 Females				8 Males			
Condylobasal length..	62.6	60.6	64.6	2.10	67.3	65.3	71.3	3.14
Zygomatic breadth...	43.6	41.0	44.8	2.83	47.1	45.2	48.5	2.43
Palatofrontal depth...	23.8	22.6	25.0	3.34	25.3	24.4	26.7	3.57
Length of palate.....	43.0	41.1	44.5	2.48	46.4	44.7	49.0	3.51
Length of nasals.....	22.0	21.0	23.3	3.24	23.8	22.1	26.1	5.83
Breadth of braincase..	32.5	30.8	34.3	3.33	34.4	32.5	35.9	3.74
Squamosal breadth...	45.8	44.6	47.4	2.10	49.0	47.0	52.3	3.83
Breadth of rostrum...	14.7	14.0	16.1	4.12	16.0	15.2	17.1	4.15
Length of rostrum....	27.3	26.3	28.8	2.89	29.3	27.6	31.7	5.15
Alveolar length of Maxillary tooth-row..	13.5	12.6	14.3	3.33	14.4	13.7	15.8	5.02
Pappogeomys (Pappogeomys) bulleri albinasus (see Fig. 1 for localities)								
	18 Females				14 Males			
Condylobasal length..	40.5	38.9	42.1	2.03	42.2	40.2	43.6	2.38
Zygomatic breadth...	27.1	24.1	29.9	4.97	28.9	27.0	31.0	3.79
Palatofrontal depth...	15.7	15.0	16.3	2.25	16.2	15.5	16.7	2.11
Length of palate.....	26.4	25.4	27.4	2.54	27.8	26.5	28.6	2.32
Length of nasals.....	14.9	13.9	16.4	4.87	15.7	14.3	17.2	6.27
Breadth of braincase..	20.3	18.8	21.8	3.48	21.1	20.4	21.9	2.01
Squamosal breadth...	24.6	22.4	26.5	3.27	25.9	24.8	27.1	2.63
Breadth of rostrum...	9.6	8.8	10.5	5.28	10.3	9.4	10.9	4.66
Length of rostrum....	18.7	17.8	20.2	3.57	19.7	18.6	21.2	4.24
Alveolar length of maxillary tooth-row..	9.0	8.1	9.8	4.35	9.3	8.2	9.8	4.30

On the following pages, specimens of all ages are listed in the terminal sections "*specimens examined*" of accounts of subspecies and monotypic species. In all other parts of those accounts, unless otherwise indicated, all measurements, descriptions, and comparisons relate to adults and old individuals. The specimens in each of several series were arranged according to date within the year in order to learn about seasonal variation. In the northern part of the geographic range of the genus the winter pelage is slightly darker, longer, softer to the touch, and appears to be more dense than the summer pelage.

After some confidence was developed in recognizing the sex and the ontogenetic age by means of cranial features, specimens of the largest series of the same sex and age from the same locality (for example *Pappogeomys gymnurus gymnurus* from Las Canoas), obtained in the same season, were measured in order to ascertain the range of variation in each of several cranial dimensions, in the three external measurements (total length, length of tail, and length of hind foot), in color pattern, and in color. The variation detected was designated "individual variation" and was considered to be of the same sort found in offspring of a single pair of parents.

Once the range of individual variation was known, specimens of the same sex, age, and season from locality A could meaningfully be compared with corresponding specimens from locality B. If the two samples were identical they were referred to one and the same subspecies. If the two samples differed, the difference was tested for subspecific *versus* specific nature. The test ordinarily involved an examination of specimens from a geographically intermediate locality, C. If intergradation was evident in animals from C, the animals from localities A and B were arranged as two subspecies of one and the same species, but if the kinds of animals at A and B did not intergrade at C or at any other locality the animals from A and those from B were arranged as two species.

In distinguishing between kinds of pocket gophers I have relied principally on females rather than males for two reasons: Adult females outnumber adult males by more than two to one in collections of study specimens; adult females are less variable than adult males, especially in the subgenus *Cratogeomys*. In nine females and eight males of *Pappogeomys* (*Cratogeomys*) *merriami merriami* the coefficient of variation for the condylobasal length was 2.35 in females versus 3.41 in males. In the subgenus *Pappogeomys*, males are no more variable in linear measurements of the skull than are females.

In lists of specimens examined, an asterisk preceding the designation of a locality signifies that it is not entered on the distribution map beyond because undue crowding or overlapping of symbols would have occurred.

In the lists of specimens examined the localities within any one county of the United States and within any one state of the Republic of Mexico are listed from north to south. If more than one locality in a given political subdivision lies on the same line of latitude, the westernmost of those on that line is recorded first.

Specimens for study were lent by the institutions listed below. The abbreviations preceding the names of institutions are used in the lists of specimens examined. Specimens for which no designation is given are in the Museum of Natural History of The University of Kansas. For the loan of specimens, I am especially indebted to these institutions and persons:

AMNH—American Museum of Natural History. S. Anderson and H. M. VanDeusen.
WLC—William L. Cutter Collection. W. L. Cutter
DM—Denver Museum of Natural History. Alfred M. Bailey.
FMNH—Field Museum of Natural History. The late C. C. Sanborn.
MCZ—Harvard University, Museum of Comparative Zoology. B. Lawrence.
LSU—Louisana State University, Museum of Natural History. G. H. Lowery.
USNM — United States National Museum, including Biological Surveys Collection. D. H. Johnson and V. S. Schantz.
OSU—Oklahoma State University. B. P. Glass.
PA—Academy of Natural Sciences of Philadelphia. R. R. Grant, Jr.

UA—University of Arizona. E. L. Cockrum.
MVZ—University of California, Museum of Vertebrate Zoology. O. P. Pearson.
UI—University of Illinois, Museum of Natural History. D. F. Hoffmeister.
UMMZ—University of Michigan, Museum of Zoology. E. T. Hooper and W. H. Burt.
NM—University of New Mexico, Museum of Southwestern Biology. J. S. Findley.
UT—University of Texas. W. F. Blair.
TCWC—Texas A and M University, Texas Cooperative Wildlife Research Collection. W. B. Davis and D. R. Patten.
TT—Texas Technological College. R. L. Packard.
MSU—The Museum, Michigan State University. R. H. Baker.
WC—Warren Collection, Colorado College. R. G. Beidelman.

Cranial measurements are in millimeters and tenths thereof. The measurements recorded beyond are the following:

Condylobasal length.—Least distance on skull from line connecting posteriormost projections of exoccipital condyles to line connecting anteriormost projections of premaxillary bones.

Zygomatic breadth.—Greatest distance across zygomatic arches of cranium at right angles to long axis of skull.

Palatofrontal depth.—Least distance between two parallel planes, one touching dorsalmost points of the two frontal bones and the other touching the ventralmost points of the two palatine bones between the molar teeth.

Length of palate.—Distance on skull from anteriormost point on posterior border of palate (palatine bones) to line connecting anteriormost projections of premaxillary bones.

Length of nasals.—Least distance between a line touching anteriormost point of nasals to a parallel line touching posteriormost point of nasals.

Breadth of braincase.—Distance, at right angles to long axis of skull, between right lateral margin of squamosal bone immediately in front of external auditory tube to corresponding place on left side of skull.

Squamosal breadth.—Greatest distance across mastoid processes of squamosal bone at right angles to long axis of skull.

Breadth of rostrum.—Greatest width, at right angles to long axis of skull, of preorbital part of skull at (or within 5 mm of) suture between premaxilla and maxilla as seen on dorsal surface of skull.

Length of rostrum.—Middle of anterior border of nasals to junction of orbital border of maxilla and lateral end of base of lacrimal process.

Alveolar length of maxillary tooth-row.—Distance from anterior lip of alveolus of P4 to posterior lip of alveolus of M3. Measurement taken with needle-point dividers and marked off on paper; then distance between two points was measured by means of calipers.

Capitalized color-terms are those of Ridgway (1912).

In 1948 when my study was begun the Recent pocket gophers here reported on were arranged as belonging to 43 kinds (including subspecies) of 13 species of 3 genera. In the present account 52 kinds of 9 species of one genus are recognized, owing to combining three genera into one genus, reducing the species from 13 to 9, and naming several heretofore unrecognized subspecies.

Genus Pappogeomys Merriam

Pseudostoma, Baird, *in* Report Stansbury's Expd. Surv. . . . Great Salt of Utah . . ., App. C, p. 313, June, 1852 (for his new species *castanops*). *Pseudostoma* is preoccupied by *Geomys*.

Geomys, LeConte; Proc. Acad. Nat. Sci. Philadelphia, 6:163, 1852, who applied the name to *Pseudostoma castanops* Baird.

Pappogeomys Merriam, N. Amer. Fauna, 8:145, January 31, 1895 (type, *Geomys bulleri* Thomas).

Cratogeomys Merriam, N. Amer. Fauna, 8:150, January 31, 1895 (type, *Geomys merriami* Thomas).

Platygeomys Merriam, N. Amer. Fauna, 8:162, January 31, 1895 (type, *Geomys gymnurus* Merriam).

Type.—*Geomys bulleri* Thomas, Ann. Mag. Nat. Hist., ser. 6, 10:196, August, 1892.

Diagnosis.—Anterior surface of upper incisors having single, deep, median sulcus; P4 having only three enamel plates, the posterior lacking; posterior face of M1 and M2 without enamel plate; trends in cranial specializations distinctly toward platycephaly.

Distribution.—Geologically, early Blancan (Benson local fauna of Arizona) to Recent; geographically in Recent time from southeastern Colorado and the panhandle of Oklahoma south through western Texas and eastern New Mexico and the Central Plateau of México to the southern slopes of the Neovolcanic Range; from Pacific Coast of Jalisco and Colima eastward onto western slopes of Sierra Madre Oriental. Altitudinal range from near sea level to 13,500 ft. in the Neovolcanic Range.

Remarks.—From 1895 until now the generic name *Cratogeomys* has been applied to the medium-sized pocket gophers of this genus (*Pappogeomys*). *Platygeomys* was applied to the largest members from 1895 to 1946 (see Hooper, 1946:399). *Pappogeomys* was restricted to the smallest members from 1895 until now. Inasmuch as my study has led to the conclusion that all of the species formerly arranged under the three generic names just mentioned belong in a single genus, the name *Pappogeomys* is used because it has priority (by page) over the other two. Like other pocket gophers, *Pappogeomys* is of stocky build, with a relatively large head, no perceptible neck, large forelegs, and shoulders more strongly developed than the hind legs and hips. The tail is nearly naked, especially the distal third. The ears do not protrude beyond the pelage, and external cheek pouches are well developed. The body form is decidedly fossorial.

Pappogeomys is referable to the tribe Geomyini, as it is defined by Russell (1968:521). The most highly specialized geomyids of the Geomyini are included in *Pappogeomys,* which genus is characterized by a combination of several specializations of the skull and dentition, as described in the subgeneric accounts beyond and in Russell (1968:533-534).

Key to Species of the Genus *Pappogeomys*

1. Small (condylobasal length 33.1–42.2 in females, 35.0–45.5 in males); nasal patch well developed in most individuals; posterior surfaces of M1 and M2 having enamel plates (sometimes absent on M1, rarely absent on M2); sagittal crest lacking, parietal impressions developed only part-way across parietal bones in adults; anterior angles of zygomata without lateral platelike expansions..................Subgenus *Pappogeomys*, p. 594
   2. Enamel plate on posterior surface of M1 thick, restricted to lingual one-fourth of posterior wall; nasals truncate posteriorly; nasal patch bright ochraceous or buffy.........................*P. alcorni*, p. 615
   2′. Enamel plate on posterior surface of M1 thin, usually extending across entire posterior wall (sometimes reduced, rarely absent); nasals emarginate posteriorly, forming V-shaped notch; nasal patch white or pale buffy, often absent....................*P. bulleri*, p. 596

1′. Small to large (condylobasal length 38.9–65.9 in females, 43.7–74.5 in males); nasal patch lacking; posterior surfaces of M1 and M2 lacking any trace of enamel; sagittal crest developed in adults of both sexes; lateral angles of zygomata enlarged into platelike expansions. Subgenus *Cratogeomys*, p. 618
   3. Skull deep and narrow (palatofrontal depth greater than 62% of breadth across squamosals and squamosal breadth less than 64% of condylobasal length); dorsal outline of lambdoidal crest convex posteriorly, never sinuous; paroccipital processes small, not enlarged into flangelike knobs; M3 specialized, its surface either quadriform or obcordate; squamosal breadth less than zygomatic breadth; angular processes short, breadth across angular processes less than greatest length of mandible.
      4. Small to medium (condylobasal length 38.9–53.2 in females, 43.7–62.6 in males); width across upper incisors midway between tip and anterior lip of alveolus less than 3.3 in females and occlusal surface of M3 quadriform, posterior loph not elongated; squamosals not overlapping parietals; basioccipital parallel-sided or hour-glass-shaped............................*P. castanops*, p. 621
      4′. Medium to large (condylobasal length 51.3–62.6 in females, 57.4–74.5 in males); width across upper incisors midway between tip and anterior lip of alveolus more than 3.3 in females and 3.6 in males; occlusal surface of M3 obcordate, posterior loph elongated and displaced toward labial side; squamosals expanded medially, with increasing age progressively overlapping parietals and completely covering parietals in old adults; basioccipital strongly wedge-shaped, its anterior end distictly narrower than posterior end.............................*P. merriami*, p. 691
   3′. Skull shallow and wide (palatofrontal depth less than 58% of breadth across squamosals and squamosal breadth greater than 66% of condylobasal length, except in *P. t. zodius*); dorsal outline of lambdoidal crest sinuous; paroccipital processes enlarged into flangelike knobs; M3 unspecialized, its surface either subtriangular or suborbicular (as in subgenus *Pappogeomys*); squamosal breadth usually equal to or greater than zygomatic breadth; angular processes long, breadth across angular processes more than greatest length of mandible.
      5. Females: Small (condylobasal length 45.6–46.7); skull smoothly rounded; rostrum relatively short (37.1–38.1% of condylobasal length) and broad (61.8–64.5% of length); adult male unknown. *P. neglectus*, p. 717
      5′. Medium to large (condylobasal length 56.1–65.9 in females and 56.5–71.3 in males); skull angular and rugose; rostrum relatively long (39.4–46.4% of condylobasal length in females [39.3–45.5% in males], except for 38.2–38.8% in females of *P. t. brevirostris*), and narrow (47.6–61.3% of condylobasal length in females and 47.8–61.6% in males).

6. Pelage harsh and bristly; squamosal breadth less than zygomatic breadth; occurring only on Pacific Coastal Plain. *P. fumosus*, p. 719
6′. Pelage soft and lax; squamosal breadth usually greater than zygomatic breadth; not occurring on Pacific Coastal Plain.
    7. Skull smaller (condylobasal length 50.4–59.1 in females and 56.5–65.0 in males) and narrower (squamosal breadth 32.0–41.6 in females and 36.7–45.1 in males).
        8. Zygomata widely spread laterally, zygomatic breadth 41.6–43.2 in females (adult male unknown). *P. zinseri*, p. 744
        8′. Zygomata not expanded laterally, zygomatic breadth 31.3–39.4 in females and 37.6–45.0 in males. *P. tylorhinus*, p. 721
    7′. Skull larger (condylobasal length 60.1–64.6 in females and 66.7–71.3 in males) and broader (squamosal breadth 41.6–47.8 in females and 43.1–52.3 in males)... *P. gymnurus*, p. 748

Subgenus **Pappogeomys** Merriam

Type.—*Geomys bulleri* Thomas, Ann. Mag. Nat. Hist., ser. 6, 10:196, August, 1892.

Diagnosis.—Size small (see below); overhair of top of head and back having only two color bands; pale nasal patch usually present; top of skull convex upward in longitudinal outline; no sagittal crest; lateral angles of maxillary arms of zygomata without platelike expansions; posterior wall of M1 and M2 usually having complete enamel blade (plate of M1 reduced to lingual fourth in *P. alcorni*).

Remarks.—The size is less than in the subgenus *Cratogeomys*. Males are slightly larger than females but sexual dimorphism is not so pronounced as in *Cratogeomys*. The recorded ranges of minimum and maximum variation in external dimensions of adult females are: Length of head and body, 142 to 183; length of tail, 53 to 82; length of hind foot, 28 to 35. Corresponding measurements of adult males are: 150 to 188; 63 to 83; 28 to 34.

The pelage is long and soft, and the body is well covered in all named kinds except *P. bulleri burti* from the Pacific Coast. Its pelage is sparse, especially on the venter, and the hairs are shorter than in other taxa of the subgenus.

The cover hairs (on upper parts and underparts) are dark gray or plumbeous basally. The remainder of the hair is uniform in color and its pigmentation varies depending on the subspecies. In paler pelages the terminal band varies between shades of bright lustrous cinnamon, orange-cinnamon, and rusty chestnut; in darker pelages tones of dull mouse gray or lustrous liver brown are typical. In either case, the terminal wash scarcely conceals the plumbeous undercolor, which thus imparts to the pelage a darker overall appearance. The blackish terminal band, characteristic of the pelage on the top of head and back in the subgenus *Cratogeomys,* is lacking. Hairs on the face are shorter than on the body and lack plumbeous bases. The hairs on the forehead and around the ears usually are blackish, although the auricular patch is small and inconspicuous in most individuals. The most remarkable facial marking is the distinct and unique nasal patch. It is composed of white or pale buffy hairs and surrounds the nasal pad and mouth. In many individuals the patch extends far up over the face, and in most it extends under the chin and around the openings to the external cheek pouches. The nasal patch is most pronounced in *P. b. albinasus* and in *P. alcorni;* in the latter the patch is a bright ochraceous-buff. The hind foot is sparsely set with short whitish hairs. The tail is superficially naked.

Condylobasal length of the skull ranges from 33.1 to 42.2 in adult females and from 35.0 to 45.5 in adult males. Excepting *P. castanops subnubilus* and *P. castanops peridoneus* of the subgenus *Cratogeomys,* all other kinds of *Cratogeomys* are larger than the largest individuals of the subgenus *Pappogeomys.*

The skull, convex in dorsal longitudinal outline, is smoothly rounded, without the extreme angularity and rugosity characteristic of *Cratogeomys.* Although no sagittal crest develops at any age, faint parietal impressions are evident near the lateral margins of the parietal bones in most adults. The zygomata are broadly spread but slender. When viewed from above, the occiput bulges posteriorly and is never flat and rugose; the lambdoidal crest is convex posteriorly. The squamosals are unspecialized, and not expanded over the parietals or so far as the glenoid notch. The paroccipital processes are small and in no specimen expanded into a broad plate. The rostrum is narrow, long, and lightly constructed. The angular processes of the mandible are short. The maxillary sheath of the upper incisor is not developed into a knoblike shelf around the alveolus of the incisor as in the specialized species of *Cratogeomys.*

On the posterior surface of M1 and M2, the complete enamel blade becomes rather thin with wear on the labial side in some older individuals. In *P. alcorni,* only a partial enamel plate is present on the inner fourth of the posterior wall of the first upper molar, the remainder of the posterior face being devoid of enamel. The reduction of the posterior enamel blade in *alcorni* evidently represents a specialized condition tending toward the complete loss of the posterior blade characteristic of the subgenus *Cratogeomys,* and suggests an evolutionary step that may have occurred in the ancestral populations of *Pappogeomys* that at an earlier time evolved into *Cratogeomys.* However, the reduction of the plate in *alcorni* is an independent development at a later time than is the reduction in *Cratogeomys.* M3 is subtriangular or suborbiculate, and partly separated by a shallow labial sulcus into an incomplete double prism.

Pappogeomys bulleri

(Synonymy under subspecies)

Range.—West-central México; Nayarit south to Colima; Pacific Coast east to Río Grande de Santiago in Jalisco. See Fig. 2. Altitudinal range sea level on the Pacific Coast up to 10,000 feet.

Diagnosis.—Small to large for subgenus; nasals emarginate posteriorly; incisive foramina long and slitlike; enamel plate on posterior wall of M1 usually well developed, variably reduced, rarely absent in specimens from Pacific Coastal Range (*P. b. bulleri, P. b. amecensis,* and *P. b. nayaritensis*); nasal patch, when present, whitish or rarely pale buffy.

Description.—Small for genus (length of head and body 120 to 183 in females and from 144 to 188 in males); tail naked, flesh-colored, less than half length of head and body; hind foot short to medium (25 to 35 in females and 28 to 34 in males).

Color: Pelage of dorsum bicolored, basally pale gray to dark gray (black in melanistic individuals), apically black to ochraceous, tawny, and cinnamon; sides and face same as back; chin and throat usually white, sometimes lightly tinged with pale buff; nasal patch usually present, small to large and white in most examples but slightly tinged with buff in others; belly pale gray to blackish basally overlaid with buff, ochraceous, or tawny (black to roots in melanistic individuals); underparts usually only slightly paler than upper parts.

Skull: Small for genus (condylobasal length 33.1 to 42.2 in females and 36.4 to 45.5 in males); relatively narrow (squamosal breadth 19.8 to 25.4 in females and 20.6 to 27.7 in males); basioccipital strongly wedge-shaped, having sides converging anteriorly, rarely hour-glass-shaped with breadth across middle less than at either end; nasals posteriorly emarginate with V-shaped notch between posterior tips; incisive foramina long and slitlike; enamel plate on posterior wall of M1 usually complete, rarely reduced or absent; M3 subtriangular or suborbicular in cross-section, with posterior heel weakly developed.

Habitat.—Pappogeomys bulleri is predominantly a montane species occurring in soils mostly of volcanic origin in the pine-oak-madroña zone in western Jalisco and Nayarit, and is most abundant at higher elevations in meadows supporting grasses and forbs. Burrows sometimes extend into adjacent forests. The species has been taken in semi-tropical environments in the larger canyons dissecting the west slope of the coastal range where *P. bulleri* occurs in association with tropical shrubs, especially in cultivated areas. The subpecies *P. b. burti* occurs in arid tropical shrub associations

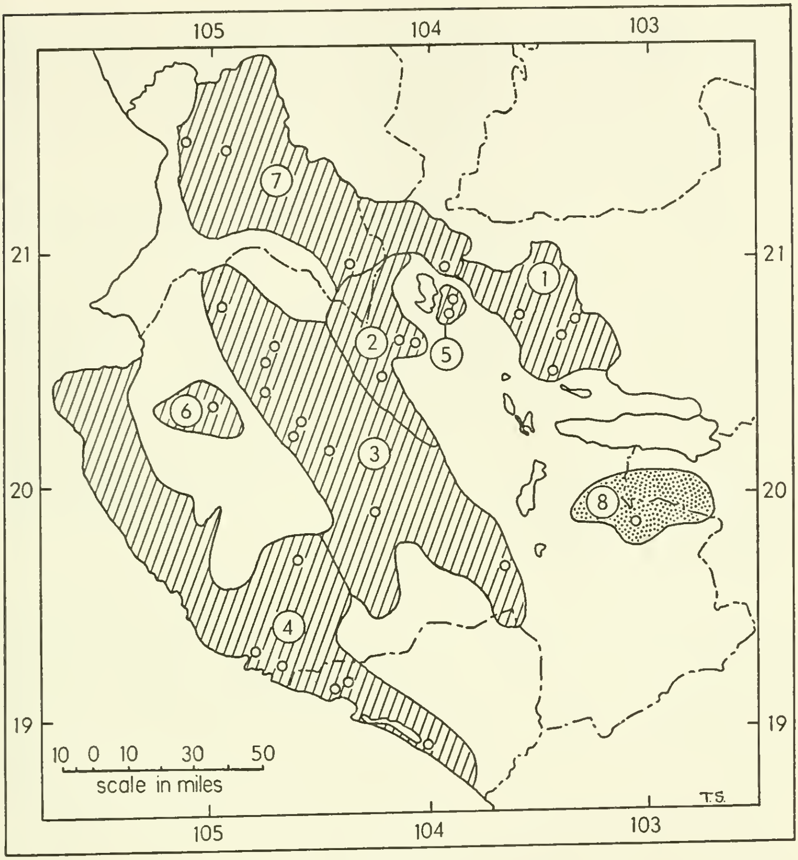

FIG. 2. Subgenus *Pappogeomys.*

1. *Pappogeomys bulleri albinasus*
2. *Pappogeomys bulleri amecensis*
3. *Pappogeomys bulleri bulleri*
4. *Pappogeomys bulleri burti*
5. *Pappogeomys bulleri infuscus*
6. *Pappogeomys bulleri lutulentus*
7. *Pappogeomys bulleri nayaritensis*
8. *Pappogeomys alcorni*

on the Pacific Coastal Plains, and *P. b. albinasus* is found in areas of desert grassland on the western edge of the Central Plateau in north-central Jalisco west of the Río Santiago. *Pappogeomys bulleri* does not occur in the chain of low interior basins of central Jalisco that begin with the Valle de Ameca in the north and continue southeastward into the valleys of Sayula and Zapotitic west and south of the Lago de Chapala and east of the Sierra Nevada de Colima.

Pappogeomys bulleri occurs in association with the larger species

Pappogeomys fumosus on the arid coastal plains of Colima, and *bulleri* possibly has limited contact with *Thomomys umbrinus* on the southern edge of the Río Santiago gorge in north-central Jalisco. However, over most of its range in the mountains of western Jalisco and Nayarit, *bulleri* is the only geomyid.

Geographic variation.—*Pappogeomys bulleri* is polytypic; seven subspecies are recognized. One group, including *amecensis, bulleri,* and *lutulentus* from the Coastal Range and adjacent mountains in Jalisco, is characterized by small size and brightly pigmented pelage. All three of the small subspecies probably differentiated from a common ancestral stock. Of the three, *lutulentus* is decidedly the smallest, and it also is the smallest representative of the genus. *P. b. bulleri* varies from small to medium and varies more in color than either *lutulentus* or *amecensis.* Specimens from lower elevations in subtropical canyons on the Pacific Slope of the mountains are the most intensely ochraceous-orange. Specimens from higher elevations have duller shades of ochraceous.

Populations from the northern part of the Coastal Range, in the mountains of southern Nayarit north of the Río de Ameca and south of the Río Grande de Santiago, the Pacific Coastal Plain of Jalisco and Colima, and the Central Plateau west of the Río Grande de Santiago and east of the Valle de Ameca in north-central Jalisco have darker and duller pelage and are larger than the group of small subspecies discussed above. This group of large subspecies includes *albinasus, nayaritensis, burti,* and *infuscus. P. b. infuscus,* restricted in range to the Sierra de Tequila, is actually of medium size, but its other features suggest that it was differentiated from the ancestral stock of large animals that also gave rise to *albinasus, burti,* and *nayaritensis. P. b. burti* is the most atypical of the species externally. Its pelage is scanty and the hairs of both upper parts and underparts are black to their roots. The thinness of the pelage and the development of melanism evidently are responses to selective pressures of the arid tropical environment in which *burti* lives. *Pappogeomys fuscus* of the subgenus *Cratogeomys,* which occurs on the tropical, coastal plains of Colima, also has developed the same characteristics in its pelage. *P. b. albinasus* is the largest subspecies of this group and of the species. Remarkably large size, especially in cranial dimensions, and the characteristic large white nasal patch, that usually extends over much of the face, clearly distinguish *albinasus* from the other subspecies. *P. b. albinasus* is more nearly isolated from other members of the species than is any other subspecies, and its unique features evidently have developed independently in the absence of high rates of gene exchange with neighboring subspecies. The low interior basin to the west of the range occupied by *albinasus* evidently restricts gene flow between *albinasus* and the small subspecies in the Coastal Range. Limited contact between *albinasus* and *nayaritensis* occurs now along the high south rim of the Río Santiago gorge.

The enamel investment on the posterior wall of M1 and M2 varies in *Pappogeomys bulleri*. Of a total of 206 M1's examined, with equal numbers of left and right teeth, 21 (10%) were characterized by lateral reduction of the enamel plate on the posterior wall; and of 206 M2's, 12 (6%) were characterized by reduction. The position and extent of lateral reduction varies, but the reduction usually is from the labial side resulting in retention of a lingual segment of the plate. Length of the enamel vestige varies; the plate is reduced to the lingual one-half (loss of labial one-half), to the lingual one-fourth (loss of labial three-fourths), to the medial one-half (approximately one-fourth of plate lost at both lingual end and labial end), to the labial one-fourth (loss of lingual three-fourths), or the entire plate may be lost. Usually left and right teeth are characterized by the same condition, but there are a few exceptions probably due to asymmetrical wear on the occlusal surface.

In the M1's which have reduced enamel plates, 6 (3% of the total) are characterized by loss of one-half the plate on the labial side (lingual one-half retained), 2 (1%) by loss of three-fourths of the plate on the labial side (lingual one-half retained as in *Pappogeomys alcorni*, but vestige not thickened as in *alcorni*), 3 (1%) by loss of enamel at both ends of the plate (approximately the medial one-half of plate retained), 2 (1%) by loss of three-fourths of the plate on the lingual side (labial one-fourth retained), and 8 (4%) by loss of all of the posterior plate.

In the M2's having reduced enamel plates, 2 (1% of the total) are characterized by loss of one-half the plate on the labial side (lingual one-half retained), 6 (3%) by loss of enamel at both ends (approximately medial one-half of plate retained), 2 (1%) by loss of one-half the plate on the lingual side (labial one-half retained), and 2 (1%) by loss of all of the posterior plate. No M2 was observed with loss of enamel from three-fourths of the labial side (lingual one-fourth retained).

Most of the dentitions showing loss of enamel in M1 and M2, or both, were in specimens from the Pacific Coastal Range in western Jalisco and Nayarit, especially in populations of *Pappogeomys bulleri bulleri, Pappogeomys bulleri nayaritensis,* and *Pappogeomys bulleri amecensis.* No reduction was observed in *P. b. burti,* on the coastal plain, or *P. b. lutulentus* and *P. b. infuscus,* which occur at higher elevations and are more or less isolated in mountain ranges. Only one of 61 specimens of *albinasus* has lost enamel on M1 (loss of labial one-half, retention of lingual one-half), and no specimen has lost enamel on M2. Of the 185 M1's with no lateral reduction of enamel, 6 (3%) were characterized by thin plates of enamel; in some the plates were so thin that their presence could be verified with certainty only upon microscopic examination. Only 4 (2%) of 194 plates of M2's that showed no lateral reduction were reduced in thickness as in M1.

Pappogeomys alcorni probably differentiated from an ancestral stock that was related to, and continuous with, the populations of *Pappogeomys bulleri* occurring in the Coastal Range. Post-Wisconsin trends toward aridity in the lowlands, and the subsequent movement of the forest zones to higher elevations in the mountains, isolated a segment of the species in the Sierra del Tigre. The isolated segment to the east evolved into *Pappogeomys alcorni.* It more closely resembles the adjacent populations of *Pappogeomys bulleri* in the Sierra Nevada de Colima and the Coast Range than it does the more peripheral subspecies of the species (*albinasus, burti* and *nayaritensis*). The loss of enamel from the posterior wall of M1 occurs also in adjacent populations of *P. bulleri,* as discussed above, but only two, or three per cent, of the 60 specimens of *bulleri* examined from this area were characterized by the same pattern of reduction present in *alcorni,* and the other features of those specimens were characteristic of *bulleri.* The enamel plate on the posterior wall of M2 is not reduced in *alcorni.*

Pappogeomys bulleri albinasus Merriam

Pappogeomys albinasus Merriam, N. Amer. Fauna, 8:149, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:268, July 1, 1905; Lyons and Osgood, Bull. U. S. Nat. Mus., 62:71, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:246, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:258, April 29, 1924; Ellerman, Families and Genera of Living Rodents, 1:528, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:374, April 9, 1942.

[*Pappogeomys*] *albinasus,* Trouessart, Cat. Mamm., 1:572, 1898; Elliot, Field Columb. Mus. Publ. 95; Zool. Ser., 4:331, 1904.

Pappogeomys bulleri albinasus, Goldman, Jour. Mamm., 20:94, February 15, 1939; Goldman, Smith. Misc. Coll., 115:371 and 433, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955; Hall and Kelson, The Mamamls of North America, 1:463, March 31, 1959.

Type.—Female, adult, skull and skin; No. 34138/46215, U. S. National Museum (Biol. Surv. Coll.); Atemajac, now a suburb of Guadalajara, Jalisco; May 21, 1892; obtained by E. W. Nelson, original number 2654.

Range.—Central Jalisco, sparsely vegetated open plains at elevations of approximately 5000 feet. See Fig. 2.

Description.—Large for species; tail relatively short (averaging 42 per cent of length of head and body in females); hind foot large. Averages and extremes of 17 females and 15 males, from the plains around Guadalajara are, respectively, as follows: Length of head and body 163 (154-172), 167 (155-178); length of tail 68 (53-78), 72 (63-80); length of hind foot, 31 (29-33), 31 (28-34). Two females from Ciudad Granja weighed 154 and 109 grams.

Color: General color effect of dorsum dark rusty brown, pelage dull Ochraceous-Tawny apically, becoming brighter Ochraceous-Orange on sides; pelage Light Mouse Gray basally on back and sides; pelage of venter Ochraceous-Orange apically and Light Mouse Gray basally; chin and throat whitish; white nasal patch large, whitish extending over anterior part of face and forehead mixing with darker hairs imparting mottled appearance to most of head; hind feet whitish.

Skull: Large and broad, especially across zygomata (zygomatic breadth exceeding length of palate in most specimens), squamosals, and angular processes.

Averages and extremes for 17 females and 15 males from the plains around Guadalajara are, respectively, as follows: Condylobasal length, 40.6 (39.5-42.1), 42.0 (40.2-43.6); zygomatic breadth, 27.3 (25.8-29.9), 28.7 (26.6-31.0); palatofrontal depth, 15.7 (15.0-16.3), 16.3 (15.5-16.7); length of palate, 26.4 (25.4-27.4), 27.7 (26.3-28.6); length of nasals, 15.0 (14.1-16.4), 15.7 (14.3-17.2); breadth of braincase, 20.4 (19.1-21.8), 21.1 (20.4-21.9); squamosal breadth, 24.8 (23.7-25.4), 25.7 (24.3-27.1); breadth of rostrum, 9.7 (8.8-10.5), 10.3 (9.4-10.9); length of rostrum, 18.7 (17.8-20.2), 19.6 (18.6-21.2); alveolar length of maxillary tooth-row, 9.0 (8.1-9.8), 9.3 (8.2-9.8); breadth across angular processes, 28.6 (26.3-29.9), 30.9 (27.9-34.1).

Comparisons.—For comparisons with *P. b. amecensis, P. b. bulleri, P. b. infuscus,* and *P. b. nayaritensis,* see accounts of those subspecies.

Remarks.—Only the type specimen of *P. b. albinasus* was available to previous revisors (Merriam, 1895:149, and Goldman, 1939b: 94). Now 61 specimens, all from the vicinity of Guadalajara, are in the University of Kansas Museum of Natural History, all but three of them because of the industry of J. R. Alcorn. This relatively large sample permits a revised and more complete diagnosis, as presented above, and for the first time an accurate estimation of the range of individual variation in the subspecies. The skull is large and unusually broad—broader than in other subspecies. Moreover, the large white nasal patch is characteristic of all specimens so far examined. In most specimens white hair on the face and forehead dilutes the ochraceous pelage.

Pappogeomys bulleri albinasus differs greatly from its smaller neighbors, *P. b. amecensis, P. b. infuscus,* and *P. b. bulleri,* which occur on the opposite (west) side of the Valle de Ameca. *Pappogeomys bulleri* does not live in the lowlands of that valley. The distinctness of *albinasus* from *bulleri,* one of the smaller subspecies to the west, led Merriam (1895:149) to regard *albinasus* as a distinct species. Although *albinasus* does not intergrade directly with any one of the smaller subspecies and probably has not done so for a long time, intergradation is thought to have occurred indirectly in the "recent past" by way of *P. b. nayaritensis* that inhabits the south rim of the gorge of the Río de Santiago whence a chain of low mountains and elevated mesas, like the Sierra Viejo de Magdalena, form an elevated corridor to the northeast around the northern end of the Valle de Ameca. By this route there probably was gene flow between *albinasus* and *amecensis* (see account of *amecensis*), although the lack of a white nasal spot in *nayaritensis* and its presence in *albinasus, amecensis, bulleri,* and *infuscus* does not support this hypothesis.

P. b. albinasus apparently is restricted to the elevated, grassy plain west of the Río Grande de Santiago and east of the drainage of the Río de Ameca. The plain is isolated from the main part of the Central Plateau by the deep gorge of the Río Grande de Santiago. That narrow, steep-walled canyon functions as an absolute barrier to the eastward movement of these pocket gophers. The plain continues without interruption to the south, but no specimens of *P. b. albinasus* have been taken from its southern part. *Pappogeomys tylorhinus,* a large species of the subgenus *Cratogeomys,* lives there. The two species have been recorded less than eight miles apart—*albinasus* at a place 10 mi. S and 8 mi. W Guadalajara and *tylorhinus* at a place 13 mi. S and 15 mi. W Guadalajara. *P. b. albinasus* may be excluded from the southern parts of the plain because of interspecific competition with its larger relative. Sympatry among species of pocket gophers usually occurs only between those that differ greatly in size, but these two species are so nearly of the same size that incompatability would be expected.

Specimens examined.—Total of 61, all from **Jalisco**, as follows: West side La Venta, 4 mi. N and 13 mi. W Guadalajara, 13; 2 mi. N and ½ mi. W Guadalajara, 20; *Ciudad Granja (a colonia in the northwest part of Guadalajara), 5100 ft., 3; 4 mi. W Guadalajara, 11; 10 mi. S and 8 mi. W Guadalajara, 14.

Pappogeomys bulleri amecensis Goldman

Pappogeomys bulleri amecensis Goldman, Jour. Mamm., 20:97, February 15, 1939; Poole and Shantz, Bull. U. S. Nat. Mus., 178:374, April 9, 1942; Goldman, Smiths. Misc. Coll., 115:386 and 433, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:463, March 9, 1959.

Type.—Male, adult, skull and skin; No. 82189, U. S. National Museum (Biol. Surv. Coll.); mountains near Ameca, 6500 feet, Jalisco; February 20, 1897; obtained by E. W. Nelson and E. A. Goldman, original number 10554.

Range.—Northwestern Jalisco, mountains bordering Valle de Ameca. See Fig. 2. Altitudinal range about 5100 feet on Sierra de Quila up to 6500 feet on Sierra de Ameca.

Description.—Small for species; tail short; hind foot small. Averages and extremes of four females and three males, respectively, from mountains northwest and southwest of Ameca are as follows: Length of head and body, 140 (137-146), 149 (144-155); length of tail, 59 (52-65), 67 (58-73); length of hind foot, 28 (27-29), 29 (28-29). A female and male weighed, respectively, 93.3 and 106.5 grams.

Color: General color effect of dorsum bright ochraceous, pelage hairs from rich Ochraceous-Orange to Orange-Cinnamon apically and Light Mouse Gray basally; sides having slightly brighter hues than back; venter bright yellowish-red, hairs Orange-Cinnamon apically and Light Mouse Gray basally; chin and throat whitish to pale buffy; nasal patch small, hairs usually whitish, rarely pale buffy; hind feet whitish.

Skull: Skull short (especially in condylobasal length and palate) and narrow across braincase, squamosals, and angular processes; cranium shallow.

Averages and extremes of four females and four adult males, respectively, from mountains northwest and southwest of Ameca are as follows: Condylobasal length, 35.7 (35.2-25.9), 37.1 (36.4-38.3); zygomatic breadth, 21.8 (21.4-22.1), 23.5 (23.0-23.7); palatofrontal depth, 13.9 (13.3-14.3), 14.4 (13.8-14.8); length of palate, 23.0 (22.2-23.7), 23.8 (23.1-24.5); length of nasals, 12.9 (11.9-13.6), 13.6 (13.3-14.1); breadth of braincase, 17.8 (17.5-18.1), 18.5 (16.8-19.6); squamosal breadth, 20.6 (20.2-21.1), 22.4 (21.6-23.2); breadth of rostrum, 7.4 (7.2-7.7), 8.1 (7.8-8.5); length of rostrum, 15.7 (15.1-16.4), 16.9 (16.0-17.8); alveolar length of maxillary tooth-row, 8.3 (7.9-8.8), 8.5 (7.7-9.0); breadth across angular processes, 22.2 (21.0-22.8), 24.0 (23.4-25.0).

Comparisons.—For comparisons with *P. b. nayaritensis* and *P. b. infuscus,* see accounts of those subspecies.

From *P. b. albinasus, P. b. amecensis* differs as follows: Smaller; dorsum and underparts brighter, less dull reddish-brown and more bright reddish-orange; nasal patch smaller, less conspicuous; skull smaller in all dimensions, with overlap only in length of maxillary tooth-row; tail shorter; hind foot shorter.

From *P. b. bulleri, P. b. amecensis* differs as follows: Slightly smaller; underparts brighter, less buffy and more ochraceous; skull shorter (nasals, condylobasal length, and palate), and narrower (especially across zygomata, rostrum, squamosals, and angular processes); skull shallower; tail slightly shorter.

Remarks.—The smallness of the skull in *amecensis* may reflect an inadequate sample but the exceptional narrowness across the zygomata, rostrum and angular processes indicates otherwise.

From *P. b. infuscus, P. b. amecensis* differs in the same characters that distinguish it from *bulleri,* and also in distinctly paler and brighter coloration, above and below. The geographic ranges of *amecensis* and *infuscus* are separated by the Valle de Ameca, 4000 to 4500 feet in elevation, from which no *Pappogeomys bulleri* is known although despite extensive search there in the vicinities of Ameca, La Vega, Ahualulco, Etzatlán, San Marcos, Cocula, El Refugio, Tala, and Tequila. The large *Pappogeomys gymnurus* has been recorded from near Refugio and Tala in the eastern part of the Valle de Ameca, and probably occurs in widely scattered colonies throughout the valley.

In the upland on either side of the Río Ameca, *Pappogeomys bulleri* occurs only at elevations of more than 4900 feet in the pine-oak-madroño forest.

P. b. amecensis is distinguished from *P. b. albinasus,* which occurs on the high plateau to the east of the Valle de Ameca, by remarkably smaller size. The only overlap in cranial measurements is in alveolar length of the maxillary tooth-row. The degree of divergence suggests long separation and that the Valle de Ameca has effectively limited or prevented gene flow between the two kinds of gophers.

The Sierra de Ameca, where *amecensis* occurs, is connected to a series of elevated ridges continuous with the Cerro El Faro, a mountainous mass in southeastern Nayarit. Two specimens from the Cerro El Faro are narrow across the braincase and squamosals as is *P. b. amecensis* (other measurements are as in *nayaritensis*, to which the specimens are referred). This narrowness suggests intergradation between *amecensis* and *nayaritensis* in southeastern Nayarit.

Specimens labeled as 13 mi. WSW Ameca probably were collected on the southwestern slope of the Sierra de Quale, an escarpment forming the southern border of the Valle de Ameca. Contrary to expectation they do not suggest intergradation between *P. b. amecensis* and *P. b. bulleri.*

Specimens examined.—Total of 9, all from Jalisco, as follows: Cerro Ameca, 5500 ft., 5 mi. NW Ameca, 1;* 5 mi. NNW Ameca, 5500 ft., 1; type locality, 5 (USNM); 13 mi. WSW Ameca (Sierra de Quale), 5100 ft., 2.

Pappogeomys bulleri bulleri (Thomas)

Geomys bulleri Thomas, Ann. Mag. Nat. Hist., ser. 6, 10:196, August, 1892.

Geomys nelsoni Merriam, Proc. Biol. Soc. Washington, 7:164, September 29, 1892 (type from N slope Sierra Nevada de Colima, 6500 ft., Colima); Lyon and Osgood, Bull. U. S. Nat. Mus., 62:72, January 15, 1909; Poole and Shantz, Bull. U. S. Nat. Mus., 178:375, April 9, 1942.

Pappogeomys bulleri, Merriam, N. Amer. Fauna, 8:159, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:268, July 1, 1905; Elliot, Field Columb. Mus. Publ. 115, Zool. Ser., 8:311, 1907; Miller, Bull. U. S. Nat. Mus., 79:246, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:258, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:528, June 8, 1940.

[*Pappogeomys*] *bulleri*, Trouessart, Cat. Mamm., 1:572, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:320, 1904.

Pappogeomys bulleri bulleri, Goldman, Jour. Mamm., 20:94, February 15, 1939; Goldman, Smiths. Misc. Coll., 115:371 and 433, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:463, March 31, 1959.

Pappogeomys bulleri nelsoni, Goldman, Jour. Mamm., 20:94, February 15, 1939; Goldman, Smiths. Misc. Coll., 115:386 and 433, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955: Hall and Kelson, The Mammals of North America, 1:464, March 31, 1959.

Pappogeomys bulleri flammeus, Goldman, Jour. Mamm., 20:95, February 15, 1939 (type from Milpillas, 5 mi. SW San Sebastian, Jalisco); Pool and Shantz, Bull. U. S. Nat. Mus., 178:374, March 6, 1942; Goldman, Smiths. Misc. Coll., 115:371 and 429, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:464, March 31, 1959.

Pappogeomys bulleri lagunensis, Goldman, Jour. Mamm., 20:96, February 15, 1939 (type from La Laguna, 6500 ft., Sierra de Juanacatlán, Jalisco); Poole and Shantz, Bull. U. S. Nat. Mus., 178:374, March 6, 1942; Goldman, Smiths. Misc. Coll., 115:386 and 433, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:340, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:464, March 31, 1959.

Type.—Female, in spirits; British Museum; Talpa, 8500 (probably about 5000) feet, west slope Sierra de Mascota, Jalisco; obtained by A. C. Buller, original number unknown.

Range.—Mountains of west-central Jalisco, from northwestern slopes of the Coastal Range south of Río de Ameca, southward including Sierra de Juanacatlán, Sierra de Mascota, Sierra de Parnosa, and Sierra de Autlán, to Sierra Nevada de Colima in south-central Jalisco. See Fig. 2. Altitudinal range from 3800 feet at Milpillas up to 9000 feet on Volcán de Nieve in Sierra Nevada de Colima.

Description.—Small to medium for species; tail relatively long (in females, averaging 44.6% of length of head and body); hind foot small. Averages and extremes of twelve females and five males, respectively, from mountains of western Jalisco are as follows: Length of head and body, 144 (120-159), 152 (149-154); length of tail, 64 (53-75), 66 (60-80); length of hind foot, 29 (26-31), 31 (30-32). Weights of three females from 14 mi. NW Cuantla were 120.2, 142.0, and 135.4 grams; weights of three males from 5 mi. NW Cuantla were 131.2, 141.1, and 142.3.

Color: Ground color of dorsum rich reddish-brown, apically hairs varying from Ochraceous-Orange in brighter specimens to Ochraceous-Cinnamon in duller specimens, darker specimens near Mikado-Brown, hairs Light Mouse Gray basally; apically hairs of belly Pinkish-Buffy in paler to Ochraceous-Buff in darker specimens, basally hairs Light Mouse Gray; chin and throat whitish, in some specimens tinged with buffy; nasal patch small, whitish, absent in some specimens; hind feet whitish.

Skull: Moderately long and broad, having most dimensions intermediate in range of variation of species; narrow across angular processes in relation to length of skull.

Averages and extremes of 13 females and four males, respectively, from mountains of western Jalisco are as follows: Condylobasal length, 37.7 (36.1-39.2), 38.0 (36.9-39.6); zygomatic breadth, 23.7 (21.4-25.1), 24.7 (23.4-26.3); palatofrontal depth, 14.8 (13.5-15.4), 14.5 (14.1-15.0); length of palate, 24.9 (23.7-26.2), 25.0 (24.3-26.1); length of nasals, 14.4 (13.7-15.2), 14.6 (14.2-15.5); breadth of braincase, 18.1 (16.6-19.1), 19.7 (18.1-19.5); squamosal breadth, 21.7 (19.8-23.3), 22.6 (21.4-24.0); breadth of rostrum, 8.4 (7.8-9.3), 8.6 (8.1-9.4); length of rostrum, 17.8 (16.7-18.6), 18.0 (17.5-19.3); alveolar length of maxillary tooth-row, 8.7 (7.8-9.5), 8.8 (8.4-9.2); breadth across angular processes, 23.8 (21.4-25.5), 25.0 (24.1-26.5).

Comparisons.—For comparisons with *P. b. amecensis, P. b. infuscus, P. b. lutulentus, P. b. nayaritensis,* and *P. b. burti,* see accounts of those subspecies.

From *P. b. albinasus, P. b. bulleri* differs as follows: Smaller; upper parts brighter, more ochraceous and less brownish; underparts paler, less ochraceous and less buffy; nasal patch smaller, less distinct; skull averaging smaller in all dimensions, and without overlap in condylobasal length and breadth across zygomata, squamosals and angular processes.

Remarks.—Until recently only six specimens of *P. b. bulleri* (near topotypes, labeled as "Talpa"), in the U. S. National Museum, had been seen by me. They were collected by E. W. Nelson and E. A. Goldman in March of 1897 above Talpa in a pine-oak-madroño zone between 4500 and 5500 feet on the southwest-facing slope of the Sierra de Mascota (see Goldman, 1951:182), which separates the semitropical valleys of the Río Talpa and the Río Mascota. The town of Talpa de Allende is in the valley of the Río Talpa. The "Talpa" series includes four females and two males of which only female No. 88114 USNM and male No. 88116 USNM are fully adult. Another female, No. 88111 USNM is as much a subadult as an adult, although it probably has been used as an adult by previous workers. On the basis of this sample, former students would have concluded that *bulleri* is small, especially in cranial dimensions. The available samples of neighboring populations were larger in most dimensions than the specimens from "Talpa." Therefore, Goldman (1939b) recognized three subspecies, *P. b. nelsoni, P. b. flammeus, and P. b. lagunensis,* here regarded as inseparable from *P. b. bulleri.* Each of the three allegedly differed from *bulleri* mainly in larger skull.

In 1964 and 1965, additional specimens of *bulleri* were obtained from the mountains southeast of Talpa de Allende and from northwest of Cuautla and demonstrate that *bulleri* is larger than previously supposed. Consequently, *P. b. bulleri* is redescribed above. The difference in size stressed by Goldman (1939) between populations that he referred to *bulleri, lagunensis,* and *flammeus* is less than he supposed.

According to the original description, *P. b. lagunensis* Goldman (*loc. cit.*:96) differs from *P. b. bulleri* ("Talpa" specimens) in larger size; broader braincase, nasals, ascending branches of premaxillae, and rostrum; less inflated auditory bullae; and heavier molariform teeth. Size of bullae and breadth of nasals and premaxillae vary so much individually as to be of little value in revealing geographic variation. On the average, the nasals are shorter and the skulls are shallower from the Sierra de Juanacatlán than in typical *bulleri* but no significant differences otherwise are apparent. The type locality of *lagunensis* (La Laguna, 6500 feet elevation) in the Sierra de Juanacatlán, is no more than 20 miles airline from the type locality of *bulleri* in the Sierra de Mascota. A low valley separates most of the two mountains, but they are connected by high ridges, around the eastern end of the valley, that provide continuous habitat of pine, oak, and madroño forest.

P. b. flammeus Goldman was based on four specimens from Milpillas, a small village five miles southwest of San Sebastian and less than 20 miles northwest of La Laguna. These specimens were collected at 3850 feet elevation in a zone of oak forest within a steep-walled canyon on the northwest slope of the Sierra de Juanacatlán. The head of the canyon opens out onto the high country, and offers an unobstructed passage from the highlands downward to the low valley of the Río de Ameca. Semitropical vegetation prevails at the canyon mouth and other elements of this extend up the canyon and merge with the boreal flora. Goldman described *flammeus* as differing from *bulleri* in the more intense reddish tones on the dorsum; larger skull; greater zygomatic breadth; more arched braincase; and heavier molariform dentition. From *lagunensis, flammeus* was thought to be distinguished by brighter reddish upper parts; smaller skull; narrowness across zygomata and squamosals; more depressed frontal region; and a heavier and more angular jugal. Arching of the skull, shape and size of the jugal, and depression of the frontal region are functions of age. Also, each feature shows much individual variation. Both the upper parts and underparts in paratypes of *flammeus* are a brighter reddish-ochraceous than is commonly observed in the duller pelages of *bulleri* and *lagunensis.* Nevertheless, the color of the dorsum in *bulleri* and *lagunensis* varies, and, even though the reddish hues may be more intense at Milpillas, some individuals of *bulleri,* especially in the "Talpa" series, are as bright dorsally as *flammeus.* The nasals of *flammeus* agree in length with those of *lagunensis,* but are slightly shorter than in the smallest examples of *bulleri.* No difference of taxonomic significance could be found in any of the other characters examined, including those suggested by Goldman (*loc. cit.*).

A month after Thomas (1892:196) named *Geomys bulleri,* Merriam (1892:164) proposed the name *Geomys nelsoni* on the basis of six specimens from 6500 feet on the north slope of the Sierra Nevada de Colima. Subsequently, Merriam (1895:147) compared *nelsoni* with near topotypes of *bulleri,* the series from "Talpa," and, finding no trenchant differences, synonomized *nelsoni* with *Pappogeomys bulleri.* The name *Geomys nelsoni* was resurrected by Goldman (1939b-94) and applied as a subspecific name to the population from the Sierra Nevada de Colima. Goldman thought that *P. b. nelsoni* differed from *P. b. bulleri* as follows: Upper parts brighter, having tones of ochraceous-orange more intensely developed; skull longer; zygomatic arches more nearly parallel-sided and less divergent anteriorly; nasals longer and narrower. But, comparison of paratypes of *nelsoni* and one additional specimen (UA 3260) from 9000 feet, Volcán de Nieve, on the north slope of the Sierra Nevada de Colima, with the larger sample of *bulleri* now available, reveals no difference of taxonomic significance in either external or cranial features except in length of nasals. They are longer actually and relatively (39.8 *versus* 34.7% of condylobasal length) even with the advantage of a larger sample of *bulleri.* On the average, specimens of *nelsoni* are also slightly darker (more Amber Brown and less Orange-Cinnamon), but some specimens of *bulleri* and especially *lagunensis* are as dark brownish as *nelsoni.* Consequently *P. b. nelsoni, P. b. flammeus,* and *P. b. lagunensis* are here arranged as synonyms of *P. b. bulleri.*

A weakly defined cline in length of nasals in *bulleri* is evident; they are longest in the south (Sierra Nevada de Colima) and shortest in the north (Sierra Juanacatlán and Sierra de Mascota; samples from "Talpa," "Mascota," La Laguna, and Milpillas). In the central part of the geographic range (15 mi. S and 9 mi. E Talpa de Allende, 14 mi. NW Cuantla, 5 mi. NW Cuantla, and Sierra de Autlán) the nasals are intermediate in length.

Intergradation with neighboring subspecies is not shown by any specimens examined, but is to be expected (with *P. b. amecensis*) in the mountains or intermontane valleys east of the Sierra de Parnosa and west of the Sierra de Quila.

At 6500 feet elevation on the north slope of the Sierra Nevada de Colima this subspecies was found in association with the remarkably larger species *Pappogeomys gymnurus.*

Specimens examined.—Total, 33, all from Jalisco, as follows: Milpillas, 3850 ft., 5 mi. SW San Sebastián, 3 (USNM); La Laguna, 6500 ft., Sierra de Juanacatlán, 1(USNM); "Mascota," actually at El Tajo but specimens labeled Mascota, 3900 ft., Sierra de Juanacatlán, 1 (AMNH) and 1 (FMNH); "Talpa" (actually SW slope Sierra de Mascota), 4500 and 5500 ft., Sierra de Mascota, 5 (USNM), 1 (MCZ); 15 mi. S and 9 mi. E Talpa de Allende, 6900 ft., 6; 14 mi. NW Cuautla, 7500 ft., 3; 5 mi. NW Cuautla, 6550 ft., 5; Sierra de Autlán, 7600 ft., 1 (UMMZ); north slope Sierra Nevada de Colima, 6500 ft., 5 (USNM); * Volcán de Nieve, north slope Sierra Nevada de Colima, 9000 ft., 1 (UA).

Pappogeomys bulleri burti Goldman

Pappogeomys bulleri burti Goldman, Jour. Mamm., 20:97, February 15, 1939; Goldman, Smiths. Misc. Coll., 115:336, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955; Hall and Kelson, The Mammals of North America, Vol. 1:463, March 31, 1959.

Type.—Female, adult, skull and skin; No. 81017, University of Michigan Museum of Zoology; Tenacatita Bay, southwestern coast of Jalisco; February 19, 1938; obtained by William H. Burt, original number 4121.

Range.—Coastal plain and lower foothills of western Jalisco and Colima. See Fig. 2. Sea level up to about 1400 feet elevation.

Description.—Large for species; tail relatively short (averaging 42 per cent of length of head and body in females); hind foot large. Averages and extremes of four females and measurements of one male, respectively, from Coastal Plains of western Jalisco and Colima are as follows: Length of head and body, 161 (152-183), 188; length of tail, 69 (66-73), 70; length of hind foot, 32 (31-34), 34. Two females weighed 141 and 134 grams.

Color: Pelage of dorsum and venter Fuscous-Black to roots, sparse, scarcely covering skin in most areas; nasal patch small, whitish.

Skull: Long and relatively narrow across zygomata, squamosals and braincase; rostrum broad and long; maxillary tooth-row long; angular processes widely spread.

Averages and extremes of four females and measurements of one male, respectively, from the Coastal Plains of western Jalisco and Colima are as follows: Condylobasal length, 39.7 (39.5-40.1), 45.5; zygomatic breadth, 25.7 (24.5-27.7), 31.5; palatofrontal depth, 15.4 (14.5-16.2), 16.7; length of palate, 26.4 (25.2-28.1), 29.8; length of nasals, 15.1 (14.3-16.4), 18.2; breadth of braincase, 19.4 (18.8-20.7), 22.8; squamosal breadth, 23.0 (21.8-25.2), 27.7; breadth of rostrum, 9.3 (8.8-9.8), 21.0; alveolar length of maxillary tooth-row, 9.4 (8.5-10.3), 10.3; breadth across angular processes, 27.5 (25.4-30.0), 33.2.

Comparisons.—For comparisons with *P. b. lutulentus,* see account of that subspecies.

From *P. b. bulleri, P. b. burti* differs as follows in: Larger size; everywhere darker, more blackish and less ochraceous; hind foot blackish above instead of white; skull longer and broader; angular processes more widely spread; rostrum broader and longer; maxillary tooth-row longer.

From *P. b. nayaritensis, P. b. burti* differs as follows: Slightly larger size; upper parts and underparts darker, more blackish and less reddish-brown; braincase narrower; maxillary tooth-row longer.

Remarks.—Goldman (1939b:97) named *P. b. burti* on the basis of a single specimen from near sea level (Tenacatita Bay) on the Pacific Coast. Additional specimens have been obtained from the coastal plains, near the coast line, of southwestern Jalisco and western Colima, and one from 5 mi. S Purificación, Jalisco, at approximately 1400 feet above sea level. The specimen last mentioned suggests that *burti* occurs also on the lower west-facing slopes of the Coastal Range. The Coastal Plains are characterized by an arid tropical scrub owing to the long dry season (late November into May). Most of the precipitation falls in a short wet season in September and October (Vivó Escoto, 1964:212). Owing to the aridity for most of the year, these pocket gophers are able to live in the Tropical Life-Zone.

The additional material substantiates the validity of *burti* and shows that it is large, more nearly like *P. b. nayaritensis* and *P. b. albinasus* than the small subspecies *P. b. bulleri* and *P. b. lutulentus* in the adjacent mountains immediately to the east.

Specimens examined.—Total of 8 as follows: Jalisco: 5 mi. S Purificación, 1; 10 mi. NNW Barrada Navidad, 2; 5 mi. NE Navidad, 200 ft., 1. Colima: 6 mi. N Santiago, 1; 4 mi. W and 1 mi. S Santiago, 10 ft., 2; 3 mi. NE Cuyutlán, 1 (UA).

Pappogeomys bulleri infuscus new subspecies

Type.—Male, adult, skull and skin; no. 33451, University of Kansas Museum of Natural History; Cerro Tequila, 10,000 feet, 7 mi. S and 2 mi. W Tequila, Jalisco; May 13, 1949; obtained by J. R. Alcorn, original number 9186.

Range.—Cerro Tequila, 9000 to 10,000 feet, and probably restricted to higher elevations of that mountain in north-central Jalisco. See Fig. 2.

Diagnosis.—Size medium for species; tail relatively short (averaging 40.5% of length of head and body in males); hind foot short to medium. Averages and extremes of five males from Cerro Tequila are as follows: Length of head and body, 159 (150-170); length of tail, 68 (63-76); length of hind foot, 30 (29-30).

Color: Ground color of dorsum dark reddish-brown, hairs of back Cinnamon-Brown distally, becoming bright Ochraceous-Tawny on sides; basally all hairs Light Mouse Gray; hairs of underparts Ochraceous-Buff apically, chin and throat whitish; upper parts of hind feet varying from whitish to buffy; nasal patch lacking.

Skull: Moderately long for species and decidedly narrow, relative to length, across zygomata and squamosals; rostrum narrow and moderately long; angular processes widely spreading.

Averages and extremes of five males from Cerro Tequila are: Condylobasal length, 38.8 (38.7-39.0); zygomatic breadth, 24.2 (22.5-25.5); palatofrontal depth, 15.1 (14.7-15.8); length of palate, 24.9 (23.4-26.2); length of nasals, 14.7 (14.4-15.3); breadth of braincase, 18.7; (17.4-19.4); squamosal breadth, 22.4 (20.6-23.4); breadth of rostrum, 8.6 (8.3-8.9); length of rostrum, 18.4 (18.0-18.7); alveolar length of maxillary tooth-row, 8.3 (7.6-9.1); breadth across angular processes, 26.2 (24.5-27.3).

Comparisons.—From *P. b. amecensis, P. b. infuscus* differs as follows: Larger; upper parts darker, more dark brownish and less bright ochraceous; nasal patch lacking; skull longer (as expressed in condylobasal length, length of palate, length of nasals, and length of rostrum); broader across angular processes.

From *P. b. bulleri, P. b. infuscus* differs as follows: Slightly larger; dorsum darker, more dark brownish and less ochraceous; underparts darker and brighter, more ochraceous and less buffy; skull narrower (as expressed in lesser distance across zygomata, braincase, and angular processes); hind foot slightly shorter.

From *P. b. albinasus, P. b. infuscus* differs as follows: Decidedly smaller; upper parts darker, more brownish and less tawny; underparts paler, more ochraceous-buffy and less bright ochraceous-orange; face without whitish markings typical of *albinasus;* skull smaller in all measurements (no overlap except in length of nasals, rostrum and maxillary tooth-row); tail and hind foot shorter.

From *P. b. nayaritensis, P. b. infuscus* differs as follows: Smaller; underparts paler, more ochraceous-buffy and less tawny; skull smaller in all dimensions (overlap only in palatofrontal depth, length of nasals, rostrum and maxillary tooth-row); tail and hind foot decidedly shorter.

Remarks.—This subspecies probably is restricted to Cerro Tequila, down the slopes to the lower edge of the oak forest zone at about 6500 feet. A low ridge supporting an oak woodland extends northwest from the base of Cerro Tequila to the Sierra Viejo de Magdalena where *P. b. nayaritensis* occurs. This ridge would be a logical place to look for intergrades between *nayaritensis* and *infuscus.* Except for the relatively low ridge mentioned above, the Cerro Tequila is isolated in all directions from adjacent highlands by the low basin formed by the Valle de Ameca (see comments in account of *albinasus*). *P. b. amecensis* occurs nearby on the Sierra de Ameca. The two mountains are separated by a distance of no more than 20 miles, but the intervening lowlands are unsuitable for the subspecies of *P. bulleri.* Consequently there is no gene flow between *infuscus* on the one hand and *amecensis* and *albinasus* on the other.

P. b. infuscus is only slightly larger in most dimensions than *P. b. bulleri,* and in this respect more closely resembles the group of small subspecies in the mountains of west-central Jalisco than the group of large subspecies primarily in the northern part of the range of the species. Probably immigrants from the northwest colonized the Cerro Tequila or an original stock resembling *nayaritensis* inhabited all of the area now occupied by *infuscus* and in *nayaritensis* as well as the intervening lowlands, when ecological conditions were more favorable than now at lower elevations. In either case, that stock probably was large like *P. b. nayaritensis* that occurs to the northwest today. Subsequent selection pressure possibly favored reduction in size. Almost all geomyids living at high elevations, and especially those isolated at high elevations, are small. The size of *infuscus,* especially the size of its skull, is postulated to have decreased until most dimensions approximated those of *P. b. bulleri.*

Another trend postulated for *P. b. infuscus* was an increase in pigmentation, especially pronounced middorsally in the form of an indistinct stripe. The underparts are darker also than in any of the neighboring populations. Interestingly, no nasal patch is developed in *infuscus,* even though such a patch is well marked in adjacent populations of both small (*amecensis*) and large (*albinasus*) subspecies. Lack of the nasal patch in *nayaritensis* lends additional support to the hypothesis that *infuscus* was derived from a *nayaritensis*-like ancestor.

Specimens examined.—Total, 10, all from **Jalisco**, as follows: Cerro Tequila, 10,000 ft., 7 mi. S and 2 mi. W Tequila, 8; 7 mi. SSW Tequila, 9000 ft., 2.

Pappogeomys bulleri lutulentus new subspecies

Type.—Female, adult, skull and skin; No. 92984 University of Kansas Museum of Natural History; Sierra de Cuale, 7300 feet, 9 km. N El Teosinte (= Desmoronado), Jalisco; October 28, 1962; obtained by Percy L. Clifton, original number 3236.

Range.—Northwestern Jalisco; known only from the type locality, and probably restricted to Sierra de Cuale (= Sierra de Desmoronado). See Fig. 2.

Diagnosis.—Size small for species; tail and hind foot short. Averages and extremes for three females (including type) and measurements of one male, respectively, all from the type locality, are as follows: Length of head and body, 129 (123-137), 138; length of tail, 53 (50-58), 60; length of hind foot, 26 (25-27), 27.5.

Color: Ground color of dorsum bright orange-red, hairs of back varying between Ochraceous-Buff and Ochraceous-Orange apically, slightly brighter on sides; all hairs Light Mouse Gray basally; hairs of belly varying from dull Ochraceous-Buff to Ochraceous-Orange; chin and throat Light Ochraceous-Buff; nasal patch small, pale buffy; hind feet whitish.

Skull: Short, and relatively narrow, especially across zygomata, squamosals, and angular processes; rostrum short and narrow; maxillary tooth-row short.

Average and extreme cranial measurements for three females (including type) and measurements of one male, respectively, all from the type locality, are as follows: Condylobasal length, 33.7 (33.1-34.3), 35.0; zygomatic breadth, 20.9 (20.5-21.2), 21.9; palatofrontal depth, 13.7 (13.4-14.0), 13.8; length of palate, 22.0 (21.8-22.1), 22.9; length of nasals, 12.6 (12.0-12.9), 11.8; breadth of braincase, 17.3 (17.1-17.5), 17.0; squamosal breadth, 20.0 (19.9-20.1), 20.2; breadth of rostrum, 7.8 (7.6-8.2), 7.8; length of rostrum, 15.7 (15.3-16.4), 16.8; alveolar length of maxillary tooth-row, 7.6 (7.0-8.2), 7.7; breadth across angular processes, 20.7 (20.1-21.2), 23.4.

Comparisons.—From *P. b. bulleri, P. b. lutulentus* differs as follows: Decidedly smaller, both externally and cranially; without overlap in length of skull, length of palate, length of nasals, zygomatic breadth, and breadth across anguar processes; and only slight overlap in palatofrontal depth, squamosal breadth, length of rostrum, and maxillary tooth-row.

From *P. b. burti, P. b. lutulentus* differs as follows: Smaller body; upper parts and underparts paler and brighter, more reddish-brown and less blackish; skull decidedly shorter, without overlap in condylobasal length, length of palate, length of nasals, length of rostrum, and maxillary tooth-row; zygomatic arches broader; cranium and rostrum broader; skull deeper.

Remarks.—The name *lutulentus*, a Latin adjective meaning muddy or dirty, refers to the fossorial habits of the animal. Morphologically, *P. b. lutulentus* is most closely allied to the other diminutive subspecies, *P. b. bulleri* and *P. b. amecensis,* that occupy the west-central highlands of Jalisco. Also *lutulentus* agrees in color with other populations from the Costal Range; all are characterized by bright tones of ochraceous-orange. In cranial dimensions, *lutulentus* most closely resembles *P. b. amecensis* but is distinguished by shorter skull, shorter palate, and greater breadth across the angular processes. Even so, *lutulentus* and *amecensis* are not contiguous geographically; their ranges are separated by that of *P. b. bulleri. P. b. lutulentus* closely resembles *bulleri* but averages smaller in all dimensions, and especially in length of skull, palate, nasals, and maxillary tooth-row. The three diminutive subspecies are closely related, and evidently were differentiated from a common ancestor characterized by a small skull.

P. b. lutulentus is so much smaller than any one of the group of the large subspecies that includes *P. b. albinasus, P. b. burti* and *P. b. nayaritensis* that the only overlap in measurements taken is a slight one in alveolar length of the maxillary tooth-row.

Pappogeomys bulleri lutulentus is known only from high elevations in the Sierra de Cuale, and probably is restricted geographically to this sierra that juts westward into the coastal lowlands at nearly a right angle to the main body of the Coastal Range. The Sierra de Cuale is separated from mountains to the east by a relatively low intermontane valley. Although *P. b. bulleri* now occupies this valley, the valley may have been unoccupied in the past. If so, the valley could have permitted *lutulentus* to diverge subspecifically from *bulleri. P. b. lutulentus* and *P. b. bulleri* are not known to intergrade but may do so on the lower, eastern slopes of the Sierra de Cuale.

Specimens examined.—Total 4, all from **Jalisco**, as follows: Sierra de Cuale, 7300 ft., 9 km. N Teosinte (= Desmoronado), 4.

Pappogeomys bulleri nayaritensis Goldman

Pappogeomys bulleri nayaritensis Goldman, Jour. Mamm., 20:94, February 15, 1939; Poole and Shantz, Bull. U. S. Nat. Mus., 178:374, April 9, 1942; Goldman, Smiths. Miscl. Coll., 115:371 and 429, July 31, 1951; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:464, March 31, 1959.

Type.—Male, adult, skull and skin; no. 88124, U. S. National Museum (Biol. Surv. Coll.); Jalisco, about 10 mi. S Tepic, 5000 feet, Nayarit; April 10, 1897; obtained by E. W. Nelson and E. A. Goldman, original number 10886.

Range.—Southern Nayarit into north-central Jalisco in foothills and mountains north of Río de Ameca. See Fig. 2. Altitudinal range 3000 feet on western slope of Coastal Range WNW Jalcocotán, up to 6800 feet on Cerro El Faro.

Description.—Large for species; tail relatively long (length averaging 48% of length of head and body in females); hind foot large. Averages and extremes of seven females and three males, respectively, from Southern Nayarit are as follows: Length of head and body, 157 (150-166), 172 (165-180); length of tail, 75 (63-82), 77 (67-83); length of hind foot, 33 (29-35), 33 (32-34).

Color: Dorsum dull ochraceous-brown, pelage near Cinnamon-Brown apically in darker specimens and Ochraceous-Tawny apically in paler specimens; slightly paler on sides; pelage of upper parts basally Light Mouse Gray; pelage of belly varying from dull Ochraceous-Tawny to Ochraceous-Buff apically, most specimens having irregular spots of white on belly and innersides of forelegs; chin and throat whitish; nasal patch lacking; innersides of hind legs, tarsi, and hind feet whitish.

Skull: Long, and narrow especially across zygomata; rostrum broad and long; angular process widely spread.

Averages and extremes of seven females and three adult males, respectively, from southern Nayarit are as follows: Condylobasal length, 40.1 (39.2-42.2), 42.3 (41.2-42.9); zygomatic breadth, 25.6 (24.8-26.6), 27.9 (25.7-30.1); palatofrontal depth, 15.7 (15.0-16.3), 16.2 (15.4-16.8); length of palate, 26.2 (25.1-26.7), 27.9 (26.9-28.9); length of nasals, 15.2 (14.2-16.7), 16.3 (14.7-16.8); breadth of braincase, 20.3 (19.5-21.2); 21.3 (20.7-21.6); squamosal breadth, 23.4 (22.1-24.0), 24.8 (24.6-24.9); breadth of rostrum, 9.0 (8.5-9.5), 9.6 (9.2-10.1); length of rostrum, 18.6 (17.9-19.3), 19.9 (18.6-20.5); alveolar length of maxillary tooth-row, 9.0 (8.2-9.6), 9.3 (9.1-9.6); breadth across angular processes, 27.1 (25.5-27.8), 29.7 (27.5-31.5).

Comparisons.—For comparisons with *P. b. infuscus*, see account of that subspecies.

From *P. b. albinasus, P. b. nayaritensis* differs as follows: Dorsum slightly brighter; underparts darker, more tawny and less ochraceous; nasal patch lacking; skull decidedly narrower, as expressed in smaller zygomatic breadth, squamosal breadth, breadth of rostrum, and breadth across angular processes; tail relatively longer (averaging 48 *versus* 42% of length of head and body in females); hind foot decidedly larger.

From *P. b. bulleri, P. b. nayaritensis* differs as follows: Larger; dorsum slightly darker and duller, more tawny and less ochraceous; underparts darker and brighter, more ochraceous and less light buff; skull longer, with only slight overlap in condylobasal length, and broader (across zygomata, braincase, squamosals, and angular processes); rostrum broader and longer; tail longer; hind foot decidedly longer; no overlap in breadth of braincase.

From *P. b. amecensis, P. b. nayaritensis* differs as follows: Larger; dorsum and venter darker, less bright ochraceous and more dull tawny-brown; nasal patch lacking; skull larger, without overlap in measurements except that of maxillary tooth-row; tail longer; hind foot decidedly longer.

Remarks.—The range of this subspecies in the mountains of southern Nayarit is south of the gorge of the Río Grande de Santiago and no specimen has been obtained from the low coastal plain west of the mountains. Nevertheless, specimens have been taken as low as 3000 feet in the foothills on the western slope, and, since the species (see *P. b. burti*) inhabits the coastal lowlands of southwestern Jalisco and western Colima, it possibly inhabits also the coastal plain of southwestern Nayarit where similar environments prevail.

The population from lower elevations may differ from *P. b. nayaritensis.* Cranial dimensions of a sample taken at 3000 feet from 2 mi. WNW Jalcocotán are decidedly larger than in topotypes from higher elevations. Compared with topotypes, the Jalcocotán series averages larger especially in condylobasal length of skull (40.9 *versus* 39.3), zygomatic breadth (25.8 *versus* 24.4), length of palate (26.8 *versus* 25.4), and length of nasals (16.0 *versus* 14.5). Also the rostrum of the Jalcocotán series is broader (9.2 *versus* 8.7) and longer (19.2 *versus* 18.1). Although the samples are small, a trend toward larger size in populations from lower elevations is indicated. Additional material from the foothills and possibly from the costal plains of southwestern Nayarit may demonstrate that the lowland population is subspecifically distinct from populations of *nayaritensis* taken at higher elevations. It seems advisable now to allocate the series from Jalcocotán to *P. b. nayaritensis*, pending acquisition of additional material.

Intergradation with *P. b. amecensis* is suggested in the small series from 6800 feet on Cerro El Faro near the southeastern border with Jalisco (see account of *amencensis*). Intergradation with the more closely related neighbors, *P. b. albinasus* and *P. b. burti*, cannot be demonstrated on the basis of current material. The ranges of *nayaritensis* and *burti* may meet in the low coastal plain, or may be separated by the Río de Ameca. Contact between *nayaritensis* and *albinasus* may occur on the plateau along the southern rim of the Río Santiago (see map, p. 597, and discussion of *P. b. albinasus*). A young female (KU 39803) from Cerro Viejo de Magdalena, 6500 feet, on the rim of the Río Santiago gorge, is referable to *nayaritensis* indicating that the zone of intergradation, if it occurs at all, is farther to the east along the narrow corridor. The specimen is without a nasal patch, and, in view of its youth, is referred to *nayaritensis* primarily on the basis of this feature.

Specimens examined.—Total of 16, as follows: **Nayarit:** 2 mi. WNW Jalcocotán, about 3000 ft., 5; type locality, 8 (USNM); Cerro El Faro [= Llorón de Ixtlán], 6800 ft., 6 mi. S Ixtlán del Río, 2. **Jalisco:** Cerro Viejo de Magdalena, 6500 ft., 3 mi. NE Magdalena, 1.

Pappogeomys alcorni Russell

Pappogeomys alcorni Russell, Univ. Kansas Publ. Mus. Nat. Hist., 9:359, January 21, 1957; Hall and Kelson, The Mammals of North America, 1:464, March 31, 1959.

Type.—Female, adult, skull and skin; no. 39806 University of Kansas Museum of Natural History; 4 mi. W Mazamitla, 6600 ft., Jalisco; obtained by J. R. Alcorn, original number 12835.

Range.—Southern Jalisco at higher elevations in Sierra del Tigre. See Fig 2.

Diagnosis.—Nasals truncate posteriorly; incisive foramina short and relatively broad; enamel plate on posterior wall of M1 on lingual one-fourth only and thick; nasal patch large, rich Cinnamon-Buff or bright Pinkish Buff.

Description.—Small for genus; tail naked, relatively short (averaging 42% of length of head and body in females and 47% in a male); hind foot short. External measurements of two females and one male are, respectively, as follows: Length of head and body, 147, 149 (holotype), 165; length of tail, 63, 61, 78; length of hind foot, 28, 29, 30.

Color: Upper parts Dark Mouse Gray basally and bright Orange-Cinnamon apically; nasal patch large, Cinnamon Buff or Pinkish Buff; underparts Light Mouse Gray overlaid with Orange-Cinnamon, becoming bright Cinnamon-Buff on throat except for small and inconspicuous white spot; hind feet and tarsi Cinnamon-Buff.

Skull: Small and relatively deep; rostrum narrow and short; nasals broadly truncate posteriorly and not decurved anteriorly; anterior palatine foramina small and rounded, not slitlike; zygomata slender, bowed laterally; narrow across squamosals; jugal long; enamel on posterior wall of M1 reduced to thick vestigial plate on inner fourth, outer three-fourths of posterior wall without trace of enamel. Measurements of the holotype and the other female are, respectively, as follows: Condylobasal length, 38.0 and 36.9; zygomatic breadth, 24.2 and 24.8; palatofrontal depth, 15.0 and 14.8; length of palate, 24.7 and 24.1; length of nasals, 12.7 and 12.8; breadth of braincase, 18.1 and 17.5; squamosal breadth, 21.5 and 21.4; breadth of rostrum, 8.4 and 8.1; length of rostrum, 16.9 and 16.3; alveolar length of maxillary tooth-row, 9.3 and 8.8.

Remarks.—This small, monotypic species was found in montane meadows in pine forest. The burrows crossed over those of the much larger *Pappogeomys tylorhinus angustirostris.* Possibly different food preferences permitted the two species to live at the same locality—*alcorni* in shallow burrows and *tylorhinus* in deep burrows.

Pappogeomys alcorni is closely related to *Pappogeomys bulleri.* The geographic ranges of the two species are separated by the broad valley containing the playas of Zapotlan and Sayula. Characters that differentiate *alcorni* from *bulleri* include: Outer (labial) three-fourths of posterior wall of M1 lacking enamel; bright buffy, instead of whitish, nasal patch; nasals broadly truncate instead of emarginate posteriorly; short, rounded (instead of long, narrow) incisive foramina. Because of the qualitative nature of the distinguishing characters of *alcorni* and its separation geographically from *bulleri, alcorni* is arranged as a species instead of as a subspecies of *P. bulleri* (Russell, 1957:360).

The reduction of enamel on the posterior wall of the first molar in *Pappogeomys alcorni* shows a stage in evolution that occurred earlier, in Pleistocene time when the subgenus *Cratogeomys* was evolving from primitive *Pappogeomys* stock. Evidently, the primitive stock of *Pappogeomys* in the early Pleistocene had, like *Pappogeomys bulleri,* a complete enamel plate across the posterior wall of M1 and M2. The trend in evolution giving rise to *Cratogeomys* may have occurred first by progressive reduction of enamel from the labial side of the M1 and ultimately the loss of all remaining enamel on the lingual side. Later, or perhaps at the same time, loss of the posterior enamel plate of M2 also occurred resulting in the enamel pattern characteristic of the advanced subgenus, *Cratogeomys.*

Specimens examined.—Total of three, all from Jalisco, as follows: 4 mi. W Mazamitla (Sierra del Tigre), 6600 ft., 2 (females, KU 39805, 39806); *3 mi. WSW Mazamitla (Sierra del Tigre), 1 (KU 61328, labeled ♀ but almost certainly ♂).

A FOSSIL SPECIES

Pappogeomys bensoni (Gidley)

Cratogeomys bensoni Gidley, U. S. Geol. Surv. Prof. Paper 131-E:123, 1922.

Type.—Left lower jaw, carrying all cheek teeth but lacking incisor; No. 10495 U. S. National Museum; Benson locality, sec. 22, T. 17 S, R. 20 E, San Pedro Valley, west of San Pedro River about 2 mi. S. Benson, Cochise Co., Arizona.

Geologic horizon.—Benson local fauna, Early Blancan mammalian provincial age, Upper Pliocene.

Geographic range.—Known only from the type locality.

Description.—Upper incisor provided with single median sulcus; ramus slenderer than in Recent *Pappogeomys castanops;* basitemporal fossa present, but not so deep as in Recent subgenus *Cratogeomys;* masseteric crest less massive; mental foramen ventral to anterior extremity of masseteric crest and posterior to that of Recent *Pappogeomys;* enamel distribution on p4-m3 as in all members of Tribe Geomyini (see Russell, 1968:521); m3 having slight constricted portion at posterior margin; size about as in *Geomys bursarius* and smaller kinds of *Pappogemys castanops.*

Remarks.—Four additional lower jaws, with various teeth, and an isolated upper and lower incisor were obtained from the Benson site. Reference to the genus *Pappogeomys* is made entirely on the basis of the upper incisor which has a single median sulcus, a feature peculiar to this genus. The characters of the lower jaw and inferior dentition described above for the fossil are not generically distinctive. The lower jaws including the teeth cannot be identified to genus in any of the Geomyini (genera *Geomys, Zygogeomys, Orthogeomys* and *Pappogeomys*). As was pointed out by Russell (1968:480), the pattern of grooving is a reliable, differential, generic character in each genus of the Geomyini. Therefore, *bensoni* is certainly referable to *Pappogeomys* on the basis of the pattern of grooving of the upper incisor.

On geological grounds, I would suspect that *P. benson* is referable to the primitive subgenus *Pappogeomys* rather than to the more specialized subgenus *Cratogeomys;* however, final judgment must await discovery of the upper dentition. Gidley (1922: 123) referred *bensoni* to the genus *Cratogeomys,* considered here to be a subgenus of *Pappogeomys.*

Subgenus Cratogeomys Merriam

Type.—*Geomys merriami* Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:217, October, 1893.

Diagnosis.—Size small to large (see below); overhair of top of head and back having three color bands; pale nasal patch lacking; top of skull flat in longitudinal outline; sagittal crest well developed in adults of both sexes; lateral angles of maxillary arms of zygomata enlarged into platelike expansions; posterior wall of M1 and M2 lacking enamel plate.

Remarks.—Although two of the subspecies of *Cratogeomys casanops* (*subnubilus* and especially *peridoneus*) overlap broadly the range of variation in size in the subgenus *Pappogeomys,* all other species of *Cratogeomys* are consistently larger than any species of the more primitive subgenus *Pappogeomys.* Moreover, sexual dimorphism is more pronounced in *Cratogeomys.* Recorded minimal and maximal measurements of adult females are: Length of head and body, 144 to 267; length of tail, 59 to 119; and length of hind foot, 29 to 54. Corresponding measurements of adult males are: 161 to 285; 67 to 126; 30 to 54.

Unworn pelage is typically long and soft; worn pelage tends to be shorter and less fine. The body is densely covered in all species except *P. fumosus,* which has a sparse, hispid, bristly pelage (seemingly an adaptation to the hot, tropical environments of the Pacific Coastal plains). The tail of all species is sparsely clothed in short, usually dusky hairs. Those on the feet are short, stiff, and mostly dusky or blackish except that those on the toes of the hind feet of most specimens are long and whitish. In most species an auricular patch of short, blackish hairs is conspicuous. Nasal patches, characteristic of *Pappogeomys,* are not present in *Cratogeomys.*

In all species, the cover hairs of the top of the head and back have three bands of contrasting colors. The broad basal band varies between pale and dark plumbeous. Each hair terminates in a narrow band of black (sometimes dark Bay). The basic ground color of the upper parts is provided by a broad subapical band (the black is absent on the sides and face, which have only two bands), the particular color depending on the species. Basically, the ground color of the upper parts is one of four types: 1) Pale yellowish shades of light buffs and ochraceous-buffs; 2) bright reddish tones of rusty, chestnut, or tawny; 3) dark brown or russet tones; 4) glossy slate black or lustrous greenish-black (both are variations of extremes in melanism). The color of the subapical band usually approximates the color of the soils in which the individual lives. In melanistic individuals (a common variation in *P. fumosus*, *P. gymnurus*, *P. tylorhinus*, and *P. merriami*), the subapical band and the terminal band are indistinguishable. Hairs of the sides and cheeks are colored like the hairs of the back except for lacking the blackish terminal band. Although the overall tone of the upper parts depends mostly on the hue of the subapical band, the terminal band may darken or lighten the general appearance of the pelage. For example, if the blackish terminal is broad, the pelage is darkened, but if narrow the overall tone of the pelage is lightened. In extremely worn pelage more of the dark grayish color of the basal band shows through and imparts to the pelage a darker and duller appearance.

The underparts, in contrast to the condition in the subgenus *Pappogeomys*, are typically paler than the upper parts, except, of course, in extremely melanistic individuals. Hairs of the underparts, especially on the chest and belly, are bicolored. The broad basal band is plumbeous, and the narrow terminal band, which is never broader than a fourth the length of the hair, varies in color. In most subspecies the terminal band is some shade of buff or a bright tone of ochraceous and rarely creamy white. In any case, the paler terminal wash scarcely conceals the plumbeous bases of the hair.

Condylobasal length in *Cratogeomys* varies from 38.9 to 65.9 in adult females and from 43.7 to 74.5 in adult males. In all samples the males are the larger. Except in the two subspecies *P. castanops subnubilus* and *P. castanops peridoneus* of the subgenus *Cratogeomys*, the minimum condylobasal length of skull, taking sex into account, falls below the maximum dimension of the subgenus *Pappogeomys*. All other taxa of the subgenus *Cratogeomys* are larger.

The skull of *Cratogeomys* is flat, broad and conspicuously angular and rugose (not smoothly rounded as in *Pappogeomys*). A sagittal crest is developed in adults of both sexes of all species. The crest is especially prominent in males. The zygomatic arches are heavily constructed and spread widely. The rostrum is relatively broad, heavy, and short. The lambdoidal crest generally is broadly convex posteriorly or, in the specialized species (*gymnurus* species-group), sinuous; the occiput is flat, and never bulges posteriorly. The angular processes of the mandible are typically short as in the subgenus

Pappogeomys and other geomyids, or are expanded laterally in the more specialized species (*gymnurus*-group). The maxillary sheath of the upper incisor is usually without specialization (as in *Pappogeomys*), or the sheath is developed into a knoblike shelf around the alveolous of the incisor (*P. merriami*). The paroccipital processes are small as in the subgenus *Pappogeomys* (in *P. castanops* and *P. merriami*), or are expanded into a large platelike knob (in the *gymnurus* species-group). The squamosals are variable, being so expanded medially that they completely cover the parietals in adults (*P. merriami*), or are so expanded laterally as to accommodate the postglenoid notch (*gymnurus* species-group), or are without either lateral or medial expansions (*P. castanops*).

The posterior surfaces of M1 and M2 lack any trace of enamel. The third upper molar is highly variable in *Cratogeomys* as pointed out by Merriam (1895:76-77 and 80-83). Its shape varies from subtriangular to quadriform and obcordate in those species with more specialized dentitions. The relatively great range of individual variation of M3, especially in *P. merriami*, suggests that the tooth is presently undergoing evolutionary changes, and that the pattern has not yet become stabilized.

castanops species-group

Diagnosis.—Skull not strongly specialized toward platycephaly; cranium, relative to length of skull, deep and narrow posteriorly; squamosal breadth averaging less than 64 per cent of condylobasal length, and always less than zygomatic breadth; lambdoidal crest broadly convex posteriorly; squamosals never expanded laterally; rami of mandible not especially wide-spread posteriorly, angular processes short, and breadth across angular processes less than greatest length of lower jaw; occlusal surface of M3 quadriform or obcordate (posterior loph developed into elongated heel having its apex directed labially), but never subtriangular.

Remarks.—The *castanops* species-group includes two species (*P. castanops* and *P. merriami*), both polytypic. *P. castanops* is the more generalized and more closely resembles the primitive morphotype of the subgenus *Cratogeomys* (for further discussion, see section on evolution beyond). Specializations, especially in cranial and dental features, distinguish *P. merriami* from *P. castanops*. Both are old species, evidently originating before the Rancholabrean. The subspecies of *castanops* differ less from one another than do those of *merriami*, suggesting that intraspecific differentiation occurred more recently in *castanops* than in *merriami*.

Pappogeomys castanops

(Synonymy under subspecies)

Range.—Southeastern Colorado southward into San Luis Potosí. See Fig. 3. Altitudinal range from about 30 feet near mouth of Rio Grande to 8700 feet in montane valleys of Sierra Madre Oriental of southeastern Coahuila.

Diagnosis.—Posterior enamel plate of M1 and M2 absent; M3 quadriform, having lateral plates reduced or absent; skull without strong platycephalic specializations, breadth across zygomata exceeding breadth across squamosals; squamosals unspecialized, expanded neither medially nor laterally; angular processes short, breadth across processes less than length of mandible; rostrum not especially broad or deep; sides of basioccipital parallel, never strongly convergent anteriorly; lambdoidal crest convex posteriorly, never sinuous; paroccipital processes small, never produced as platelike expansions.

Description.—Features additional to those mentioned in the diagnosis are as follows: Small to medium, extremes in external measurements of adult females and males are, respectively: Length of head and body 144-212, 161-255; length of tail, 50-105, 67-105; length of hind foot, 27-42, 30-42.

Color: Pelage of upper parts varying in overall tones from pale yellowish-buff to dark reddish-brown, with mixture of dark-tipped hairs on back and top of head; underparts whitish to bright ochraceous-buff; basally all hairs grayish, usually with slightly darker hues on dorsum.

Skull: Small to medium-sized (condylobasal length 38.9-52.8 in females and 43.7-62.6 in males); angular processes of mandible short, width across angular processes less than anteroposterior length of lower jaws; squamosals having well-developed postglenoid notch; upper incisors relatively slender; basioccipital narrow, its sides nearly parallel; M3 quadriform and monoprismatic, its posterior loph weakly developed, labial re-entrant fold shallow if present, and lateral enamel plates becoming reduced with age, often one (usually the inner) or occasionally both lacking in old individuals.

Relationships.—Specializations of *P. castanops* are: Absence of enamel plates on the posterior wall of M1 and M2, prominent sagittal crest in adults of both sexes, and platelike expansion at angle of the zygomatic arm of the maxillary bone. Otherwise, *Pappogeomys castanops* is generalized as compared with other species of the subgenus.

Morphologically, *Pappogeomys castanops* most closely resembles *Pappogeomys merriami.* Smaller size, less massive skull, paler pelage, and lack of cranial and dental specialization distinguish *P. castanops* from its larger relative. The close relationship of *P. castanops* and *P. merriami* is emphasized by uniting them in the same species-group (the *castanops*-group).

The relationship of *Pappogeomys castanops* with the species of the *gymnurus* group is more remote. The distinctive platycephalic

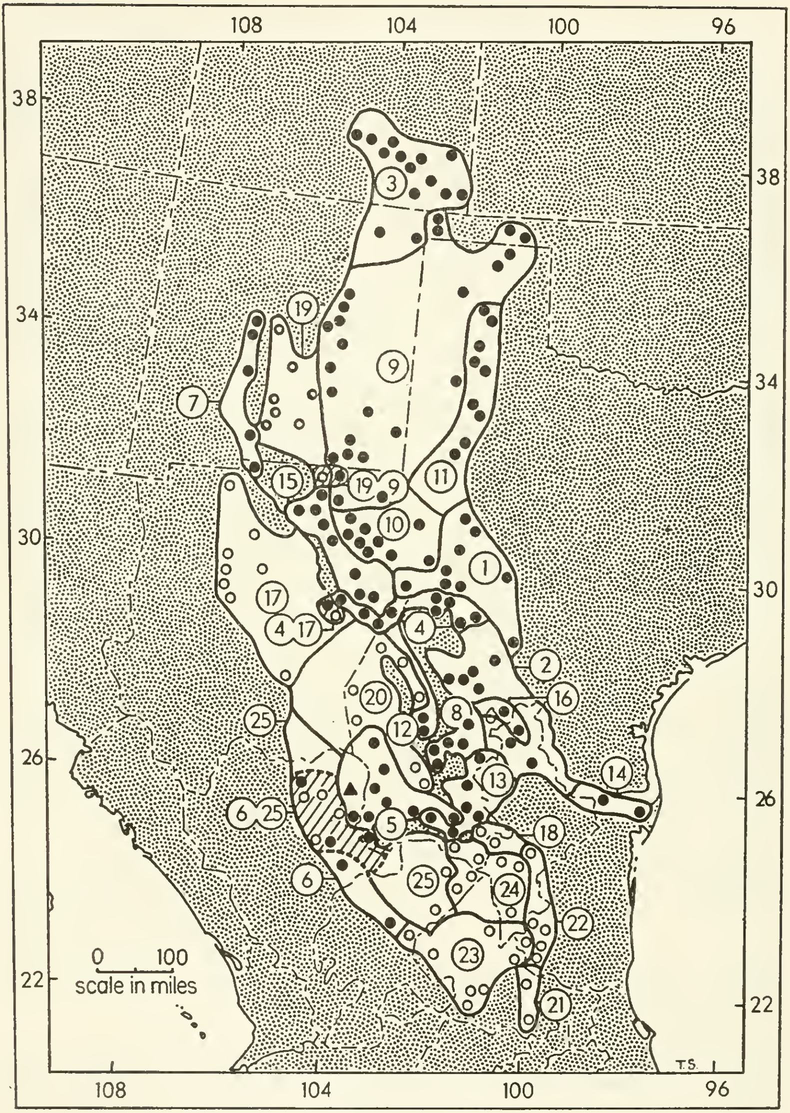

Fig. 3. *Cratogeomys castanops.*

excelsus-group ●:
1. *angusticeps*
2. *bullatus*
3. *castanops*
4. *clarkii*
5. *excelsus*
6. *goldmani*
7. *hirtus*
8. *jucundus*
9. *perplanus*
10. *pratensis*
11. *simulans*
12. *sordidulus*
13. *subsimus*
14. *tamaulipensis*
15. *torridus*
16. *ustulatus*

subnubilus-group ○:
17. *consitus*
18. *elibatus*
19. *parviceps*
20. *perexiguus*
21. *peridoneus*
22. *planifrons*
23. *rubellus*
24. *subnubilus*
25. *surculus*

specializations of the skull of members of the *gymnurus* group contrast remarkably with the generalized cranial features of *Pappogeomys castanops.* Also the generally larger size, especially in cranial dimensions, and darker coloration distinguish species of the *gymnurus* group from *Pappogeomys castanops,* the only exception being the small species *Pappogeomys neglectus* of the *gymnurus* group.

Habitat.—Pappogeomys castanops inhabits arid and semi-arid desert plains and basins in local sites that are mantled with relatively deep sandy soil or sandy loam supporting desert vegetation consisting of xerophytic shrubs, forbs, and grasses. Preferred habitat for *Pappogeomys castanops* is usually found in the deep deposits of alluvial fill that occur in the inner valley and on the lower bajada between the backwalls of the mountain ranges. On the bajadas, the habitat becomes progressively poorer for this species towards the base of the mountains. On the upper slopes the topsoil becomes gradually thinner toward the base of the mountains, and the content of rock debris increases both in amount and size of stones. *Pappogeomys castanops* rarely occurs on the upper bajadas where it is replaced by *Thomomys.* However, where stream courses penetrate the bajadas from the mountains above, *Pappogeomys castanops* may extend its range into the uplands, and sometimes finds access to lower elevations of the mountains, living in the alluvial stream-side deposits. In some areas the inner valleys become broad desert flats supporting large, almost continuous populations of this species.

At higher elevations in the Sierra Madre Oriental, *Pappogeomys castanops* occurs in dark, friable soils of volcanic origin. And in the interior desert basins of southwestern Coahuila, extreme northeastern Durango and southeastern Chihuahua, the species lives in the deep sands deposited by large Pleistocene lakes that dried up in post-Wisconsin times.

Agriculture tends to favor the occurrence of *Pappogeomys castanops,* especially in irrigated areas, and roadbeds often support colonies of this rodent.

Geographic variation.—The 25 subspecies of *Pappogeomys castanops* can be divided into two well-defined groups—the *excelsus* group occurring in the northern and eastern part of the range and the *subnubilus* group occurring in the southern and western part of the range. The two groups do not interbreed in most places where populations meet and there behave towards one another as full species, but are joined by interbreeding populations at some places, the resulting chain of intergrading subspecies thereby forming a *rassenkreis*.

The *subnubilus* and *excelsus* groups are distinguished principally on the basis of size of the skull; the degree of difference in most cranial dimensions, especially in length, is as great as usually distinguishes species. Condylobasal length, length of palate, length of nasals, length of rostrum, or squamosal breadth can be used to distinguish the two groups. A combination of two or more of these dimensions provides an even more reliable basis of distinction; for instance, the two groups may be readily separated by plotting condylobasal length against length of palate (see Fig. 4).

Most parts of the ranges of the *subnubilus* and the *excelsus* groups are separated geographically by the high Sierra de Guadelupe and Sierra de Parras. This mountain chain is oriented in an east-west direction. Ranges of the two groups of subspecies are in close proximity in at least one high pass, near the mouth of Santo Domingo Cañon southwest of General Cepeda, where *P. c. subsimus* of the *excelsus* group and *P. c. subnubilus* occur at localities less than a mile apart (see subspecies accounts for exact localities) without indication of interbreeding. Limited contact between the two groups may occur in other high passes that penetrate these ranges. Six of the nine subspecies of the *subnubilus* group occur south of the Sierra de Guadalupe-Sierra de Parras mountain chain, suggesting that earlier in the Pleistocene the *subnubilus* group was isolated by these mountains and became different from other populations of the species.

In northeastern Durango on the high plateau (elevations of 6000 feet and higher) west and south of the Bolsón de Mapimí (at elevations of 3500 to 4000 feet), populations of the *subnubilus* and *excelsus* groups are sympatric (depicted by cross hatched area on Fig. 3), although the two probably do not occur in the same local environment. In this area the *subnubilus* group is represented by *Pappogeomys castanops surculus* and the *excelsus* group by *Pappogeomys castanops goldmani*. Adjacent lowlands of the Bolsón de Mapimí to the east are occupied by *Pappogeomys castanops excelsus*, another large subspecies also of the *excelsus* group. *P. c. surculus* evidently does not occur in the lowlands of the Bolsón; therefore, its range and that of *P. c. excelsus* do not overlap. However, both *surculus* and *goldmani* occur on the high plateau to the west, and both subspecies have been taken together in the valley of the Río Nazas, 6 mi. NE Rodeo. There is no indication that the

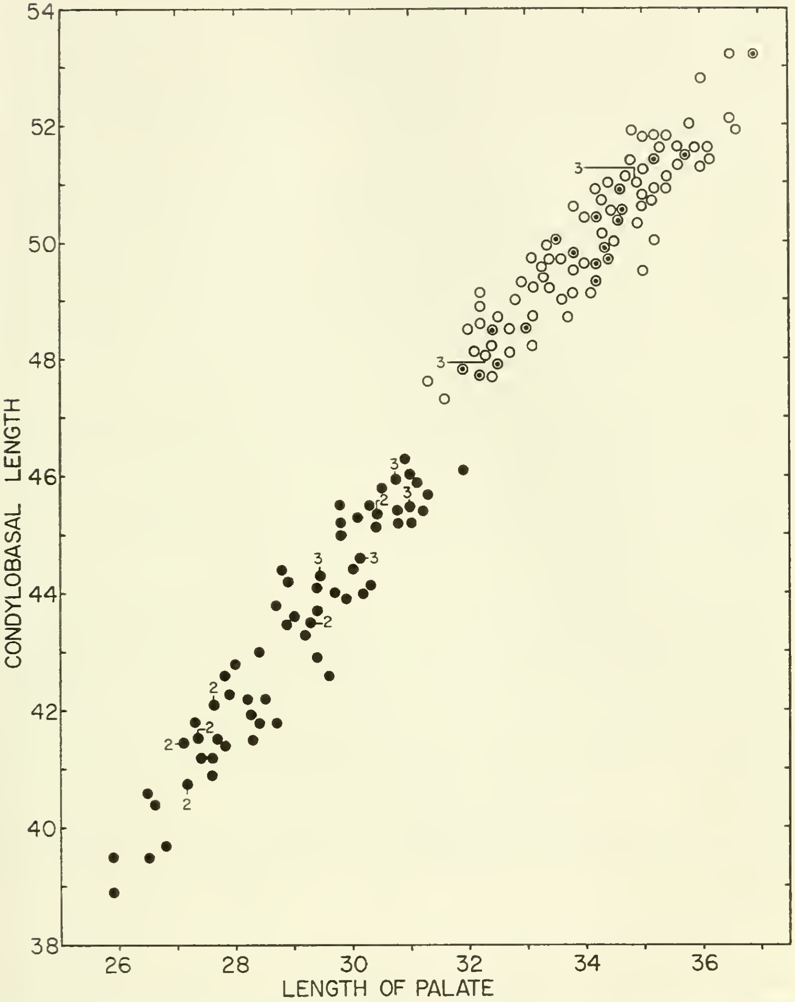

FIG. 4. Females of *subnubilus* group (solid circles), and *excelsus* group (open circles), of *Pappogeomys castanops.* An open circle enclosing a dot indicates two specimens.

two interbreed, and the characters ascribed to both subspecies are maintained in the area of sympatry without alteration. Adults are readily identified with either *surculus* or *goldmani,* and no individual with features intermediate between the two is known. In the portions of their ranges to the east, *surculus* and *goldmani* seem not to overlap.

Since *surculus* occurs only at higher elevations, it is probably ecologically separated from *excelsus.* On the less elevated desert plains of western Coahuila the ranges of *P. c. excelsus* and *P. c. perexiguus* interdigitate. The latter belongs to the *subnubilus* group. Both are pale, probably an adaptation to the unusually pale sands in which they burrow; but *excelsus* is remarkably larger than *perexiguus* cranially; therefore, there is no difficulty in identifying adults. Also, on the average, *perexiguus* is paler than *excelsus.* Boundary lines can be drawn for *excelsus* and *perexiguus* indicating that their geographic ranges do not overlap (see Fig. 3), but if more localities of occurrence were known, the two subspecies might be found to be sympatric over most of the northern part of the range of *excelsus* in west-central Coahuila. No individuals with characters intermediate between *excelus* and *perexiguus* are known.

P. c. perexiguus also has contiguous, if not overlapping, range with *Pappogeomys castanops sordidulus,* another large subspecies of the *excelsus* group, in the Llano de Ocampo of northwestern Coahuila. There is no indication that the large and small subspecies interbreed in this area, and in fact, the ranges of the two may be sympatric in the northern part of the Llano. Although no specimens of *sordidulus* are known north of Ocampo, there is indication that the population of *Pappogeomys castanops clarkii,* also of the *excelsus* group, from the Big Bend area of Texas is made up of intergrades between *clarkii and sordidulus.* Therefore, the range of *sordidulus* must extend northward to the Río Grande, thus overlapping the range of *perexiguus,* the occurrence of which is substantiated in the northern part of the Llano de Ocampo by actual specimens. Again the distribution map (Fig. 3) was drawn so that overlapping ranges are not indicated, but I suspect additional specimens will disclose sympatry.

In northeastern Chihuahua, the ranges of *P. c. clarkii* of the *excelsus* group and *Pappogeomys castanops consitus* of the *subnubilus* group are sympatric in a small area in the valley of the Río Grande around Ojinaga. Specimens of both subspecies have been identified from the valley, on the basis of large and small cranial dimensions. *P. c. clarkii* is known from Chihuahua only in the Ojinaga Valley, although it is common in the Rio Grande Valley in southern Presidio and Brewster counties in Texas. Probably *clarkii* has only recently extended its range across the Rio Grande in this area, and, therefore, until recently the habitat west of the river was occupied only by *consitus.* As elsewhere, there is no indication of gene exchanges between the populations of *clarkii* and *consitus* in this area. Desert uplands to the west of Ojinaga are inhabited only by *consitus.*

P. c. parviceps, the northernmost subspecies of the *subnubilus* group, occurs mainly in the Tularosa Valley of New Mexico between the ranges of *Pappogeomys castanops hirtus* of the *excelsus* group and other subspecies of the *excelsus* group to the east. Presently, *P. c. parviceps* is not in contact with *consitus* to the southwest, the only adjacent subspecies of the *subnubilus* group, and the intervening Río Grande Valley and plains of extreme northeastern Chiahuahua are now occupied by *Geomys arenarius.* It is especially abundant in cultivated areas, and it may have moved into the Río Grande Valley south of El Paso and Ciudad Juarez, at the expense of *Pappogeomys,* with the initiation of intensified agriculture. *P. c. parviceps* is not known to intergrade with either *hirtus* or *torridus* of the *excelsus* group, but the small size of *torridus* suggests the possibility of intergradation. *P. c. parviceps* and *P. c. torridus* are more nearly the same size than are any other adjacent pair of subspecies of the two groups, and the possibility of gene exchange between those two can not be ruled out. The range of *parviceps* and *perplanus* are in contact at Pine Springs Canyon in the Guadalupe Mountains as indicated on the map (Fig. 3). One adult female (PA 17211) from the west foot of Pine Canyon is referable to *parviceps* (condylobasal length measuring 45.3) and another adult female from the same locality (PA 17212) is referable to *Pappogeomys castanops perplanus* of the *excelsus* group on the basis of its large size (condylobasal length measuring 48.2). As in other areas of sympatry, there is no suggestion of intergradation between *parviceps* and *perplanus.*

As pointed out in the foregoing discussion, the *subnubilus* and *excelsus* groups are broadly contiguous, and in places are sympatric, from northeastern Durango northward into northeastern Chihuahua, extreme western Texas, and south-central New Mexico. Complementary subspecies of the two groups do not interbreed anywhere along this line of contact, and the two groups of subspecies there behave as species. Also the highest degree of difference is developed between those subspecies that are in contact (except for *goldmani,* which is discussed beyond). For example, the largest individuals, especially in cranial dimensions, are members of subspecies of the *excelsus* group that are in contact with members of subspecies of the *subnubilus* group. Examples of the *excelsus* group are *subsimus, excelsus, jucundus, sordidulus, clarkii, hirtus, pratensis,* and *per-*

planus. Other subspecies, such as *ustulatus, castanops,* and *simulans,* are also large and, although they do not have direct contact with subspecies of the *subnubilus* group, they do have ranges adjacent to those larger subspecies which do, and gene flow may account for their large size. The smaller subspecies of the *excelsus* group, including *angusticeps, bullatus* and *tamaulipensis,* occur along the eastern margin of the range of the species (see Fig. 3), and the range of none meets that of a subspecies of the *subnubilus* group. *P. c. angusticeps, P. c. bullatus* and *P. c. tamaulipensis,* and also *P. c. torridus* in the Trans-Pecos of Texas, differ less from subspecies of the *subnubilus* group than do their larger relatives whose geographic ranges overlap or meet those of the small subspecies. The geographic range of *P. c. torridus* may meet that of *P. c. parviceps,* but the records of occurrence of each as presently known are separated by the Sierra Diablo Mountains and the barren salt flats of northern Hudspeth County, Texas, and the ranges of *torridus* and *consitus* are physically separated by the Sierra Viejo-Sierra Chianti Mountain Chain and the Río Grande.

The greater degree of difference between subspecies of the *excelsus* group on the one hand and the subspecies of the *subnubilus* group on the other hand along the line separating the ranges of the two groups provides an exceptionally good example of character displacement as described by Brown and Wilson (1956:49) and Mayr (1960:82-86). Evidently the two groups were isolated by mesic forest in a Wisconsin pluvial cycle. After contact was made with the small gophers of the *subnubilus* group in the post-Wisconsin, selection favored trends toward larger size in populations of the *excelsus* group that were contiguous with populations of the *subnubilus* group. Populations of the *excelsus* group from the eastern part of the range that had lacked contact with the *subnubilus* group have not been affected by these selection pressures; they are smaller and less clearly differentiated from the *subnubilus* group.

Interbreeding between these two groups does occur, involving *P. c. goldmani* of the *excelsus* group and *P. c. rubellus* of the *subnubilus* group. Intergradation is demonstrated in a sample from Villa de Cos in southeastern Zacatecas. As a result of gene exchanges between these two subspecies in eastern Zacatecas, and subsequent introgression of genes into neighboring populations, *goldmani* is smaller than other subspecies of the *excelsus* group whose geographic ranges meet those of the smaller subspecies (except for *torridus*), and *rubellus* is larger than usual for the *subnubilus* group. But *goldmani* does intergrade with *excelsus* in the valley of the Río Aquanaval in southwestern Coahuila and *rubellus* does intergrade with *surculus* and *planifrons*. Consequently, there is a chain of gene flow from *excelusus* to *goldmani* to *rubellus*, and from *rubellus* to both *surculus* and *planifrons*. If gene flow between the *excelsus* and *subnubilus* groups were interrupted in the narrow zone where interbreeding occurs, the two groups of subspecies could be considered as two distinct species.

For discussion of the early evolution and formation of the *castanops* semispecies, see the account dealing with speciation (p. 769).

Pappogeomys castanops is highly variable geographically, having 25 subspecies. As discussed in the introduction, each subspecies is thought of as a center of differentiation within the species. Each center is characterized by a cluster of characters in a combination that is distinctive. The degree of differentiation between centers is not the same. In each of several geographic regions the subspecies more closely resemble each other than any one of them resembles any subspecies in another region.

The number of centers of differentiation and, therefore, the number of subspecies that warrant formal recognition, is a matter of judgment. In practical taxonomy the degree of distinction, or more correctly the range between minimum and maximum distinctiveness, is considered in deciding for or against subspecific recognition. Subspecific recognition implies the existence of a differentiation center. The 25 subspecies of *Pappogeomys castanops*, segregated into two subspecies groups, are recognized on the basis of criteria that seem to me to be descriptive of the geographic variation presently developed in the species. On the basis of less sophisticated criteria, closely allied subspecies, especially those composing geographic clusters, might be united, and the total number of subspecies reduced. On varying magnitudes of minimum criteria, combining of currently recognized subspecies would probably follow this sequence. First, *P. c. simulans* might be synomized with *pratensis*, *sordidulus* with *clarkii*, *torridus* with *angusticeps*, *bullatus* with *tamaulipensis*, *jucundus* with *excelsus*, *ustulatus* with *subsimus*, *elibatus* with *planifrons*, and *surculus* and *parviceps* with *consitus*. Therefore, a total of 17 subspecies would be recognized, as follows: *castanops*, *perplanus*, *hirtus*, *pratensis*, *clarkii*, *angusticeps*, *tamaulipensis*, *excelsus*, *subsimus* and *goldmani* in the *excelsus* subspecies-group and *consitus*, *perexiguus*, *rubellus*, *planifrons*, *subnubilus*, and *peridoneus* in the *subnubilus* subspecies-group.

If the minimum of criteria used to recognize the 17 subspecies listed above is raised so as to be even more inclusive, then: *perplanus, hirtus,* and *pratensis* might be synonymized with *castanops,* the oldest name, in keeping with the rule of priority; *tamaulipensis* with *angusticeps; excelsus* and *subsimus* with *clarkii; planifrons* with *rubellus;* and *perexiguus* with *consitus.* Thereby the total number of subspecies would be diminished from 17 to eight, as follows: *castanops, clarkii, angusticeps,* and *goldmani* in the *excelsus* subspecies-group and *consitus, rubellus, subnubilus* and *peridoneus* in the *subnubilus* subspecies-group.

Ultimate steps in synonymy would result in combining *clarkii, angusticeps,* and *goldmani* with *castanops,* and *subnubilus, rubellus,* and *peridoneus* with *consitus,* thereby recognizing but two subspecies, *castanops* and *consitus,* each of which is representative of one of the two groups of subspecies mentioned in this taxonomic study. Intergradation between the two groups occurs in southeastern Zacatecas, but so far as known, nowhere else.

Statistical analysis discloses no clinal variation. The absence of clines may be due to the restriction of gene flow between peripheral populations of adjacent subspecies. Restriction of interbreeding pocket gophers is usually a result of adverse edaphic factors. The contiguous populations that comprise each subspecies usually are remarkably uniform, and the transition from one subspecies to another is abrupt.

The subspecies *P. c. hirtus, P. c. sordidulus, P. c. tamaulipensis, P. c. perexiguus,* and *P. c. parviceps* probably are geographic isolates.

excelsus subspecies-group

Pappogeomys castanops angusticeps (Nelson and Goldman)

Cratogeomys castanops angusticeps Nelson and Goldman, Proc. Biol. Soc. Washington, 47:139, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:364, April 9, 1942; Hooper, Jour. Mamm., 29-302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959.

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, January 31, 1895 (part); Bailey, N. Amer. Fauna, 25:132, October 24, 1905 (part).

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Cratogeomys castanops lacrimalis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, June 13, 1934 (part); Herrmann, Texas Jour. Sci., 2:378, September 30, 1950.

Type.—Male, adult, skin and skull No. 24503/31908 U. S. National Museum; Eagle Pass, Maverick County, Texas; November 11, 1890; obtained by Clark F. Streator, original No. 434.

Range.—Semi-desert plains of the Texas Trans-Pecos area. See Fig. 3. Altitudinal range from about 900 feet at type locality to approximately 2600 feet at Black Gap.

Description.—Small for species; tail short relative to length of head and body (averaging 40% in females); hind foot short. Averages and extremes of 14 females and four males, respectively, from localities labeled with reference to Eagle Pass and Sheffield are: Length of head and body, 176 (165-190), 203 (195-214); length of tail, 70 (50-83), 84 (74-94); length of hind foot, 33 (30-36), 38 (35-40).

Color: Upper parts Mouse Gray basally and Cinnamon Buff apically, admixed with Bay-tipped hairs on back but pure Cinnamon Buff on face and sides; underparts Light Mouse Gray overlaid with Salmon-Buff; hind foot whitish; tail sparsely set with buffy hairs.

Skull: Short and shallow for species; narrow across zygomata and squamosals; rostrum relatively broad (averaging 52.2% of length); nasals, palate, and maxillary tooth-row short; tympanic bullae small, not inflated.

Average and extreme cranial measurements of 14 females and four males, respectively, from the Pecos and Rio Grande valleys of Texas are as follows: Condylobasal length, 46.9 (46.2-48.3), 53.1 (52.0-55.0); zygomatic breadth, 29.4 (27.2-31.2), 35.2 (32.4-39.7); palatofrontal depth, 18.2 (17.5-19.0), 20.1 (19.2-21.3); length of palate, 31.6 (30.8-32.5), 36.5 (35.4-37.6); length of nasals, 16.6 (15.3-18.2), 19.0 (18.2-19.6); breadth of braincase, 19.9 (18.8-20.9), 21.6 (21.0-22.5); squamosal breadth, 26.8 (25.7-27.9), 30.6 (29.4-32.4); breadth of rostrum, 10.5 (9.7-11.5), 12.5 (11.4-13.4); length of rostrum, 20.1 (19.0-21.8), 22.9 (21.7-24.3); alveolar length of maxillary tooth-row, 9.0 (8.0-9.7), 9.6 (8.9-10.0).

Comparisons.—For comparisons of *angusticeps with P. c. simulans, P. c. pratensis, P. c. clarkii,* and *P. c. bullatus,* see accounts of those subspecies.

From *Pappogeomys castanops perplanus, P. c. angusticeps* differs as follows: Smaller; tail relatively shorter (averaging 40 *versus* 44% of length of head and body); hind foot shorter; skull averaging smaller in all dimensions, with no overlap in condylobasal length, palatofrontal depth, length of palate, breadth of braincase and squamosal breadth; tympanic bullae smaller and less inflated.

Remarks.—Distinguished by a combination of small size, relatively short tail, and small and narrow skull, *angusticeps* is easily separated from the decidedly larger *pratensis, perplanus, clarkii,* and *simulans.* Of contiguous subspecies, *P. c. bullatus* most closely resembles *angusticeps,* but *bullatus* ranges south of the Río Grande, and differs from *angusticeps* in several features (for details, see account of *bullatus*).

Features distinguishing *angusticeps* are best developed in specimens from the lower valley of the Pecos River as evidenced in examples from along Independence Creek 15-20 mi. S Sheffield. Topotypes of *angusticeps,* collected in 1890, average smaller in condylobasal length, length of palate and length of maxillary tooth-row than do specimens from localities to the north and northwest. Recent attempts to obtain additional topotypes from Eagle Pass have been unsuccessful. *Geomys personatus fuscus* is common in this area today, and may have replaced *angusticeps* in the agricultural districts around Eagle Pass. Perhaps *angusticeps* does not occur in the Río Grande Valley south of Del Rio at present.

Intergradation of *angusticeps* with *perplanus* is clearly demonstrated in specimens from 1-3 mi. W Dryden, Texas. This sample differs from typical *angusticeps* in longer skull and palate, and greater breadth across braincase and squamosals (see account of *pratensis* for further discussion). However, considering the series as a whole, it is best referred to *angusticeps*. On the other hand, intergrades from 2 mi. E Sanderson, approximately 15 miles to the west of the aforementioned localities west of Dryden, more closely resemble *pratensis* and are referred to that subspecies. The steep gradient in variation and the narrower zone of intergradation between *angusticeps* and *pratensis* as demonstrated in the Dryden-Sanderson series, suggests secondary rather than primary intergradation.

Two females from Black Gap (TCWC 6081-82) are adult, judging from the degree of cranial development; however, they have smaller skulls than observed in other samples, especially in length and depth. The Black Gap material is even more divergent from *pratensis* and *clarkii*, both of which are known from localities nearby, and, therefore, they are best referred to *angusticeps*.

Specimens examined.—Total of 62, all from Texas, as follows: *Crockett County:* Ft. Lancaster, 1 (USNM); 5 mi. S Howard Springs, 1 (USNM). *Brewster County:* Black Gap, 50 mi. SSE Marathon, 2500 ft., 2 (TCWC); Black Gap, 2600 ft., 3 (2 TU, 1 TCWC). *Terrell County:* 15 mi. S Sheffield, 8 (TU); *16 mi. S Sheffield, 1 (TU); *19 mi. S Sheffield, 13 (TU); *20 mi. S Sheffield, 6 (TU); 3 mi. W Dryden, 2200 ft., 9; *2 mi. W Dryden, 2200 ft., 5; *1 mi. W Dryden, 2. *Val Verde County:* 20 mi. E. Juno, 1 (USNM); Samuels, 19 mi. W Langtry, 1 (USNM); 8 mi. S Langtry, 1 (USNM). *Maverick County:* Eagle Pass, 8 (7 USNM, 1 KU).

Pappogeomys castanops bullatus (Russell and Baker)

Cratogeomys castanops bullatus Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:597, March 15, 1955; Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:224, June 15, 1955; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959.

Cratogeomys castanops ustulatus Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:598, March 15, 1955 (part); Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959 (part).

Type.—Female, adult, skull and skin; No. 48498, Univ. Kansas Mus. Nat. Hist.; 2 mi. S and 6½ mi. E Nava, 810 ft., Coahuila, Republic of México; June 16, 1952; obtained by Robert J. Russell, original number 276.

Range.—Foothills of Sierra del Carmen in Coahuila, on Coastal Plains west of Río Grande southward to Vallecillo, Nuevo León. See Fig. 3. Altitudinal range from 810 feet in Río Grande Valley up to 1900 feet in foothills of Sierra del Carmen.

Description.—Small to medium sized for species; tail moderately long (averaging 43% of length of head and body); hind foot large. Averages and extremes of 11 females and four males, respectively, from eastern Coahuila (specimens labeled with reference to Nava, La Gacha, and Sabinas) are as follows: Length of head and body, 176 (164-190), 186 (180-208); length of tail, 76 (67-85), 79 (70-85); length of hind foot, 36 (33-37), 35 (33-37).

Color: Upper parts Dark Mouse Gray basally, Ochraceous-Buff to Orange-Buff apically, with some Bay-tipped hairs on back, but pure Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with white or pale buffy; hind feet white.

Skull: Size medium for species; palate and nasals short; narrow across squamosals and zygomata; rostrum short and narrow; maxillary tooth-row long.

Average and extreme cranial measurements of 12 females and 4 males (for localities, see externals above) are, respectively, as follows: Condylobasal length, 47.3 (46.3-48.2), 50.9 (49.7-52.1); zygomatic breadth, 30.4 (29.9-31.1), 34.5 (33.2-35.3); palatofrontal depth, 18.9 (18.6-19.4), 19.5 (19.2-19.9); length of palate, 32.3 (31.5-32.9), 35.0 (34.4-35.7); length of nasals, 16.5 (15.5-16.9), 17.6 (16.6-18.4); breadth of braincase, 20.9 (19.9-21.6), 21.3 (20.4-22.0); squamosal breadth, 27.8 (26.6-28.8), 29.4 (28.4-30.5); breadth of rostrum, 10.8 (10.0-11.6), 12.0 (11.4-12.6); length of rostrum, 19.9 (18.8-21.0), 21.3 (20.6-22.0); alveolar length of maxillary tooth-row, 9.5 (8.9-9.8), 9.7 (9.3-10.2).

Comparisons.—For comparisons with *P. c. ustalatus, P. c. jucundus,* and *P. c. tamaulipensis,* see accounts of those subspecies.

From *Pappogeomys castanops clarkii, bullatus* differs as follows: Smaller; hind foot shorter; skull averaging smaller in all dimensions (except length of nasals and maxillary tooth-row), especially in condylobasal length, breadth across zygomata and squamosals, and length of nasals; rostrum shorter and narrower.

From Pappogeomys castanops angusticeps, bullatus differs as follows: Tail relatively longer (43 *versus* 40% of length of head and body); hind foot longer; upper parts paler, more buffy and less ochraceous, especially on sides; skull slightly longer; zygomata more widely spreading; palate slightly longer; decidedly broader across braincase and squamosals; maxillary tooth-row longer.

Remarks.—P. c. bullatus is characterized by the combination of medium size, narrow skull, short nasals, short rostrum, and short hind foot. This differentiates *bullatus* from other subspecies in northeastern México, and especially from the large subspecies *P. c. ustulatus, P. c. jucundus,* and *P. c. clarkii. P. c. bullatus* most closely resembles *P. c. angusticeps,* from north of the Rio Grande, in size, but *bullatus* differs significantly from *angusticeps* in several features (see comparisons above). The only other subspecies of medium size in northeastern México is *Pappogeomys castanops tamaulipensis* from the lower valley of the Río Grande on the Mexican side of the river. But, *P. c. tamaulipensis* is distinctly larger than *bullatus* in several external and cranial features (see account of *tamaulipensis* for account of differences).

Specimens from 3 mi. N Lampazos, 1 mi. N Vallecillo, and Vallecillo in Nuevo León were erroneously assigned to *P. c. ustulatus* by Russell and Baker (1955:599).

The great disparity in size between *bullatus* and its two larger neighbors, *ustulatus* and *jucundus,* may reduce the frequency of interbreeding. There is no indication of intergradation in specimens of *bullatus* taken on the desert plains 9 mi. S and 11 mi. E Sabinas, although the type locality of *ustulatus* in the valley of the Río Salado at Don Martín is less than 15 miles distant to the south. *P. c. ustulatus* has not been taken outside the valley of the Río Salado where deep, sandy soils are developed. I suspect that if interbreeding between *bullatus* and *ustulatus* occurs, it is in a narrow zone between the flood plain of the river and the desert uplands. Also, specimens of *bullatus* obtained 3 mi. N. Lampazos, Nuevo León, show no evidence of intergradation with the larger subspecies. But, in specimens of *subsimus* from Hisachalo, Coahuila, the maxillary tooth-row is as short as in *bullatus* (see discussion in account of *subsimus*).

Differences between *bullatus* and *P. c. tamaulipensis* of the lower Río Grande Valley on the Mexican side) are not so great as between *bullatus* and *ustulatus,* and intergradation between the two may have occurred recently in the area between Reynosa in Tamaulipas and Vallecillo in Nuevo León. A search in this area for pocket gophers at Sabinas Hidalgo, Ciénegas de Flores, El Alamo, General Treviño, Doctor Coss, General Bravo, and China was fruitless; not even mounds were found. The area is heavily overgrazed by domestic livestock, and vegetation is scarce on the thin, rocky soil. Perhaps *Pappogeomys castanops* has been extirpated in this area, owing to the destruction of its food.

A specimen of *P. c. clarkii* (KU 35764) from 11 mi. W Hda. San Miguel, on the northeastern slope of the Serranías del Burro is small, suggesting intergradation between *bullatus* and *P. c. clarkii.* Attempts to locate a contact between the two subspecies in the valley of the Río Grande in the area around Jiménez, 20 mi. S Villa Acuña, and Piedras Negras failed. Nasals in the population of *clarkii* from northeastern Coahuila are shorter than in more nearly typical *clarkii* from the west in Texas and Chihuahua (see account of *P. c. clarkii*) and agree with those of *bullatus,* perhaps indicating the influence of *bullatus* in this area.

Specimens from the type locality and near topotypes have longer tails and nasals and a greater zygomatic breadth than other samples of *bullatus.* In the series from 29 mi. N and 6 mi. E of Sabinas the hind feet and skull are slightly shorter, and in specimens from 3 mi. N Lampazos the skull is narrower and the palate shorter, than elsewhere in the range of the subspecies.

Specimens examined.—Total of 32, as follows: **Coahuila:** 10 mi. E Hda. La Mariposa, 2000 ft., 1; La Gacha (= La Concha), 1600 ft., 8; 8 mi. S and 8 mi. E Hda. La Mariposa, 1900 ft., 1; 29 mi. N and 6 mi. E Sabinas, 5; * 2 mi. S and 6½ mi. E Nava, 810 ft., 2; * 2 mi. S and 12 mi. E Nava, 800 ft., 1; * 3 mi. S and 12 mi. E Nava, 800 ft., 4; 9 mi. S and 11 mi. E Sabinas, 1050 ft., 2. **Nuevo León:** 3 mi. N Lampazos [= Lampazos de Naranjo], 4; 1 mi. N Vallecillo, 1000 ft., 1; * Vallecillo (20 mi. S Río Salado), 1000 ft., 3.

Pappogeomys castanops castanops (Baird)

Pseudostoma castanops Baird, in Report Stansbury's Expl. Surv. . . . Great Salt of Utah . . ., App. C, p. 313, June, 1852; Audubon and Bachman, The Quadrupeds of North America, 3:304, 1854; Lyon and Osgood, Bull., U. S. Nat. Mus., 62:72, January 15, 1909; Poole and Shantz, Bull. U. S. Nat. Mus., 178:364, April 9, 1942.

Geomys castanops, Le Conte, Proc. Acad. Nat. Sci. Philadelphia, 6:163, 1852; Baird, in Exp. and Surv. . . . 8(1):xxxix, July 14, 1858; Coues, Proc. Acad. Nat. Sci. Philadelphia, 13:133, June 1, 1875; Coues, Rept. Powell's Expl. Colorado River, p. 233, 1875; Coues and Yarrow, Rept. Wheeler's Expl. West 100th Merid., p. 111, 1876; Coues, *in* Coues and Allen, Monogr. N. Amer. Rodentia, p. 616, August, 1877 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:106, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:266, July 1, 1905 (part); Warren, The Mammals of Colorado, p. 90, 1910; Cary, N. Amer. Fauna, 33:130, August 17, 1911; Rinker, Jour. Mamm; 22:88; February 14, 1941; Warren, The Mammals of Colorado, p. 172, 1942; Hibbard, Trans. Kansas Acad. Sci., 47:74, 1944; Glass, Proc. Oklahoma Acad. Sci., for 1949:29, 1949.

[Cratogeomys] castanops, Elliot, Field Columb. Mus. Publ. 45, Zool. Ser., 2:220; April 10, 1901 (part); Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:315, 1904 (part).

[Cratogeomys castanops] castanops, Trouessart, Cat. Mamm., 1:573, 1898.

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 79:247, December 1, 1910 (part): Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part): Nelson and Goldman Proc. Biol. Soc. Washington, 47:136, June 13, 1934; Ellerman, Families and Genera of Living Rodents, 1:529, June 8, 1940; Hooper, Jour. Mamm., 29: 302, August 31, 1948; Cockrum, Univ. Kansas Publ., Mus. Nat. Hist., 7:249, August 25, 1952; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959.

Type.—Sex unknown, skull and skin; No. 4007/3861 U. S. National Museum; along prairie road to Bent's Fort, near the prairie town of Las Animas, Bent County, Colorado; 1845; obtained by Lieutenant Abert. The specimen was at first mounted; later it was made into a study skin.

Range.—Southwestern Colorado and northeastern New Mexico. See Fig. 3. Altitudinal range 3300 to 5000 feet.

Description.—Size medium for species; tail relatively short (averaging 39% of length of head and body in females); hind foot large. Averages and extremes of 12 females and seven males from southeastern Colorado are, respectively, as follows: Length of head and body, 191 (180-202), 207 (193-213); length of tail, 74 (60-84), 75 (67-95); length of hind foot, 36 (34-38), 37 (35-39).

Color: Upper parts in fresh winter pelage Mouse Gray basally and Ochraceous-Orange apically, suffused with Bay-tipped hairs imparting reddish-brown tone to back and top of head, sides pure Ochraceous-Orange; underparts Light Mouse Gray basally overlaid with Light Ochraceous-Buff. Upper parts in fresh summer pelage paler and brighter, Cinnamon-Buff to Ochraceous-Buff apically in "brighter" individuals.

Skull: Length medium for species, broad across zygomata, braincase, and squamosals; nasals short, usually emarginate posteriorly; rostrum narrow (averaging 47.3% of length of rostrum); maxillary tooth-row long; mastoid bullae inflated and large in relation to size of skull.

Averages and extremes of 12 females and seven males from southeastern Colorado are, respectively, as follows: Condylobasal length, 49.7 (48.7-51.0), 54.8 (52.0-56.4); zygomatic breadth, 31.6 (30.5-32.5), 37.0 (34.1-38.9); palatofrontal depth, 19.6 (19.1-19.9), 21.1 (20.5-22.3); length of palate, 34.4 (33.4-35.5), 38.3 (37.2-39.4); length of nasals, 17.9 (17.0-18.5), 20.7 (19.1-21.3); breadth of braincase, 29.1 (20.8-22.8), 23.2 (22.8-24.3); squamosal breadth, 27.8 (26.7-28.5), 30.8 (28.9-33.6); breadth of rostrum, 10.7 (10.2-11.2), 12.3 (11.8-12.9); length of rostrum, 21.7 (20.9-22.4), 24.7 (22.6-25.9); alveolar length of maxillary tooth-row, 9.8 (9.3-10.6), 10.2 (9.7-10.7).

Comparisons.—For comparisons with *P. c. perplanus*, *P. c. hirtus*, and *P. c. simulans*, see accounts of those subspecies.

Remarks.—The combination of features that distinguish *castanops* from other subspecies are relatively short tail, short skull with relatively deep cranium and broad braincase, and relatively long maxillary tooth-row. Some of these features are shared with *P. c. simulans* but *castanops* has a longer palate and relatively shorter tail. The two subspecies are separated geographically by the range of *P. c. perplanus*. *P. c. castanops* shows less resemblance to *perplanus* and *hirtus*. Smaller size in all dimensions, save breadth of braincase and maxillary tooth-row, and the especially shorter hind foot, skull and breadth across the zygomata readily separate *castanops* from *perplanus*. *P. c. hirtus* is remarkably smaller than *castanops* except in breadth across squamosals and rostrum; there is no overlap in condylobasal length, breadth across zygomata, palatofrontal depth, and length of palate and rostrum.

Specimens of *castanops* from southeastern Colorado are surprisingly uniform. Interrelationships of *castanops* with *perplanus* are expressed in two series. One of these, from Cimarron County, Oklahoma (see specimens examined of *P. c. perplanus* for exact localities), consists of intergrades between *castanops* and *perplanus*. Some measurements fall within the range of variation of typical *castanops* from southeastern Colorado, but most of the measurements fall within the range of variation of *perplanus;* for instance, an adult female (OSU 1101) from Black Mesa resembles *perplanus* and is larger than *castanops.* Another adult female (OSU 1108) from 2 mi. E and 7 mi. S Kenton has longer nasals and a broader braincase like *perplanus,* but otherwise is like *castanops.* The tail of the Cimarron County specimens averages shorter relative to the length of head and body than in typical samples of either *castanops* or *perplanus.* The same is true in the second series, also referred to *perplanus,* from 2 mi. W and 1 mi. S Conchos Dam, New Mexico, that shows intergradation between *castanops* and *perplanus,* and that is discussed in the account of *perplanus.*

There is no evidence of direct intergradation between *castanops* and *hirtus;* intervening high plateaus and mountainous country in central New Mexico, from which *P. castanops* is absent, separate the geographic ranges, as now known, of the two subspecies.

P. c. castanops is the northermost subspecies of the species and the genus. It inhabits the High Plains of the Short Grass Prairie Association of southeastern Colorado and adjacent areas in New Mexico, Oklahoma, and possibly southwestern Kansas. Rinker (1941:88) and Hibbard (1944:74) report two skulls of *P. castanops* of Recent, or more correctly of sub-Recent, age from Meade County, Kansas. One was found in a fresh mound of earth thrown up by *Geomys bursarius.* Extensive collecting by Rinker and Hibbard failed to provide evidence for the present occurrence of *P. castanops* in Kansas, nor were the efforts of Cockrum (1952:279) or other workers successful in obtaining specimens of this subspecies in southwestern Kansas. It is my notion that *P. castanops* is presently excluded from this area by competition with *Geomys bursarius.* Areas having 18 or more inches of annual precipitation are more favorable for *Geomys* than *Pappogeomys* whereas the reverse is true for areas having less than 18 inches. The precipitation in southwestern Kansas fluctuates around 18 inches; it is more in the present cycle. Alternating cycles of precipitation may be responsible for the presence of first one and then the other genus in southwestern Kansas.

Specimens examined.—Total of 46, as follows: **Colorado:** *Pueblo County:* Arkansas River, mesa about 26 mi. below Canyon City, 1 (MVZ); 3 mi. W Pueblo 4900 ft., 1 (WC). *Crowley County:* Olney (= Olney Springs), 2 (USNM). *Otero County:* 4 mi. W Rocky Ford, 3; 12 mi. E La Junta, 2. *Bent County:* Las Animas (topotypes), 5 (USNM). *Prowers County:* Lamar, mesa 1½ mi. S town . . . at Willow Springs Arroyo, 1 (WC). *Las Animas County:* Irwing's Ranch (T-39S, R.52W), 5000 ft., 7 (WC). *Baca County:* Gaum's Ranch (NW corner Baca Co.), 2 (WC); Bear Creek bottom, Springfield, 6 (WC); Johnson's Ranch, Monon, 2 (WC); Ragnier, 2 (DM); * Furnace Canyon, 9 (DM). **New Mexico:** *Colfax County:* Chico (= Chico Springs), 2 (USNM). *Union County:* Clayton, 1 (USNM).

Pappogeomys castanops clarkii (Baird)

Geomys clarkii Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:322, April, 1855; Baird, Mammals, in Repts. Expl. and Surv. . . ., 8(1)xxxix, p. 383, July 14, 1858 (part); Baird, Mammals of the Boundary, U. S. Mexican Bound. Surv., p. 41, 1859; Gerrard, Cat. Bones British Mus., p. 222, 1862; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:72, January 15, 1909; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 9, 1942.

Geomys castanops, Coues, Rept. Powell's Expl. Colorado River, p. 233, 1875 (*G. clarkii* allocated as a synonym of *Geomys castanops*); Coues, Proc. Acad. Nat. Sci. Philadelphia, p. 133, 1875; Coues, *in* Coues and Allen, Monogr. N. Amer. Rodentia, p. 616, August, 1877 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, January 31, 1895 (part); Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Cratogeomys castanops clarkii, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, June 13, 1934 (part); Hooper, Jour. Mamm., 29:302, August, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959.

Cratogeomys castanops lacrimalis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, June 13, 1934 (part); Borell and Bryant, Univ. California Publ. Zool., 48:22, August 7, 1942; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Cratogeomys castanops convexus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:142, June 13, 1934, type from 7 mi. E Las Vacas (= Villa Acuña), Coahuila; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Russell and Baker, Univ. Kansas Publ., Mus. Nat. Hist., 7:595, March 15, 1955; Baker, Univ. Kansas Publ., Mus. Nat. Hist., 9:226, June 15, 1956; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959.

Type.—Female, adult, skull and skin, No. 6/1624 U. S. National Museum; Presidio del Norte, at or near the present town of Ojinaga, on the Río Grande, Chihuahua; date unknown; obtained by J. H. Clark, original number unknown.

Range.—Valley of Río Grande from Presidio on both sides of river southeastward on the Texas side to Boquillas, and eastward on Coahuilan side to Villa Acuña. See Fig. 3. Altitudinal range from about 950 feet at Villa Acuña to 2450 feet at Ojinaga, Chihuahua.

Description.—Size large for species; tail relatively long (averaging 45% of length of head and body in topotypes and specimens from near Presidio, Texas); hind foot large. Averages and extremes of 13 females and six miles from the Rio Grande Valley of Texas (Boquillas NW to Presidio and Ojinaga) are, respectively, as follows: Length of head and body, 186 (173-202), 204 (187-228); length of tail, 80 (68-92), 90 (77-101); length of hind foot, 37 (36-39), 39 (37-40). Three females and two males from near Ojinaga weighed, respectively, 260, 252, 225, 297, and 275 grams.

Color: Upper parts Mouse Gray basally and Ochraceous-Buff (fresh summer pelage) to Orange-Buff (fresh winter pelage) apically, admixed with Bay-tipped hairs on top of head and back; pure Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with Light Ochraceous-Buff or Pale Ochraceous-Salmon in brighter specimens; hind feet whitish.

Skull: Size medium to large for species; zygomata widely spreading; palate long; nasals relatively short; squamosals and braincase broad; rostrum broad and long.

Averages and extremes of 13 females and seven males from the Río Grande Valley (Boquillas NW to Presidio and Ojinaga) are, respectively, as follows: Condylobasal length, 49.6 (48.1-50.8), 54.8 (53.6-57.0); zygomatic breadth, 32.1 (30.7-34.7), 37.1 (36.4-37.6); palatofrontal depth, 19.6 (19.0-20.1), 21.2 (20.6-22.0); length of palate, 33.5 (32.0-34.6), 37.0 (36.5-37.7); length of nasals, 17.6 (16.6-18.5), 19.8 (19.3-21.6); breadth of braincase, 21.3 (20.5-22.4), 23.4 (22.0-26.8); squamosal breadth, 29.4 (27.7-31.0), 32.6 (31.1-35.5); breadth of rostrum, 11.5 (10.5-12.5), 13.3 (12.7-14.5); length of rostrum, 21.3 (20.3-22.3), 24.2 (23.5-25.0); alveolar length of maxillary tooth-row, 9.5 (9.0-10.0), 10.2 (9.6-10.5).

Comparisons.—For comparisons with *P. c. pratensis, P. c. torridus, P. c. hirtus, P. c. sordidulus,* and *P. c. consitus,* see accounts of those subspecies. From *P. c. angusticeps, P. c. clarkii* differs as follows: Larger, tail relatively longer (43 *versus* 40 percent of length of head and body); hind foot longer; upper parts paler, more buffy and less ochraceous; underparts paler, more buffy and less pinkish; skull averaging larger in all dimensions, but especially in condylobasal length, palatofrontal depth, length of palate, and zygomatic breadth.

Remarks.—Coues (1875:235) demonstrated that *Geomys clarkii,* described by Baird as a species, and *Geomys* [=*Pappageomys*] *castanops* were conspecific. Subsequently, *clarkii* was allocated as a synonym of *castanops,* until Nelson and Goldman (1934:140) revived it as a subspecies of *Cratogeomys castanops. P. c. clarkii* was known to Nelson and Goldman (*loc. cit.*) by the holotype, and a skull only of an adult male paratype (USNM 1623) that formed the basis of the original description, and an adult female from near the Río Grande, opposite Samuels, Texas, in Coahuila. Owing to the paucity of specimens, especially topotypes, the diagnosis provided by the authors mentioned was incomplete. Nine topotypes have been available to me, and make possible a more accurate appraisal of individual variation in *clarkii.* Deficiencies in the original description and in the description by Nelson and Goldman (*loc. cit.*) are corrected in the new description above.

Specimens from Presidio, directly across the Rio Grande from Ojinaga, average less in length of body and condylobasal length than do topotypes, but the differences are slight, and, in my opinion, have no taxonomic significance. Evidently, here as elsewhere along its course, the Rio Grande from time to time permits the movement of these rodents from one side to the other. Specimens of *Geomys arenarius arenarius* from the two sides of the Río Grande in the El Paso region are indistinguishable. The colony of *clarkii* in the Ojinaga valley was likely formed by immigrants from the Texas side of the Rio Grande, probably in Recent times.

Habitat characterized by deep sandy soils, found mainly in the valley of the Rio Grande, is continuous on the Texas side of the river from Presidio southeast to Boquillas in the Big Bend area. Pocket gophers from the Big Bend in Brewster County agree with topotypes of *clarkii* and specimens from within a radius of seven miles of Presidio, except for longer head and body (194 *versus* 182 mm.), relatively shorter tail (40 *versus* 45% of length of head and body), and slightly broader skull (zygomatic breadth, 32.5 *versus* 31.9 mm.; breadth of braincase, 21.8 *versus* 21.0; and squamosal breadth, 29.8 *versus* 29.1). In the features just mentioned, the Big Bend series resembles *Pappogeomys castanops sordidulus* of the Llano de Ocampo in Coahuila, directly south of the Big Bend region, and the resemblance may reflect gene flow between the two. But, taking into account all characters, the Big Bend gophers are best allocated to *P. c. clarkii.* Previously, Nelson and Goldman (1934:137) and Borell and Bryant (1942:22) referred all specimens from the Big Bend to *Cratogeomys castanops lacrimalis* (synonomized with *P. c. perplanus* in my study). Not only does the geographic range of *P. c. pratensis,* newly described beyond, occur between the Big Bend and the geographic range ascribed to *P. c. perplanus,* but the skull of *perplanus* is significantly larger (see especially condylobasal length and length of palate and nasals). Judging from records of occurrence, *clarkii* in the Big Bend area, as at Presidio and Ojinaga, is restricted to the valley of the Rio Grande, and does not occur in the adjacent desert uplands. All specimens have been taken within 10 miles of the river channel.

Nelson and Goldman (1934:142) based their original description of *Pappogeomys castanops convexus* on a single adult female obtained from 7 mi. E Las Vacas (= Villa Acuña), in the Río Grande Valley (below the Big Bend), Coahuila. According to them *convexus* differed from *clarkii* in paler underparts, longer and broader (more massive) skull having the longitudinal dorsal profile more strongly and evenly convex, broader rostrum, longer nasals, more inflated mastoids, more excavated supraoccipital region, and more depressed lambdoid crest (near mid-line). In *P. castanops,* considering the additional specimens from the Río Grande Valley of northern Coahuila, including five near topotypes, I find that from *clarkii* of the Presidio-Ojinaga region, *convexus* differs only in smaller size, relatively longer tail (50 as opposed to 45% of length of head and body), shorter nasals (16.6 as opposed to 17.8), and narrowness across squamosals and braincase (squamosal breadth

28.6 *versus* 29.1; breadth of braincase 20.4 *versus* 21.0). Except for length of nasals, none of these differences is of taxonomic significance. Moreover, nasal length varies in a cline, increasing gradually from southeast to northwest along the Rio Grande. For example, length of nasals averages 16.6 in the sample from northern Coahuila, 17.2 in the Big Bend, 17.6 at Presidio, and 17.9 at Ojinaga. I find no characters that distinguish *P. c. convexus* from *clarkii* and therefore arrange *convexus* as a synonym of the older name *clarkii*.

The skull of a female from 11 mi. W Hacienda San Miguel, almost an adult, is considerably smaller than the other specimens of *clarkii* of comparable age, and may show intergradation with the smaller *Pappogeomys castanops bullatus*. Eleven miles west of Hacienda San Miguel is near the head of the Cañon de la Babia that opens out on the lowlands to the south occupied by *bullatus*.

Specimens examined.—Total of 55, from Texas and México, as follows:

Texas: *Presidio County:* 3 mi. NW Presidio, 2400 ft., 2 (AMNH); * Presidio, 8; * 1 mi. S and 2 mi. E Presidio, 2400 ft., 1; * 1 mi. S and 4 mi. E Presidio, 2400 ft., 2; * 3 mi. S and 6 mi. E Presidio, 2400 ft., 2; * 7 mi. ESE Presidio, 2 (AMNH). *Brewster County:* Lajitas, 2200 ft., 4; Boquillas, 2 (USNM); * 1 mi. SW Boquillas, 1800 ft., 1 (AMNH); * Rio Grande, 1 mi. SW Boquillas, 1850 ft., 1 (MVZ); mouth of Santa Elena Canyon, 2100 ft., Big Bend National Park, 1 (TCWC); * Castalon, Big Bend National Park, 1 (UMMZ); * Johnson's Ranch, 2060 ft., on Big Bend of Rio Grande, 2 (UMMZ); * Big Bend of Rio Grande (= Johnson's Ranch), 2000 ft., 3 (MVZ).

Chihuahua: 2 mi. WNW Ojinaga, 2400 ft., 1 (AMNH); * 1½ mi. WNW Ojinaga, 2400 ft., 1 (AMNH); * Presidio del Norte (= Ojinaga), 1 (USNM); Ojinaga, 2400 ft., 5 (3 AMNH, 2 KU); * 1½ mi. SE Ojinaga, 2500 ft., 1 (AMNH).

Coahuila: Río Grande, 17 mi. S Dryden, Texas, *in* Coahuila, 6; Río Grande, opposite Samuels, Texas, *in* Coahuila, 1 (USNM); Villa Acuña, about 950 ft., 5; Cañon del Conchino, 16 mi. N and 21 mi. E Piedro Blanco, 3200 ft., 1; 11 mi. W Hda. San Miguel (eastern foothills of Sierra de Carmen), 2200 ft., 1.

Pappogeomys castanops excelsus (Nelson and Goldman)

Cratogeomys castanops excelsus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:143, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:365, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:603, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:226, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959 (part); Baker and Greer, Michigan State Univ. Publ. Museum, Biol. Ser., 2:96, August 27, 1962 (part).

Type.—Male, adult, skull and skin; No. 246533 U. S. National Museum; San Pedro [= San Pedro de las Colonias], 10 mi. W Laguna de Mayrán, Coahuila, Republic of México; March 28, 1926; obtained by E. A. Goldman, original number 23561.

Range.—Arid Bolsón de Mapimí in southwestern Coahuila and northeastern Durango. See Fig. 3. Altitudinal range 3500 to 3800 feet.

Description.—Large for species; tail relatively long (averaging 44% of length of head and body); hind foot of medium length. Average and extreme external measurements of 12 females and eight males from the Balsón de Mapimí (specimens labeled with reference to Acatita, Torreón, San Pedro, Nuevo Mundo, and Americanos) are, respectively, as follows: Length of head and body, 197 (184-209), 213 (201-226); length of tail, 86 (77-101), 87 (71-97); length of hind foot, 37 (35-40), 39 (36-41).

Color: Upper parts Mouse Gray basally, Pale Yellow-Orange apically, some hairs on back faintly tipped with brownish, pure Pale Yellow-Orange on sides and face; underparts Light Mouse Gray overlaid with whitish, tinged with Pale Ochraceous-Buff along mid-ventral line; hind feet whitish.

Skull: Large; zygomata widely spreading; palate and nasals long; broad across braincase and squamosals; rostrum broad and long; maxillary tooth-row moderately long.

Average and extreme cranial measurements of 12 females and eight males from the Bolsón de Mapimí (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 50.6 (49.1-51.6), 54.0 (53.0-55.3); zygomatic breadth, 33.3 (31.4-34.9), 36.7 (35.3-38.9); length of palate, 34.7 (33.4-36.1), 37.6 (36.2-40.1); length of nasals, 18.3 (17.0-20.1), 20.0 (18.9-22.4); breadth of braincase, 22.4 (19.8-24.1), 23.1 (20.9-26.0); squamosal breadth, 30.1 (28.4-31.7), 32.2 (30.5-36.0); breadth of rostrum, 11.3 (10.3-12.3), 12.7 (11.3-14.7); length of rostrum, 21.3 (20.0-22.4), 23.4 (22.3-26.2); alveolar length of maxillary tooth-row, 9.6 (8.9-10.2), 10.1 (9.7-10.6).

Comparisons.—For comparisons with *P. c. jucundus, P. c. sordidulus, P. c. perexiguus, P. c. surculus,* and *P. c. goldmani,* see accounts of those subspecies.

From *Pappogeomys castanops subsimus, P. c. excelsus* differs, as follows: Hind foot shorter; upper parts paler, more buffy and less yellowish-brown; underparts paler, more whitish and less ochraceous-buff; skull decidedly shorter; palatofrontal depth less; palate, rostrum, and maxillary tooth-row shorter.

Remarks.—This large, pale subspecies inhabits the interior basin formerly occupied by the Laguna de Mayrán in the late Pleistocene. As the lake receded in the post-Wisconsin, large areas of deep, light-colored sands were deposited. *P. c. excelsus* occurs mostly in these well-developed sandy soils, and the diluted pigmentation of the pelage closely matches the color of the soil.

P. c. excelsus is another of the large subspecies that occurs in the desert basins of northeastern México. The combination of smaller size, shorter tail and hind foot, paler dorsum and especially paler venter, and decidedly shallower skull distinguishes *excelsus* from its closest relative, *Pappogeomys castanops jucundus.* High ridges of the Sierra de la Madera and Sierra de San Marcus separate the geographic ranges of the two subspecies at present, but low passes between the Bolsón de Mapimí and the Cuatro Ciénegas Basin may have permitted gene flow when more favorable conditions prevailed.

P. c. excelsus resembles *Pappogeomys castanops subsimus* in color but differs significantly in shorter and narrower skull. Ranges of the two subspecies meet along the periphery of the Bolsón de

Mapimí and the highly dissected uplands to the southeast and east. Intergradation between *excelsus* and *subsimus* can not be demonstrated in any of the specimens available to me, but can be expected in habitat intermediate between the deep sands of the Bolsón and the less well-developed soils of the uplands. An adult female from 3 mi. N and 5 mi. W La Rosa is clearly referable to *excelsus*, although it was taken from a point less than 20 miles from the type locality of *subsimus* at Jaral. The habitat of the female was deep sand in a narrow valley that connects to the west with the eastern part of the Bolsón de Mapimí.

All along the western and northern border of its geographic range, *excelsus* of the *excelsus* group interdigitates, and in places may overlap, the ranges of two of the small subspecies of the *subnubilus* group, *Pappogeomys castanops surculus* and *Pappogeomys castanops perexiguus.* Both *surculus* and *perexiguus* are remarkably smaller than *excelsus*, and there is no indication that *excelsus* interbreeds with them. Certainly they do not inhabit the same local habitat. *P. c. excelsus* seems to prefer the deep sandy soils of the central basin and *perexiguus* occurs in the thinner soils of the uplands. West of the basin in northeastern Durango the plain becomes progressively higher, and *excelsus* gives way abruptly to *surculus.*

Intergradation with *Pappogeomys castanops goldmani* occurs to the southwest in the valley of the Río Aquanaval (for details, see account of *P. c. goldmani*).

Specimens of *excelsus* from 4 mi. N Acatita in the northern part of its range are slightly paler, have a longer hind foot (37 *versus* 36) and nasals (18.7 *versus* 17.8), and are broader across the squamosals (30.8 *versus* 29.8) and braincase (23.1 compared with 21.9) than specimens from 2 mi. E Torreón in the southern part of the range.

Specimens examined.—Total of 26, as follows: **Durango:** 4 mi. WSW Lerdo, 3800 ft., 2 (1 MSU, 1 KU). **Coahuila:** 8 mi. E and 2 mi. S Americanos, 3700 ft., 3; 4 mi. N Acatita, 3600 ft., 8; Nuevo Mundo, 33 mi. NW Torreón, 2; San Pedro, 2 (USNM); *1 mi. SW San Pedro de las Colonias, 3700 ft., 4; 11 mi. N and 10 mi. W San Lorenzo, 3700 ft., 2; 3 mi. N and 5 mi. W La Rosa, 1; 2 mi. E Torreón, 3700 ft., 12. Solid triangle = Tlahualilo (Nelson and Goldman, 1934:144).

Pappogeomys castanops goldmani (Merriam)

Cratogeomys castanops goldmani Merriam, N. Amer. Fauna, 8:160, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:266, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:73, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924; Nelson and Goldman, Proc. Biol. Soc. Washington, 47:145, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:365, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Russell and Baker, Univ. Kansas Publ. Mus. Nat.

Hist., 7:606, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:227, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959; Baker and Greer, Michigan State Univ. Publ. Mus., Biol. Ser., 2:96, August 27, 1962.

[*Cratogeomys castanops*] *goldmani*, Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool Ser., 4:316, 1904.

Cratogeomys castanops consitus, Baker and Greer, Michigan State Univ., Publ. Museum, Biol. Ser., 2:96, August 27, 1962 (part).

Type.—Female, young adult, skull and skin; No. 57965 U. S. National Museum; Canitas, Zacatecas; December 24, 1893; obtained by Edward A. Goldman, original number 286.

Range.—High and arid plateau of eastern Durango, southwestern Coahuila, and central Zacatecas, mainly in upper drainages of Río Aguanaval and Río Nazas and their tributaries. See map, Fig. 3. Altitudinal range 4600 to approximately 7000 feet.

Description.—Large for species; tail relatively short (averaging 38% of length of head and body in females); hind foot short. Average and extreme external measurements for six females and three males from the drainage of the Río Aguanaval and Río Nazas are, respectively, as follows: Length of head and body, 189 (178-199), 207 (190-225); length of tail, 71 (55-90), 72 (65-78); length of hind foot, 34 (31-36), 37 (36-38). An adult female and male from 4 mi. NNE Boquilla, Durango, weighed 233 and 380 grams, respectively.

Color: Upper parts Mouse Gray basally and from Ochraceous-Buff to Orange-Buff apically, mixed with Bay-tipped hairs on back, but pure Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with Light Ochraceous-Buff; hind feet whitish.

Skull: Size medium for species; zygomata moderately spreading; palate, nasals, and rostrum long; moderately broad across squamosals.

Average and extreme cranial measurements for six females and three males, respectively, from the drainage of the Río Aguanaval and Río Nazas are as follows: Condylobasal length, 48.4 (47.9-49.0), 54.2 (52.7-56.7); zygomatic breadth, 30.8 (29.1-31.9), 37.7 (36.7-39.4); palatofrontal depth, 18.9 (18.2-19.6), 22.1 (21.4-23.1); length of palate, 32.7 (32.3-33.7), 37.7 (36.2-40.2); length of nasals, 17.7 (16.6-18.9), 20.4 (19.5-22.1); breadth of braincase, 21.0 (19.8-21.7), 23.7 (23.2-24.1); squamosal breadth, 28.2 (27.0-29.3), 32.3 (31.6-33.4); breadth of rostrum, 10.7 (9.8-11.4), 12.9 (12.2-13.3); length of rostrum, 20.7 (19.7-21.4), 24.1 (23.3-24.5); alveolar length of maxillary toothrow, 9.2 (8.9-9.5), 9.8 (9.2-10.4).

Comparisons.—For comparisons with *P. c. surculus, P. c. subnubilus,* and *P. c. rubellus,* see accounts of those subspecies.

From *Pappogeomys castanops excelsus, P. c. goldmani* differs as follows: Slightly smaller; tail relatively shorter (averaging 38 *versus* 44% of length of head and body); hind foot shorter; upper parts brighter, more orange-buff and less pale yellowish-buff; underparts darker, more ochraceous and less whitish; skull averaging shorter in all dimensions, especially in condylobasal length, zygomatic breadth, length of palate, and breadth across braincase and squamosals.

Remarks.—Since its description by Merriam in 1895, *P. c. goldmani* has been known only from the five original specimens. Additional material now available from several localities in northeastern Durango and extreme southwestern Coahuila make possible a more reliable estimate of the characteristics of this subspecies. *P. c. goldmani* is characterized by large size externally, relatively short tail and hind foot, and medium-sized skull that is relatively broad across zygomata. The rostrum is long and relatively narrow, and the maxillary tooth-row and nasals are long.

P. c. goldmani occurs sympatrically with *Pappogeomys castanops surculus,* one of the group of small subspecies that share a contiguous range with the exceptionally large subspecies of the *excelsus*-group. In most places *goldmani* and *surculus* do not occupy the same local habitat, but both have been taken from the canyon floor of the Río Nazas, 6 mi. NW Rodeo, Durango. All specimens from 6 mi. W Rodeo are referable to *goldmani* except for two adult females (KU 62472 and 62475). There is no suggestion of interbreeding in any of the samples that have been studied. Niche exclusion seems effectively to segregate populations of the two subspecies in the area of sympatry, with *goldmani* occurring most commonly in the deep, well-developed alluvial soils in the valleys of the Río Nazas and Río Aguanaval, and their tributaries, and *surculus* occurring most commonly in the thin, poorly-developed upland soils of the desert flats. However, in places, such as at the aforementioned locality 6 mi. NW Rodeo, the ranges of the two are in close proximity, and their populations may mingle. Probably the two compete in such situations, and their occurrence in the same local habitat is only temporary, with one or the other becoming dominant to the exclusion of the other.

In allopatric parts of their ranges, niche exclusion is of no consequence, and populations of both *goldmani* and *surculus* occur in all available habitats, both upland and lowland. For instance, on the high plateau of east-central Durango and central Zacatecas, where *goldmani* occurs alone, samples have been taken on the desert uplands at Hda. Atotonilco and the type locality.

Specimens from the valley of the Río Aguanaval, 1 mi. S Jimulco, and from the west foot of Pico de Jimulco, Coahuila, are intergrades between *goldmani* and *Pappogeomys castanops excelsus.* In color of the dorsum these specimens closely resemble *excelsus,* and, therefore, they are decidedly paler than typical *goldmani.* The specimens are intermediate between *goldmani* and *excelsus* in most cranial features. The sample is referred to *goldmani.* Intergradation between *goldmani* and *Pappogeomys castanops rubellus* is reflected in specimens from Villa de Cos in southeastern Zacatecas (for a discussion, see account of *P. c. rubellus*).

Specimens examined.—Total 24, as follows: **Durango:** 4 mi. NNE Boquilla, 6300 ft., 3 (MSU); Río Nazas, 6 mi. NW Rodeo, 4200 ft., 8 (1 in alc.); *6 mi. NW Rodeo, 4200 ft., 2; Hacienda de Atotonilco, 6680 ft., 2. **Coahuila:** Valley Río Aguanaval, 1 mi. S Jimulco, 4600 ft., 4; *W-foot Pico de Jimulco, 4600 ft., 1. **Zacatecas:** Canitas, 4 (USNM).

Pappogeomys castanops hirtus (Nelson and Goldman)

Cratogeomys castanops hirtus, Nelson and Goldman, Proc. Biol. Soc. Washington, 47-138, June 14, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:365, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, January 31, 1895 (part).

Cratogeomys castanops [*castanops*], Bailey, N. Amer. Fauna, 53:242, March 1, 1932 (part).

[*Cratogeomys castanops*] *castanops,* Trouessart, Cat. Mamm., 1:573, 1898 (part).

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Cratogeomys castanops lacrimalis, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, June 14, 1934 (part); Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955 (part); Hall and Kelson. The Mammals of North America, 1:466, March 31, 1959 (part).

Type.—Male, adult, skull and skin, No. 58358 U. S. National Museum; Albuquerque, Bernalillo Co., New Mexico; January 17, 1894; obtained by J. A. Loring, original number 1558.

Range.—Desert plains east of Rio Grande and west of north-south mountain chain composed of the Sandia, Manzano, Oscura, and San Andres mountains, from Albuquerque, New Mexico, southward through the Jornado del Muerto to El Paso, Texas. See Fig. 3. From 3700 to 7000 feet elevation.

Description.—Small for species; tail moderately long; hind foot small. Averages and extremes of seven females and measurements of two males from upper Rio Grande Valley (El Paso north to Albuquerque) are, respectively, as follows: Length of head and body, 185 (175-207), 184 and 205; length of tail, 78 (70-92), 81 and 78; length of hind foot, 35 (33-38), 35 and 37. An adult female from South Valley, Albuquerque, weighed 185.5 grams.

Color: Ground color of dorsum dark reddish-brown, hairs near Cinnamon-Buff apically, heavily overlaid with black-tipped hairs on back and top of head giving pelage a darker appearance, less blackish and more pure Cinnamon-Buff on sides, hairs Dark Mouse Gray basally; hairs of underparts Light Mouse Gray basally and varying from Pinkish Buff to Cinnamon-Buff apically; hind feet whitish.

Skull: Small to moderate for species; skull shallow; nasals relatively long; rostrum relatively broad (averaging 22.7% of condylobasal length in females); maxillary tooth-row short.

Averages and extremes of seven females and the measurements of two males from the upper Rio Grande valley (see external measurements) are, respectively, as follows: Condylobasal length, 48.0 (47.3-49.7), 50.3 and 51.7; zygomatic breadth, 30.5 (29.2-32.2), 34.1 and 32.6; palatofrontal depth, 18.9 (18.4-19.4), 19.8 and 19.6; length of palate, 32.4 (31.6-33.1), 33.6 and 34.7; length of nasals, 17.8 (16.7-17.6), 17.9 and 20.6; breadth of braincase, 20.2 (19.4-21.4), 21.1 and 20.6; squamosal breadth, 27.8 (27.1-29.1), 29.5 and 30.0; breadth of rostrum, 10.9 (10.0-11.2), 11.0 and 11.3; length of rostrum, 20.9 (20.0-22.0), 21.9 and 21.9; alveolar length of maxillary tooth-row, 9.0 (8.5-9.8), 9.1 and 10.2.

Comparisons.—For differences from *P. c. pratensis, P. c. torridus, P. c. consitus,* and *P. c. parviceps,* see accounts of those subspecies.

From *P. c. castanops, P. c. hirtus* differs as follows: Tail relatively longer (averaging 43 *versus* 39% of length of head and body); hind foot shorter; upper parts darker, more brownish and less yellowish-buff; skull shorter (especially condylobasal length and palate) and narrower (especially across zygomata and braincase); rostrum shorter and relatively broader; maxillary tooth-row shorter.

From specimens of *P. c. perplanus* from upper Pecos River Valley, *P. c. hirtus* differs as follows: Hind foot shorter; upper parts darker, more dark brownish and less yellowish-buff; skull averaging smaller in all dimensions, especially condylobasal length, length of palate, and breadth across zygomata, braincase and squamosals, and with no overlap in length of palate; rostrum narrower but broader relative to length of skull; maxillary tooth-row slightly shorter.

From *P. c. clarkii, P. c. hirtus* differs, as follows: Tail and hind foot shorter; upper parts darker, more reddish brown and less pale yellowish-buff; skull averaging smaller in all dimensions save length of nasals; especially smaller in condylobasal length and breadth across zygomata and squamosals.

Remarks.—Topotypes of *P. c. hirtus* are few, and, consequently, diagnosis of its variation remains incomplete. Nelson and Goldman (1934:138) had only the holotype and two paratypes, collected in 1898 and first allocated to *Cratogeomys castanops* [*castanops*] by Bailey (1932:242), upon which to base their description of *hirtus.* James S. Findley, of the Museum of Southwestern Biology in Albuquerque, informs me (*in. litt.*) that pocket gophers of the genus *Thomomys* are common today on the desert plains and in the valley of the Rio Grande around Albuquerque, but that *Pappageomys castanops* is rare. Efforts by Findley and his students to secure topotypes have provided only one additional specimen, an adult female obtained in 1962 by C. J. Jones in South Valley, Albuquerque. If *hirtus* was ever common at the type locality, it evidently has since been largely replaced by *Thomomys.* Populations from eastern Bernalillo County, east of the Sandia Mountains, clearly are not referable to *hirtus* (see remarks in the account of *P. c. parviceps*).

P. c. hirtus does not range north of Albuquerque, and no specimen of *P. castanops* has been taken west of the Rio Grande in New

Mexico, although the genus *Thomomys* and, to the south, *Geomys arenarius,* occur abundantly. South of Albuquerque and beyond the Los Pinos Mountains lies the Jornado del Muerto, an extremely arid desert plain bordered to the west by the Rio Grande and to the east by a range of high mountains, including from north to south the Sierra Oscura, San Andres and Organ mountains. *P. c. hirtus* is unknown from the desert flats of the Jornado, but specimens from Rhodes Pass in the San Andres Mountains and from Parker Lake just east of San Augustin Pass between the San Andres and Organ mountains are best referred to *hirtus.* Also, a specimen from El Paso, Texas, is referable to *hirtus* although larger samples from El Paso and Parker Lake may show that the populations from these areas are referable instead to *Pappogeomys castanops torridus.*

Specimens examined.—Total of 12, as follows: New Mexico: *Bernalillo County:* Albuquerque, 2 (USNM); South Valley, Albuquerque, 1 (NM). *Socorro County:* Rhodes Pass, San Andres Mts., 7000 ft., 4 (PA). *Dona Ana County:* Parker Lake, east of Organ Mts., 4 (USNM). Texas: *El Paso County:* Municipal Golf Course, El Paso, 1 (MVZ).

Pappogeomys castanops jucundus (Russell and Baker)

Cratogeomys castanops jucundus Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:599, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:227, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Cratogeomys castanops tamulipensis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:141, June 13, 1934 (part); Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955 (part).

Type.—Female, adult, skull and skin; No. 56603 University of Kansas Museum of Natural History; Hermanas, 1205 ft., Coahuila; December 5, 1953; obtained by Robert W. Dickerman, original number 2051.

Range.—Upper drainage of Río Salado in east-central Coahuila. See Fig. 3. Altitudinal range 1200 to about 2300 feet.

Description.—Large for species; tail relatively short (averaging 40% of length of head and body); hind foot long. Average and extreme external measurements of eight females and the measurements of one male, respectively, from the upper valley of the Río Salado (specimens labeled with reference to Hermanas, Monclova, and Cuatro Ciénegas) are as follows: Length of head and body, 199 (186-212), 231; length of tail, 79 (67-90), 80; length of hind foot, 38 (35-42), 42.

Color: Upper parts Dark Mouse Gray basally, Ochraceous-Buff to Antimony-Yellow apically, mixed with Bay-tipped hairs on back, but pure yellowish-brown on sides and face; underparts Light Mouse Gray overlaid with Pale Ochraceous-Buff; hind feet whitish.

Skull: Large for species; zygomata widely spreading; palate and nasals moedartely long; broad across braincase and squamosals; rostrum broad and long; maxillary tooth-row long.

Average of extreme cranial measurements of eight females and the measurements of one male (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 50.2 (49.2-51.8), 56.9; zygomatic breadth, 33.2 (31.6-34.4), 38.7; palatofrontal depth, 20.0 (18.9-20.8), 22.4; length of palate, 34.2 (33.1-35.0), 40.1; length of nasals, 17.7 (16.2-18.6), 21.0; breadth of braincase, 22.6 (22.0-23.2), 24.1; squamosal breadth, 29.9 (29.0-31.4), 32.3; breadth of rostrum, 11.4 (10.9-11.6), 13.4; length of rostrum, 21.2 (20.4-21.9), 25.0; alveolar length of maxillary tooth-row, 9.6 (9.1-10.3), 9.9.

Comparisons.—For comparison with *P. c. sordidulus, P. c. subsimus,* and *P. c. ustulatus,* see accounts of those subspecies.

From *Pappogeomys castanops excelsus, P. c. jucundus* differs as follows: Tail relatively shorter (40 *versus* 44% of length of head and body); hind foot shorter; upper parts and underparts decidedly darker, more ochraceous and less pale buffy; skull deeper, nasals slightly shorter.

From *Pappogeomys castanops bullatus, P. c. jucundus* differs as follows: Larger; tail relatively shorter (40 *versus* 43% length of head and body); upper parts less bright, more yellowish-brown and less reddish-brown; underparts darker, more ochraceous and less buffy; skull averaging larger in all dimensions, except for length of maxillary tooth-row, and without overlap in condylobasal length, zygomatic breadth, length of palate, breadth of braincase, and squamosal breadth.

Remarks.—*P. c. jucundus* is distinguished from the other large subspecies by the combination of relatively short tail, yellowish-brown dorsum, and short skull. *P. c. jucundus* is decidedly larger in both cranial and external dimensions than *P. c. bullatus* and *P. c. tamaulipensis.*

Among the large subspecies, *juncundus* most closely resmbles *P. c. excelsus.* The two subspecies agree in size in most cranial dimensions, but *jucundus* is distinctly darker. The ranges of *jucundus* and *excelsus* are apparently separated by the Sierra de la Madera and Sierra de San Marcos; however, limited contact may occur in the lower passes. Usually the canyons that dissect the mountains of this area are narrow and have thin, rock soils. For example, in the canyon north of Cuatro Ciénegas I found only *Thomomys* living in the thin soils of the canyon floor, although *P. c. jucundus* occurred in the balsón to the south and *P. c. sordidulus* on the llano to the north. In this case, *jucundus* and *sordidulus* seem to be effectively isolated by the intervening mountains.

On the other hand, the series of small basins along the course of the Río Salado from its headwaters near Cuatro Ciénegas eastward to San Buenaventura are connected by wide canyons that offer continuous habitat to these gophers.

Nelson and Golman (1934:141) referred two specimens, a subadult and young female, from Monclova, Coahuila, to *P. c. tamau-*

lipensis. Comparison of these specimens and others from 2 mi. N and 1 mi. E Monclova and from 5 mi. N and 2 mi. W Monclova with topotypes of *jucundus* and *tamaulipensis* reveals that the Monclova specimens are referable to *jucundus,* as expected on geographical grounds. Specimens from Hisachalo, southeast of Monclova, were referred to *jucundus* by Russell and Baker (1955:599), but reexamination of these specimens, which have unusually broad skulls and short tooth-rows, suggests that they more closely resemble *P. c. subsimus,* to which they are here referred. The specimens from Hisachalo also may be intergrades between *subsimus* and *jucundus* (for further discussion, see account of *subsimus*).

Intergradation with *P. c. ustulatus* is not evident in known specimens but may be expected in the valley of the Río Salado east of Hermanas.

Specimens examined.—Total of 19, all from Coahuila, as follows: Hermanas, 1205 ft., 9 (1 in alc.); *1 mi. S Hermanas, 1; 6 mi. W Cuatro Ciénegas, about 2300 ft., 2; 16 kms. S Cuatro Ciénegas, 1; 1 mi. N and 13 mi. E Cuatro Ciénegas, 2; 5 mi. N and 2 mi. W Monclova, 1; *2 mi. N and 1 mi. E Monclova, 1; * Monclova, 2 (USNM).

Pappogeomys castanops perplanus (Nelson and Goldman)

Cratogeomys castanops perplanus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:136, June 13, 1934 (part); Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Blair, Texas Jour. Sci., 6:246, September, 1954 (part); Miller and Kellogg, Bull. U. S. Nat. Mus., 205:324, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959.

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:160, January 31, 1895 (part); Stone and Rehn, Proc. Acad. Nat. Sci. Philadelphia, 55:23, May 7, 1903; Bailey, N. Amer. Fauna, 25:132, October 24, 1905 (part); Elliot, Field Columb. Mus. Publ. 115, Zool. Ser., 8:311, 1907; Bailey, N. Amer. Fauna, 53:242, March 1, 1932 (part).

[*Cratogeomys*] *castanops,* Elliot, Field Columb. Mus. Publ. 45, Zool. Ser., 2:220, April 10, 1901 (part); Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:315, 1904 (part).

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Cratogeomys castanops lacrimalis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:137, June 13, 1934 (part), type from Roswell, 3500 ft., Chaves Co., New Mexico; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940 (part); Poole and Schantz, Bull. U. S. Nat. Mus., 178:365, April 9, 1942; Davis and Robinson, Jour. Mamm., 25:267, September 8, 1944; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:341, March 3, 1955 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Type.—Male, adult, skull and skin; No. 97171, U. S. National Museum; from Tascosa, Oldham County, Texas; June 5, 1899; obtained by Vernon Bailey, original number 6941.

Range.—Panhandle of Oklahoma, Llano Estacado of western Texas and eastern New Mexico; southward into northern part of the Trans-Pecos area of Texas. See Fig. 3.

Description.—Large for species; tail relatively long (averaging 44% of length of head and body in females); hind foot large. Averages and extremes of 13 females and eight males, respectively, from the Pecos River Valley of southeastern New Mexico and adjacent parts of Texas are as follows: Length of head and body, 187 (182-212), 198 (177-212); length of tail, 83 (66-105), 89 (78-98); length of hind foot, 37 (35-38), 37 (35-39).

Color: Upper parts (summer pelage) Cinnamon Buff, pure on sides and face, but suffused with Bay-tipped hairs on back and top of head resulting in a darker reddish-brown appearance, basally Dark Mouse Gray; underparts Light Mouse Gray overlaid with Salmon-Buff; hind foot whitish; tail thinly covered with buffy hairs.

Skull: Large for species; breadth across zygomata and squamosals especially great; palatofrontal depth great; nasals, rostrum, and especially palate long; rostrum broad and massive; tympanic bullae inflated; horizontal process of lacrimal large; maxillary tooth-row short in relation to length of skull; rostrum broad (averaging 51.4% of its length).

Averages and extremes of 15 females and eight adult males, respectively, from the Pecos River valley of southeastern New Mexico and adjacent parts of Texas are as follows: Condylobasal length, 50.6 (49.3-51.8), 54.9 (53.0-57.8); zygomatic breadth, 32.6 (31.2-34.2), 37.0 (34.8-40.3); palatofrontal depth, 19.9 (19.2-20.8), 21.2 (20.4-22.1); length of palate, 34.7 (33.3-36.1), 37.8 (36.3-40.4); length of nasals, 18.4 (17.3-19.4), 20.1 (19.2-21.8); breadth of braincase, 21.9 (21.1-22.5), 22.8 (21.4-25.4); squamosal breadth, 29.6 (28.5-30.7), 32.1 (30.7-35.0); breadth of rostrum, 11.2 (10.7-11.7), 12.7 (11.7-13.7); length of rostrum, 21.8 (20.6-22.9), 23.8 (22.7-25.5); alveolar length of maxillary tooth-row, 9.6 (8.9-10.2), 10.1 (9.3-10.6).

Comparisons.—For comparisons with *P. c. hirtus, P. c. simulans, P. c. pratensis, P. c. parviceps, P. c. torridus,* and *P. c. angusticeps,* see accounts of those subspecies.

From *P. c. castanops, perplanus* differs, as follows: Averaging slightly larger; tail relatively longer (averaging 39 *versus* 44% of length of head and body); hind foot longer; underparts brighter, more ochraceous and less buffy; skull averaging significantly longer and broader, especially in breadth across zygomata and squamosals; horizontal process of lacrimal larger (when viewed in dorsal aspect); tympanic bullae more inflated; last upper molar smaller; rostrum broader (averaging 51.4 *versus* 49.3% of its length).

Remarks.—Judging from trapping records, *P. c. perplanus* is most abundant in the broad valley of the Pecos River in New Mexico and adjacent parts of Texas. Deep, sandy soils and xerophytic shrubs are common to the Pecos River Valley, and the combination of both features provides ideal environment for this species. *P. c. perplanus* is less common on the higher, grass-covered plains, but evidently is locally numerous in the valleys of the Colorado (of Texas), Brazos, Red, and Canadian rivers. The Sacramento-Guadalupe mountains, a north-south range continuous from central

New Mexico southward into the Trans-Pecos area of Texas, forms an impassable barrier which physically separates much of the geographic ranges of *perplanus* and *parviceps* in most areas.

Cratogeomys castanops lacrimalis Nelson and Goldman is treated as a synonym of *C. c. perplanus,* the latter having page priority, because specimens from the Llano Estacado and the Pecos River Valley, including the type series of both *perplanus* and *Cratogeomys castanops lacrimalis,* are uniform, except for an old, lactating, female (KU 66143) from 3 mi. N Hobbs, in southeastern New Mexico, which has a remarkably long skull (condylobasal length, 53.1), palate (38.0), and maxillary tooth-row (11.2).

Specimens from Hooker and 4 mi. E Elmwood, Oklahoma, in comparison with typical examples of *perplanus* from the Llano Estacado and Pecos River Valley are slightly smaller, and the tail is relatively short (38% of length of head and body) as in *castanops* and *simulans;* the hind foot averages larger (38.2); the breadth across the squamosals is less (28.6); and the maxillary tooth-row is slightly longer (10.0). In relative length of tail and breadth across squamosals, the Oklahoma specimens more closely approximate *castanops* and *simulans;* the longer hind foot and longer maxillary tooth-row are distinctive of these samples. Considering all features, these specimens are referable to *perplanus,* but the genetic influence of *castanops,* or most probably *simulans,* is evident.

P. c. perplanus occurs sympatrically with *P. c. parviceps* of the *subnubilus*-group in Pine Springs Canyon of the Guadalupe Mountains of extreme northwestern Culberson County, and without any indication of intergradation. Most of the specimens from the canyon are referable to *parviceps* (see account of that subspecies), but an adult female (PA 17212) is distinctly referable to *perplanus.*

Five specimens from 2 mi. W and 1 mi. S Conchas Dam, New Mexico, previously mentioned in the account of *castanops,* are intergrades between *perplanus* and *castanops.* The length of hind foot, length of skull, and length of nasals and rostrum of these specimens approximates those of *castanops.* The length of tail relative to length of head and body (34%) is remarkably shorter than in either *perplanus* or *castanops.* Otherwise these specimens agree with typical *perplanus,* the subspecies to which the sample is referred. Specimens from Cimarron County, Oklahoma (discussed in the account of *castanops*), also are intergrades between *perplanus* and *castanops,* but, as pointed out before (see account of *castanops*), are more nearly like *perplanus* to which they are referred.

Specimens from 17 mi. SE Washburn, and from several localities in the vicinity of Lubbock and Lemesa, Stranton, and Big Springs, were formerly assigned either to *perplanus* or *lacrimalis* by other authors (Nelson and Goldman, 1934:137; Blair, 1954:246). All of these localities are along, or to the east of, the Cap-rock escarpment that separates the Llano Estacado from the Rolling Prairie to the east and the specimens are significantly smaller than *perplanus*. They are uniform in their features, cannot be identified with *perplanus,* and are here described as a new subspecies (with type locality 17 mi. SE Washburn, Armstrong Co., Texas).

A specimen (KU 7348) from 2 mi. E Carlsbad, New Mexico, labeled female, is an adult male. Another specimen (TCWC 667) from Scott Canyon, Texas, labeled male is an adult female. An old adult male (KU 100664) from Carlsbad is remarkably larger cranially than any other adult male; it measures 62.6 in condylobasal length, 44.4 in length of palate, and 25.2 in palatofrontal depth.

Specimens examined.—Total of 99, as follows:

New Mexico: *San Miguel County:* 2 mi. W and 1 mi. S Conchas Dam, 4250 ft., 5; Bell Ranch, 1 (NM). *Guadalupe County:* Cuerro (= Cuervo), 1 (USNM); Santa Rosa, 1 (USNM). *De Baca County:* 8 mi. N Fort Sumner, 1 (USNM). *Chaves County:* 35 mi. N Roswell, 1 (USNM); * Roswell, 15 (5 USNM, 10 KU); * along Dry Hondo Creek, Roswell, 2 (PA); 7 mi. N Maljamar, 4100 ft., 4. *Eddy County:* Ligon Bird Farm, 3 mi. NW Carlsbad, 1 (NM); * 2 mi. NE Carlsbad, 2; * Carlsbad (Eddy), 3200 ft., 6 (3 USNM, 3 KU); * Pecos River Bank, 1 mi. E Carlsbad, 8; * 2 mi. E Carlsbad, 5; 2 mi. S and 1 mi. W White City, 1; 5 mi. S and 1 mi. E Black River Village, 1; Rattlesnake Springs Ranger Station, Carlsbad Cavern Nat'l Park, 4000 ft., 2. *Lea County:* 3 mi. N Hobbs, 4.

Oklahoma: *Cimarron County:* 7 mi. N Kenton, 7; * north Carrizo Creek, 6 mi. N Kenton, 2 (OS); * north side of Black Mesa, 6 mi. N Kenton, 4 (OS); 7 mi. E and 2 mi. S Kenton, 1 (UA); * head Tesequite Canyon, 5 mi. S Kenton, 1 (OS); * 2 mi. E and 7 mi. S Kenton, 1 (OS). *Texas County:* Hooker, railroad right-of-way just west of town, 5 (OS). *Beaver County:* 4 mi. E Elwood P. O., 4 (OS).

Texas: *Hansford County:* Paladuro Canyon, 3 (FMMH); 6 mi. S and 3 mi. W Gruver, 3300 ft., 1 (WLC). *Oldham County:* Tascosa, 2 (USNM). *Hale County:* Hale Center, 1 (USNM). *Culberson County:* foot of Pine Canyon, Guadalupe Mts., 5740 ft., 1 (PA, No. 17212); Scott Canyon, Delaware Mts., 2 (TCWC). *Reeves County:* Pecos, 2500 ft., 3 (PA).

Pappogeomys castanops pratensis new subspecies

Type.—Female, adult, skin and skull; no. 52051, Museum of Natural History, University of Kansas; 8 mi. W and 3 mi. S Alpine, 5100 ft., Brewster Co., Texas; December 30, 1952; obtained by Gerd H. Heinrich, original number 5684.

Range.—Desert plains of central part of Trans-Pecos area of western Texas. See Fig. 3. Altitudinal range 2775 to 5600 feet.

Diagnosis.—Small for species; tail relatively long (averaging 40% of the length of head and body); hind foot of medium length. Averages and extremes of 17 females and eight males from Davis Mountain area of Texas (localities labeled with reference to Fort Davis, Limpia Canyon, Madera Canyon, Fort Stockton, and Alpine) are, respectively, as follows: Length of head and body, 179 (164-199), 203 (179-255); length of tail, 81 (70-90), 86 (80-96); length of hind foot, 35 (30-37), 38 (35-45).

Color: Upper parts Dark Mouse Gray basally overlaid with pale Cinnamon-Buff, sides and face pure Cinnamon-Buff, back and top of head darker owing to mixture of Bay-tipped hairs, especially prominent in unworn pelage; sides of face pale yellowish-brown; underparts Light Mouse Gray basally suffused with whitish or pale buffy; hind feet whitish; tail scantily set with buffy hairs.

Skull: Medium in size for species and deep; braincase narrow; palate short; broad across zygomata in relation to length of skull; rostrum narrow and short.

Averages and extremes of 18 females and nine males from Davis Mountain area of Texas (see localities listed above) are, respectively, as follows: Condylobasal length, 48.7 (47.6-49.9), 54.8 (52.6-58.1); zygomatic breadth, 30.9 (29.7-32.2), 37.1 (35.1-40.5); palatofrontal depth, 19.2 (18.5-20.1), 21.3 (20.2-22.8); length of palate, 32.7 (31.3-33.4), 37.5 (36.2-39.5); length of nasals, 17.3 (16.5-17.8), 20.0 (18.2-21.9); breadth of braincase, 20.7 (19.5-22.3), 22.3 (20.4-24.3); squamosal breadth, 28.4 (27.0-30.1), 32.2 (29.6-34.8); breadth of rostrum, 10.4 (9.7-11.0), 12.3 (11.4-13.2); length of rostrum, 20.6 (19.4-21.6), 23.9 (22.1-25.2); alveolar length of maxillary tooth-row, 9.6 (8.9-10.5), 9.8 (9.3-10.2).

Comparisons.—For comparison with *P. c. simulans, P. c. torridus,* and *P. c. parviceps,* see accounts of those subspecies.

From ***P. c. perplanus, P. c. pratensis*** differs as follows: Smaller; hind foot shorter; skull averaging smaller in all dimensions except maxillary tooth-row, which is essentially the same.

From ***P. c. clarkii, P. c. pratensis*** differs as follows: Smaller; hind foot shorter; skull and palate shorter; narrower across zygomata and squamosals; rostrum slightly shorter and especially narrower.

From ***P. c. angusticeps, P. c. pratensis*** differs as follows: Tail relatively longer (averaging 44 *versus* 40% of length of head and body); hind foot longer; skull, nasals, and palate longer; palatofrontal depth greater; skull broader, especially across zygomata and squamosals.

Remarks.—Most of the specimens from the Davis Mountain area, which form the basis for the recognition of *pratensis,* previously were identified as *Cratogeomys castanops lacrimalis,* Nelson and Goldman (see Nelson and Goldman, 1934: 138; Blair, 1940: 27-28; Blair and Miller, 1949: 13-14). In my study, *lacrimalis* (type locality, Roswell, New Mexico) is synonymized with *P. c. perplanus,* and the range of variation ascribed to *perplanus* significantly exceeds that of the population in the Trans-Pecos area in most cranial dimensions. Specimens from the central Trans-Pecos area cannot be conveniently assigned to any of the neighboring subspecies, least of all to *perplanus.* This circumstance was one reason for naming the subspecies, namely *P. c. pratensis.*

A female, AMNH 136726, from along the highway 6 mi. W Alpine, is adult, as judged by cranial morphology, but is remarkably small (condylobasal length 42.1) for adults of *pratensis.* Cranial measurements of this specimen are actually within the range of variation ascribed to subspecies of the *subnubilus*-group; however, the nearest point of occurrence of one of the *subnubilus* subspecies (*parviceps*) is north of the Davis Mountains more than 70 miles distant. Perhaps the specimen is a subadult with precocious closure of sutures.

Specimens from 2 mi. E Sanderson and those from 1-3 mi. W Dryden, Texas, are intergrades between *pratensis* and *angusticeps.* In both series, the average measurements of condylobasal length, length of palate, and length of nasals are intermediate between the corresponding measurements of the larger *pratensis* and smaller *angusticeps.* In the Sanderson series palatofrontal depth and the breadths across zygomata, braincase, and squamosals approximate averages of those dimensions in *pratensis,* and therefore, these specimens are referred to *pratensis.* In the Dryden series squamosal breadth is about as in *pratensis,* whereas palatofrontal depth and the breadth across the zygomata are about as in *angusticeps,* and the breadth of braincase is intermediate. The Dryden series is referred to *angusticeps* on the basis of palatofrontal depth and zygomatic breadth.

The adult male from Kent in Culberson Co. is referred to *pratensis* on geographical grounds. No female is known from that locality, and males alone cannot be identified to subspecies with certainty. Specimens numbered TCWC 2344 and 2346 from 2 mi. S Paisano and TCWC 2333 and 2337 from 2 mi. E Sanderson are labeled females but are adult males. A specimen from Marathon (USNM 108600) and one from 2 mi. S Paisano (TCWC 2343) are labeled males but are probably adult females.

Specimens examined.—Total of 92, all from Texas, as follows: *Culberson County:* Kent, 1 (USNM). *Pecos County:* Ft. Stockton, 4. *Jeff Davis County:* Madera Canyon, 4400 ft., 3 (TCWC); * Davis Mts., 15 mi. S Toyahvale, 1 (USNM); * 16 mi. NE Fort Davis, 2 (TCWC); Upper Limpia Canyon, 5 mi. W Mt. Livermore, 2 (UMMZ); * Limpia Canyon, Mt. Livermore, 5400 ft., 2 (TCWC); * Limpia Canyon, 5 mi. E Mt. Livermore, 5600 ft., 1 (TCWC); * Limpia Canyon, 7½ mi. E Mt. Livermore, 1 (TCWC); 1 mi. N Fort Davis, 4 (TCWC); * Limpia Canyon, 9 mi. W Fort Davis, 5200 ft., 3 (TCWC); * 5 mi. W Fort Davis, 9 (TCWC); * Limpia Canyon, 9 mi. E Fort Davis, 1 (TCWC); * Fort Davis, 5 (UMMZ); * 3.8 mi. SE Fort Davis, 1 (TT); * 4.1 mi. SE Fort Davis, 1 (TT). *Presidio County:* Marfa, 3 (USNM); * 2 mi. S Paisano, 5000 ft., 10 (TCWC). *Brewster County:* 10 mi. W and 3 mi. S Alpine, 5200 ft., 2; * 8 mi. W and 3 mi. S Alpine, 5100 ft., 5; * 6 mi. W and 2 mi. S Alpine, 5100 ft., 2; * 6 mi. W Alpine (along highway), 3 (AMNH); * 5 mi. W Alpine, 1 (UI); * 2 mi. W and ½ mi. S Alpine, 4 (UI); * Alpine, 1 (USNM); * 6 mi. E Alpine, 1; 10 mi. W and 4 mi. N Marathon, 4800 ft., 1; * Marathon, 5 (USNM). *Terrell County:* 2 mi. E Sanderson, 2775 ft., 13 (11 TCWC, 2 KU).

Pappogeomys castanops simulans new subspecies

Type.—Female, adult, skull and skin; No. 222, Texas Natural History Collection, University of Texas; July 10, 1947; 17 mi. SE Washburn, Armstrong County, Texas; obtained by W. Frank Blair, original number 1817.

Range.—High plains of western Texas generally east of the cap-rock escarpment, from vicinity of Amarillo south to Big Springs. See Fig. 3.

Diagnosis.—Large for species; tail of medium length (averaging 40% of length of head and body); hind foot short. Averages and extremes of 13 females and nine males from rolling plains of West Texas are, respectively, as follows: Length of head and body, 185 (158-205), 178 (170-221); length of tail, 76 (65-90), 82 (73-95); length of hind foot, 34 (31-37), 37 (33-40).

Color: Pelage of upper parts Dark Mouse Gray basally overlaid with Cinnamon-Buff, darkened on top of head and back in unworn pelage by admixture of Bay-tipped hairs, sides pure Cinnamon-Buff; buffy wash in worn pelage strongly mixed with dark plumbeous of basal portion of hairs giving pelage a darker appearance; sides of face yellowish-brown; underparts Light Mouse Gray basally overlaid with buffy or whitish; hind feet whitish; tail thinly covered with buffy hairs.

Skull: Medium in size for species, approximating that of *P. c. castanops;* narrow across zygomata and especially across squamosals; palate, nasals, and rostrum relatively long; rostrum narrow.

Averages and extremes of 14 females and nine males from rolling plains of West Texas are, respectively, as follows: Condylobasal length, 49.2 (48.2-50.1), 56.3 (53.4-59.7); zygomatic breadth, 31.4 (30.3-33.2), 38.6 (34.7-42.3); palatofrontal depth, 19.5 (18.8-20.2), 22.1 (20.8-23.5); length of palate, 33.7 (31.4-34.8), 39.6 (37.2-42.6); length of nasals, 18.1 (16.7-19.9), 21.3 (19.1-23.5); breadth of braincase, 21.3 (20.4-22.2), 23.8 (22.5-25.1); squamosal breadth, 27.5 (26.5-29.3), 32.1 (30.0-34.1); breadth of rostrum, 10.4 (9.6-11.9), 12.7 (11.8-14.7); length of rostrum, 21.5 (19.8-22.5), 25.5 (23.5-27.6); alveolar length of maxillary tooth-row, 9.7 (9.2-10.3), 10.3 (9.4-11.6); breadth across angular processes, 31.1 (27.9-34.0), 41.9 (38.7-43.2).

Comparisons.—From *P. c. perplanus* (females from southeastern New Mexico), *P. c. simulans* differs as follows: Averaging slightly smaller; tail relatively short (averaging 41 *versus* 44% of length of head and body); hind foot shorter; skull smaller, especially in length (condylobasal length averaging 49.2 *versus* 50.6); breadth across zygomata, squamosals, and rostrum decidedly less; palate shorter.

From *P. c. angusticeps, P. c. simulans* differs as follows: Averaging larger; hind foot longer; skull averaging significantly larger in all dimensions save breadth and length of rostrum; no overlap in range of variation in palatofrontal depth, basilar length, and length of palate, and only slight overlap in condylobasal length and breadth of braincase.

From *P. c. pratensis, P. c. simulans* differs as follows: Averaging larger; hind foot shorter; skull averaging slightly longer (condylobasal length averaging 49.2 *versus* 48.7 in *pratensis*); palate, nasals, and rostrum longer; narrower across squamosals and angular processes.

Remarks.—*P. c. simulans* is based on specimens formerly referred to *P. c. perplanus.* The name *perplanus* now is restricted to apply to the remarkably large pocket gopher that occurs west of the cap-rock escarpment on the Llano Estacado of extreme western Texas and southeastern New Mexico. The name *simulans* is proposed for those populations inhabiting the western limits of the rolling prairie at lower elevations east of the cap-rock escarpment. Samples of the populations assigned to *simulans* measure significantly smaller than those referred to *perplanus*.

P. c. simulans closely resembles *P. c. castanops* from northeastern New Mexico and southeastern Colorado. The two subspecies are separated geographically by the range of *perplanus*. From *P. c. castanops*, *simulans* differs as follows: Relatively longer tail (averaging 41 *versus* 39% of length of head and body); shorter hind foot; and slightly shorter palate. Also, *simulans* is allied *to P. c. pratensis* of the Trans-Pecos region of Texas; *simulans* is the larger, especially in breadth of braincase and length of palate, nasals, and rostrum. Of the neighboring subspecies, *P. c. angusticeps* differs most from *simulans*. The range of cranial variation in *simulans* is larger than in *angusticeps* in all dimensions, save breadth and length of rostrum.

Consideration of the subspecies in western Texas, eastern New Mexico, southeastern Colorado, and the panhandle of Oklahoma permits formulation of a hypothesis as follows: The primitive stock in this region was morphologically homogenous; structurally, it approximated that of *castanops* and *simulans;* subsequent subspeciation resulted in increased size in those populations inhabiting the Llano Estacado and the upper Pecos River Valley; collectively these populations of large pocket gophers are now referable to *perplanus; castanops* and *simulans*, although no longer contiguous, have retained, little changed, the features of the primitive stock.

Examples of *simulans* from Big Springs and Stanton, localities at the southern limits of the known range, have slightly shorter nasals than those from elsewhere, and, in this respect, resemble *P. c. pratensis*. Specimens from Big Springs, 8 mi. NE Lamesa, and 2 mi. N Lubbock have shorter tails than do topotypes. A female from Stanton is broader across the squamosals than is usual for *simulans* and in this respect resembles *perplanus*, but otherwise is like *simulans*.

Specimens examined.—Total of 37, all from Texas, and distributed as follows: *Potter County:* 2 mi. E Amarillo, 2 (TCWC). *Armstrong County:* 17 mi. SE Washburn, 8 (TU). *Lubbock County:* 9 mi. NW Lubbock, 1 (UMMZ); * 7.5 mi. N Lubbock, 4 (TT); * 7.4 mi. N Lubbock, 2 (TT); * 5 mi. N Lubbock, 3 (TT); 2 mi. E Reese Air Force Base, 1 (TT); * 3 mi. NE Lubbock, 4 (TT); * 2 mi. N Lubbock, 2 (UMMZ); * Mackenzie State Park, 2 mi. NE Lubbock, 2 (TT); 6.5 mi. W Lubbock, 2 (TT). *Dawson County:* 8 mi. N Lamesa, 1 (UMMZ); * 8 mi. NE Lamesa, 1 (OS); 10 mi. E Lamesa, 2 (TU). *Martin County:* Stanton, 1 (USNM). *Howard County:* Big Springs, 1 (USNM).

Pappogeomys castanops sordidulus (Russell and Baker)

Cratogeomys castanops sordidulus Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:600, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:228, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959 (part).

Type.—Female, adult, skull and skin; No. 56614, University of Kansas Museum of Natural History; 1½ mi. NW Ocampo, 3300 ft., Coahuila; December 16, 1953; obtained by Robert W. Dickerman, original number 2164.

Range.—Llano de Ocampo in central Coahuila, probably northward into Río Grande Valley on south side of river. See Fig. 3.

Description.—Body large for species; tail relatively short (averaging 39% of length of head and body); hind foot long. Averages and extremes of three females and the measurements of one male from the type locality are, respectively, as follows: Length of head and body, 201 (194-205), 219; length of tail, 79 (75-85), 88; length of hind foot 37 (36-39), 37.

Color: Upper parts Mouse Gray basally and Orange-Buff (fresh winter pelage) apically, with some Bay-tipped hairs on back and top of head but pure Orange-Buff on sides and face; underparts Light Mouse Gray overlaid with Pale Ochraceous-Salmon; hind feet white.

Skull: Size large for species; relatively narrow across zygomata (averaging 62.9% of condylobasal length in females); palate decidedly long; rostrum narrow (averaging 50.0% of length); broad across squamosals; maxillary tooth-row short.

Averages and extremes of three females and the measurements of one male from the type locality are, respectively, as follows: Condylobasal length, 50.4 (49.5-51.4), 57.5; zygomatic breadth, 31.7 (30.6-32.4), 39.6; palatofrontal depth, 19.6 (19.2-20.4), 22.7; length of palate, 34.6 (33.8-35.2), 40.3; length of nasals, 18.2 (17.7-18.5), 22.1; breadth of braincase, 21.4 (20.9-21.7), 22.9; squamosal breadth, 30.0 (29.8-30.1), 33.1; breadth of rostrum, 10.9 (10.3-11.4), 13.6; length of rostrum, 21.8 (21.3-22.4), 24.9; alveolar length of maxillary tooth-row, 9.1 (8.9-9.2), 10.3.

Comparisons.—From *Pappogeomys castanops clarkii, sordidulus* differs as follows: Head and body longer; tail relatively shorter (39 versus 43% of length of head and body); upper parts brighter, more ochraceous-orange and less ochraceous-buff; palate decidedly longer; nasals slightly longer; slightly broader across squamosals; rostrum narrower.

From *Pappogeomys castanops jucundus, sorididulus* differs as follows: Hind foot shorter; upper parts brighter, more ochraceous and less buffy; underparts darker, more ochraceous and less whitish; skull decidedly shorter and shallower; zygomata less widely spreading; palate and nasals slightly shorter; braincase decidedly narrower; rostrum relatively narrower (averaging 50.0 *versus* 53.8% of its length).

From *Pappogeomys castanops excelsus, sordidulus* differs as follows: Tail relatively shorter (39 *versus* 43% of length of head and body); upperparts darker and brighter, more rich ochraceous and less pale buffy; zygomata less widely spreading; braincase and rostrum narrower; maxillary tooth-row shorter.

From *Pappogeomys castanops perexiguus, sordidulus* differs as follows: Head and body markedly longer; hind foot longer; upperparts darker, more bright ochraceous and less pale buffy; underparts darker, more pinkish-buff and less whitish; skull larger in all respects, especially (and without overlap) in condylobasal length, zygomatic and squamosal breadth, palatofrontal depth, and length of palate and nasals.

Remarks.—*P. c. sordidulus* is one of a group of large-sized subspecies (*perplanus, clarkii, jucundus, excelsus, subsimus,* and *ustulatus*) each of which is distinguished from the others by a combination of morphological features, primarily quantitative. For instance, *sordidulus* is distinguished from the others by the combination of relatively short tail, narrow skull, and short maxillary toothrow. No one of these features separates *sordidulus* from all of the other subspecies, but the combination of features does so. The geographic range of each of the large subspecies, excepting *perplanus,* adjoins the range of one or more of the other large subspecies.

Of the other large-sized subspecies, *clarkii* most closely resembles *sordidulus.* The population of *clarkii* from the Big Bend area of Texas (see remarks in the account of *P. c. clarkii*) in particular approximates *sordidulus* in greater length of head and body (194), relatively short tail (40%), and breadth across squamosals (29.8). I take this to be evidence of gene exchange between populations of *sordidulus* and the Big Bend population of *clarkii,* and those features of the Big Bend population of *clarkii* that agree with *sordidulus* reflect the acquisition of these genes.

The high mountains that border the Llano de Ocampo, on all sides except to the northwest, function to isolate *sordidulus* from other subspecies of the *excelsus* group, especially *jucundus* and *excelsus.* In the summer of 1952 I failed to find any pocket gophers of this species in the long, narrow canyon immediately north of Cuatro Ciénegas, although *jucundus* occurs in the basin to the south and *sordidulus* on the desert plains to the north. Contact with *excelsus,* to the southwest, is prevented by the Sierra de la Madera. The isolation of *sordidulus* from other subspecies, except perhaps *clarkii,* seems to have played an important role in its differentiation.

P. c. sordidulus shares its range with *Pappogeomys castanops perexiguus,* at least on the northern part of the Llano de Ocampo. *P. c. perexiguus* enters the Llano de Ocampo *via* low mesas north of the flanks of the Sierra del Pino. These mesas connect the Llano with the arid desert plains of extreme western Coahuila and Chihuahua, a region that is inhabited exclusively by the small subspecies of the *subnubilus* group. Specimens referable to *perexiguus* have been taken 18 mi. S and 14 mi. E Tanque Alvarez, 50 mi. N and 20 mi. W Ocampo, and 3 mi. N and 9 mi. E El Pino. As elsewhere in this region, there is no evidence of intergradation between the representative of the small *subnubilus* group and the large *excelsus* group (for full discussion see section on speciation of *P. castanops*). The southern two-thirds of the Llano de Ocampo is separated from the desert plains to the west by continuous highlands, namely the Sierra del Pino-Sierra de la Madera axis.

P. c. sordidulus is not common on the Llano de Ocampo. Colonies are widely scattered and small. One colony 5 mi. N and 19 mi. W Cuatro Ciénegas had been almost eradicated by badgers, which had recently dug out most of the burrows. Only one subadult male gopher was trapped from the area inhabited by the colony.

Specimens examined.—Total of 8, all from Coahuila, as follows: 1.5 mi. NW Ocampo, 3300 ft., 7; 5 mi. N and 19 mi. W Cuatro Ciénegas (just east of Hda. El Oso), 1.

Pappogeomys castanops subsimus (Nelson and Goldman)

Cratogeomys castanops subsimus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:144, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Russell, Jour. Mamm., 35:122, February 10, 1954; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:603, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:230, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, January 31, 1895 (part); Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:266, December 6, 1905 (part).

[*Cratogeomys*] *castanops*, Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:315, 1904 (part).

[*Cratogeomys castanops*] *castanops*, Trouessart, Cat. Mamm., 1:573, 1898 (part).

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 79:247, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Cratogeomys castanops jucundus, Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:599, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:227, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Cratogeomys castanops goldmani, Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:606, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:227, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959 (part).

Type.—Male, adult, skull and skin; No. 51048, U. S. National Museum; Jaral [= San Antonio de Jaral], Coahuila; January 14, 1893; obtained by Clark P. Streator, original number 2555.

Range.—Southeastern Coahuila within the drainage of the Río Salinas and its tributaries, and probably west-central Nuevo León. See Fig. 3. Altitudinal range 3800 to 6500 feet.

Description.—Large for the species; tail relatively long (averaging 45% of length of head and body); hind foot long. Averages and extremes of the six females and three males, respectively, from south-central Coahuila (specimens labeled with reference to Jaral, Hipolito, Parras, and Santa Cruz) are as follows: Length of head and body, 201 (191-211), 220 (210-227); length of tail, 90 (80-104), 95 (89-105); length of hind foot, 38 (36-40), 40 (40-40).

Color: Upper parts Dark Mouse Gray basally and Pale Yellow-Orange apically (fresh summer pelage), with some Bay-tipped hairs on back and top of head, but pure Pale Yellow-Orange on sides and face; underparts Light Mouse Gray overlaid with Pale Ochraceous-Buff; hind foot whitish.

Skull: Largest in species; zygomata widely spreading; palate and nasals long; broad across braincase and squamosals; rostrum broad and long; maxillary tooth-row long.

Averages and extremes of six females and three males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 52.4 (51.0-53.2), 57.4 (56.4-58.2); zygomatic breadth, 32.9 (30.9-34.9), 36.5 (35.3-37.9); palatofrontal depth, 20.0 (19.2-20.8), 22.3 (22.2-22.5); length of palate, 36.0 (34.4-37.0), 39.7 (39.2-40.3); length of nasals, 18.9 (17.8-19.6), 21.2 (20.8-21.7); breadth of braincase, 22.1 (21.6-23.0), 23.4 (21.6-24.6); squamosal breadth, 30.4 (29.3-31.7), 33.6 (32.1-34.8); breadth of rostrum, 11.3 (10.5-12.6), 13.2 (12.5-14.1); length of rostrum, 22.1 (21.0-22.9), 25.0 (24.5-25.5); alveolar length of maxillary tooth-row, 10.2 (9.9-10.9), 10.5 (10.3-10.7).

Comparisons.—For comparisons with *P. c. excelsus, P. c. ustulatus, P. c. tamaulipensis, P. c. elibatus,* and *P. c. subnubilus,* see accounts of those subspecies.

From *Pappogeomys castanops jucundus, subsimus* differs, as follows: Tail relatively longer (averaging 45 *versus* 40% of length of head and body); hind foot slightly longer; skull, palate, nasals and maxillary tooth-row longer; rostrum relatively narrower (averaging 51.4 *versus* 53.8% of its length).

From *Pappogeomys castanops bullatus, subsimus* differs, as follows: Larger; tail and hind foot longer; upper parts paler, more yellowish-buff and less reddish-buff; skull averaging larger in all dimensions, especially in condylobasal length, zygomatic and squamosal breadth, and length of palate, rostrum and maxillary tooth-row.

Remarks.—*P. c. subsimus* occurs in the upper drainage of the Río Salinas and is distinguished by large size, relatively long tail, yellowish-buff upper parts, and long skull. The skull averages longer than in any other subspecies of *Pappogeomys castanops.* Considering its great length, the skull is relatively narrow, especially in the rostrum. Excepting the great condylobasal length and length of palate, nasals, rostrum, and maxillary tooth-row, each of the other cranial dimensions is equaled in one or another of the large subspecies, the ranges of which adjoin that of *subsimus.*

P. c. jucundus most closely resembles *subsimus* in color but *ustulatus* most closely approaches *subsimus* in condylobasal length and length of palate, nasals, and rostrum. Subspecies adjacent to *sub-*

simus on the Coastal Plain to the east, namely *P. c. bullatus* and *P. c. tamaulipensis*, are markedly smaller with differently proportioned skulls; and, evidently, they were derived from a different ancestral stock than the large gophers that differentiated into *subsimus* and the other large subspecies of the arid desert basins of central Coahuila and adjacents parts of Texas and Nuevo León.

Although the distribution of *subsimus* centers in southeastern Coahuila, part of its range extends westward across the foothills of the Sierra Guadelupe and Sierra Parras, at least to the town of Parras de la Fuente (a specimen from 1½ miles N Parras was erroneously assigned to *P. c. goldmani* by Russell and Baker, 1955:607). This western segment of its range lies south of that of *Pappogeomys castanops excelsus*, which occurs in the deep, light-colored sands of the basin formerly occupied by the Laguna de Mayrán. The northwestern limits of the range of *subsimus* are unknown but probably are along the eastern slopes of the Sierra de los Alamitos and Sierra de San Marcos in central Coahuila. Specimens from the west and north sides of these mountains are referable to *P. c. excelsus* and *P. c. jucundus*, respectively.

The ranges of *subsimus* and *P. c. subnubilus*, one of the small subspecies to the south, meet in Domingo Canyon in the Guadelupe Mountains. *P. c. subsimus* occurs near the mouth of the canyon, at localities 10 mi. S and 5 mi. W General Cepeda, 6500 feet, and 9 mi. S and 5 mi. W General Cepeda, 6200 feet, and *P. c. subnubilus* occurs at 6700 feet in the canyon, at a point 11 mi. S and 4 mi. W General Cepeda. There is no indication of intergradation between these populations, and the specimens are clearly referable to either *subsimus* or *subnubilus*.

An adult and subadult, labeled female, from Hisachalo [= Huisachalo], previously were referred to *P. c. jucundus* by Russell and Baker (1955:600) but here are referred to *subsimus*. The adult has a shorter tooth-row and is broader across the zygomata and braincase than any other female of *subsimus* (or of *jucundus* or *bullatus*) but, considering all features, is best assigned to *subsimus*. The subadult also is here assigned to *subsimus*. The tooth-row of the adult (KU 58078) measures 8.9, which is as small as the smallest example of *bullatus*, suggesting intergradation with *bullatus*, which occurs at Lampazos nearby. If the adult is a male, its dimensions agree even more closely with those of *subsimus*, except for the lesser condylobasal length and shorter maxillary tooth-row, and, therefore, it might be considered as an intergrade between *subsimus* and *jucundus*, and perhaps also *bullatus*.

Two specimens examined (USNM 51049 and KU 5585) that are labeled as males actually are adult females.

Specimens examined.—Total of 23, all from Coahuila, as follows: Hisachalo [= Huisachalo], 2; 3 mi. S and 3 mi. E Muralla, 3800 ft., 3; * 2 mi. N Santa Cruz, 2; Jaral, 3860 ft., 4 (USNM); *¼ mi. SE San Antonio de Jaral, 4400 ft., 5 (MVZ); *Hda. El Tulillo, 5 km. S Hipolito, 2; 17 mi. N and 18 mi. W Saltillo, 5200 ft., 1; 12 mi. N and 10 mi. E Parras, 5000 ft., 1; * 1½ mi. N Parras, 1; N foot Sierra Guadelupe, 9 mi. S and 5 mi. W General Cepeda, 6200 ft., 1;*N foot Sierra Guadelupe, 10 mi. S and 5 mi. W General Cepeda, 6500 ft., 1.

Pappogeomys castanops tamaulipensis (Nelson and Goldman)

Cratogeomys castanops tamaulipensis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:141, June 13, 1934 (part); Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955 (part); Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959 (part); Alvarez, Univ. Kansas Publ. Mus. Nat. Hist., 15:428, May 20, 1963 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:159, January 31, 1895 (part).

Type.—Female, adult, skull and skin; No. 116535 U. S. National Museum; Matamoros, Tamaulipas; February 8, 1902; obtained by E. W. Nelson and E. A. Goldman, original number 14885.

Range.—Lower valley of Río Grande in northeastern Tamaulipas; unknown from uplands of Coastal Plain to the west of valley. See Fig. 3. Altitudinal range 30 to 125 feet.

Description.—Size medium for species; tail moderately long (averaging 42% of length of head and body); hind foot long. Average and extreme external measurements of three females and the measurements of one male from type locality and Reynosa, are, respectively, as follows: Length of head and body, 183 (179-187), 220; length of tail, 75 (74-77), 81; length of hind foot, 37 (35-40), 40.

Color: Upper parts Light Mouse Gray basally and Ochraceous-Buff apically, mixed with Bay-tipped hairs on back, but sides and face pure Ochroceous-Buff; underparts Pale Mouse Gray overlaid with Light Buff; hind feet whitish.

Skull: Medium for species; skull short for *excelsus*-group; zygomata widely spreading; palate and nasals short; relatively broad across squamosals and especially braincase; rostrum broad; maxillary tooth-row long.

Average and extreme cranial measurements of three females and the measurements of one male from the type locality and Reynosa, are, respectively, as follows: Condylobasal length, 47.7 (46.8-48.9), 57.3; zygomatic breadth, 31.4 (30.8-31.8), 41.3; palatofrontal depth, 18.7 (18.6-18.8), 22.4; length of palate, 32.7 (32.1-33.3), 39.4; length of nasals, 17.1 (16.7-17.6), 22.0; breadth of braincase, 22.2 (21.5-23.3), 25.9; squamosal breadth, 28.3 (27.6-29.1), 34.1; breadth of rostrum, 10.4 (10.1-10.6), 13.3; length of rostrum, 20.5 (20.2-20.7), 25.4; alveolar length of maxillary tooth-row, 10.1 (9.9-10.4), 10.5.

Comparisons.—For comparison with *P. c. planifrons* of the *subnubilus* group, see account of that subspecies.

From *Pappogeomys castanops bullatus, tamaulipensis* differs as follows: Slightly larger; hind foot longer; zygomata more widely spreading; nasals slightly longer; braincase decidedly broader, rostrum relatively narrower (averaging 50.7 *versus* 54.3% of its length); maxillary tooth-row longer.

From *Pappogeomys castanops jucundus, tamaulipensis* differs as follows: Smaller; hind foot shorter; upper parts paler, more buffy and less yellowish-brown; undeparts paler, more buffy and less ochraceous; skull averaging smaller in all dimensions, except maxillary tooth-row, without overlap in condylobasal length and breath of rostrum; maxillary tooth-row actually and relatively longer (averaging 21.2 *versus* 19.1% of condylobasal length).

From *Pappogeomys castanops subsimus, tamaulipensis* differs as follows: Smaller; tail and hind foot shorter; upper parts more buffy and less yellowish-brown; skull averaging smaller in all dimensions, without overlap in condylobasal length, palatofrontal depth, length of palate and squamosal breadth.

From *Pappogeomys castanops ustulatus, tamaulipensis* differs as follows: Smaller; tail relatively longer (averaging 42 *versus* 36% of length of head and body); hind foot longer; upper parts paler, more buffy and less bright reddish-brown; underparts paler, more buffy and less ochraceous; skull averaging larger in all cranial dimensions except breadth of braincase and length of maxillary tooth-row; without overlap in condylobasal length, length of palate, and breadth of rostrum.

From *Pappogeomys castanops angusticeps, tamaulipensis* differs as follows: Larger; tail relatively longer (averaging 42 *versus* 40% of length of head and body); hind foot decidedly longer; upper parts paler, more buffy and less cinnamon; skull, palate, and nasals longer; zygomata more widely spreading; maxillary tooth-row decidedly longer; breadth across squamosals and especially braincase greater.

Remarks.—In comparison with other subspecies of the *excelsus*-group, *P. c. tamaulipensis* is small—about the size of *P. c. bulleri. P. c. tamaulipensis* is remarkably smaller than the large subspecies of the *excelsus*-group that occur to the west at higher elevations on the Central Plateau. Its closest relative among adjacent subspecies is *bullatus,* and evidently both *bullatus* and *tamaulipensis,* and possibly *angusticeps* from east of the Río Grande, differentiated from ancestral stock of small to medium size that occurred on the Coastal Plain in the late Pleistocene.

P. c. tamaulipensis is characterized particularly by its long foot, small skull, broad braincase, long maxillary tooth-row, small auditory bulla, and relatively broad, concave-sided basioccipital. The last two features have not been observed in other subspecies.

Apparently, *tamaulipensis* is restricted to the Río Grande Valley. No sign of pocket gophers was noted on the Coastal Plain south and west of the river valley in Tamaulipas and Nuevo León (for further discussion, see account of *bullatus* above) and only one colony was found 3 mi. SE Reynosa in the Río Grande Valley in 1954. Evidently, *tamaulipensis* is not common even in the river flood plain. Nelson and Goldman trapped the series in 1902 upon which the original description was based and no specimens have been reported from there since. *Geomys personatus* occurs along the coast and *Orthogeomys hispidus* occurs to the south in the Tropical Life-zone. *P. c. tamaulipensis* probably does not occur in the same habitat as these other genera.

Specimens examined.—Total of 8, all from Tamaulipas as follows: 3 mi. SE Reynosa, about 125 ft., 3; Matamoros, about 30 ft., 5 (USNM).

Pappogeomys castanops torridus new subspecies

Type.—Female, adult, skull and skin; No. 84461 University of Kansas Museum of Natural History; 3 mi. E Sierra Blanca, about 4000 ft., Hudspeth Co., Texas; August 13, 1960, obtained by M. R. Lee, original number 2659.

Range.—Western part of Trans-Pecos area of western Texas, from Van Horn and vicinity of Sierra Blanca south across Valentine Plain to six miles south of Terlingua. See Fig. 3. Altitudinal range 2200 to 4000 feet.

Diagnosis.—Small for species; tail relatively long (averaging 43% of length of head and body in females); hind foot short. Averages and extremes for 13 females and 10 males from the western part of Texas Trans-Pecos (Sierra Blanca and Van Horn SE to 6 mi. S Terlingua) are, respectively, as follows: Length of head and body, 176 (162-192), 200 (188-213); length of tail, 76 (60-90), 77 (60-96); length of hind foot, 35 (31-37), 36 (32-40). An adult female (holotype) and an adult male weighed, respectively, 215 and 310 grams.

Color: Ground color of dorsum yellowish-brown to cinnamon, hairs varying from Light Ochraceous-Buff to Cinnamon-Buff subapically, basally hairs Mouse Gray; tips of hairs on back black, hairs on sides without blackish band; underparts Light Mouse Gray basally, hairs varying from creamy white to Pale Ochraceous-Buff distally; hairs of tail dusky; hind feet whitish or pale buffy.

Skull: Short (in condylobasal length and length of palate and nasals), shallow (in palatofrontal depth), and narrow (across zygomata).

Averages and extremes of 13 females and 10 males from western part of Texas Trans-Pecos (see external measurements) are, respectively, as follows: Condylobasal length, 46.7 (46.0-47.7), 52.4 (49.6-54.7); zygomatic breadth, 29.8 (28.1-31.5), 34.6 (31.4-37.1); palatofrontal depth, 18.4 (18.0-18.8), 20.2 (19.0-21.1); length of palate, 31.5 (31.0-32.2), 35.8 (33.1-37.6); length of nasals, 16.5 (15.5-17.7), 19.3 (18.0-21.5); breadth of braincase, 20.6 (19.8-21.7), 22.0 (22.0-23.8); squamosal breadth, 27.6 (26.7-29.6), 30.8 (28.3-33.1); breadth of rostrum, 10.6 (9.9-11.1), 12.0 (11.1-12.9); length of rostrum, 20.0 (19.2-20.8), 22.8 (21.1-24.5); alveolar length of maxillary tooth-row, 9.4 (8.5-9.9), 9.9 (9.4-10.4).

Comparisons.—For comparison with *P. c. parviceps* and *P. c. consitus,* see accounts of those subspecies.

From *P. c. hirtus, P. c. torridus* differs as follows: Smaller; upperparts averaging paler, more buffy and less reddish; underparts distinctly paler, more pale buff and less ochraceous; skull shorter (condylobasal length and length of palate and nasals) and slightly narrower across zygomata; rostrum longer.

From *P. c. pratensis, P. c. torridus* differs in: Upper parts paler, more buffy and less brownish; skull shorter (in condylobasal length and length of palate and nasals), and shallower; averaging narrower across zygomata and squamosals.

From *P. c. clarkii, P. c. torridus* differs as follows: Smaller; tail shorter; hind foot decidedly shorter; upper parts and underparts slightly paler; skull averaging smaller in all dimensions, without overlap in condylobasal length and palatofrontal depth and with only slight overlap in length of palate and breadth of rostrum.

From *P. c. perplanus* (specimens from upper Pecos River Valley), *P. c. torridus* differs as follows: Smaller; tail and hind foot shorter; skull decidedly smaller in all dimensions; no overlap in condylobasal length, palatofrontal depth, and length of palate; only slight overlap in length of rostrum.

Remarks.—Until recently adequate samples of *Pappogeomys castanops* were not available from the Valentine Plain and adjacent desert lowlands. For instance, when Nelson and Goldman (1934: 138) reviewed the genus *Cratogeomys* they saw only one subadult female from Sierra Blanca, a young female from Valentine, and an adult male from Van Horn. The distinctive features of the population in this area were undetected, and Nelson and Goldman (*op. cit.*:137), mainly on geographic grounds, allocated the three specimens to *Cratogeomys castanops lacrimalis,* here arranged as a synonym of *Pappogeomys castanops perplanus.* Following Nelson and Goldman, Blair and Miller (1949:13) assigned specimens from 10-11 mi. W Valentine to *lacrimalis.* Subsequent authors (Miller and Kellogg, 1955:341 and Hall and Kelson, 1959:466) also referred these pocket gophers to *lacrimalis.*

Study of the specimens mentioned above and additional material labeled with reference to Sierra Blanca and Terlingua discloses that the Valentine Plain population is distinctly smaller cranially than contiguous subspecies, especially *Pappogeomys castanops perplanus* and *Pappogeomys castanops clarkii.* Morphologically, *P. c. torridus* most closely resembles the even smaller subspecies, *Pappogeomys castanops angusticeps,* from the lower Pecos River Valley to the east. Close affinity is also evident between *torridus* and *P. c. pratensis* to the east and *P. c. hirtus* to the northwest, but most parts of the skull of *torridus* are smaller than in either *hirtus* or *pratensis.*

Specimens from within an eight-mile radius of Terlingua differ from typical examples of *torridus* from Sierra Blanca and Valentine in relatively longer tail (50 *versus* 40% of length of head and body), longer hind foot (36 *versus* 34), and, with respect to its length, relatively broader rostrum (55.0 *versus* 51.0%). These variations are indicative of intergradation with the larger and longer-tailed *P. c. clarkii* that occurs nearby in the Río Grande Valley (at Lajitas, mouth of Santa Helena Canyon, and Castalon).

A skin only (TU 3177) from La Mota Rancho, Texas, has a short hind foot (34), and is referred to *torridus* on this basis. Tamsitt (1954:49) previously assigned the specimen to *lacrimalis*. Specimens from Marfa, on the northeastern edge of the Valentine Plain, are referable to *P. c. pratensis;* a larger sample from there probably will show the animals to be intergrades between *torridus* and *pratensis*.

Specimens examined.—Total of 48, all from Texas, as follows: *Hudspeth County:* Bat Cave, Diablo Mts., 1 (TCWC); 1 mi. N and ½ mi E Sierra Blanca, 7 (UI); * 3 mi. W Sierra Blanca, 1 (TCWC); * ¼ mi. W Sierra Blanca, 4 (UI); * Sierra Blanca, 2 (1 USNM, 1 UI); * Methodist Church Yard, Sierra Blanca, 3 (UI); * 3 mi. E Sierra Blanca, 3; 12 mi. N. Allmore, 1 (TCWC). *Culberson County:* Van Horn, about 4000 ft., 1 (USNM). *Jeff Davis County:* Valentine, 1 (USNM). *Presidio County:* * 10 mi. W Valentine, 1 (TU); * 11 mi. W Valentine, 9 (TU); Harper Ranch, 37 mi. S Marfa, 4000 ft., 2 (TCWC); La Mota Rancho, about 3900 ft., 53 mi. S Marfa, 1 (TU). *Brewster County:* 8 mi. N Terlingua, 2700 ft., 3; * Terlingua Creek, 4 mi. E Terlingua, 2200 ft., 9; * Terlingua Creek, 5 mi. S Terlingua, 2200 ft., 1; * 6 mi. S Terlingua, 1.

Pappogeomys castanops ustulatus (Russell and Baker)

Cratogeomys castanops ustulatus Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:598, March 15, 1955 (part); Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:230, June 15, 1956; Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959 (part).

Type.—Female, adult, skull and skin; No. 34589, University of Kansas Museum of Natural History; Don Martín, 800 ft., Coahuila; August 19, 1949; obtained by W. Kim Clark, original number 1034.

Range.—Valley of Río Salado in northeastern Coahuila and northern Nuevo León. See Fig. 3.

Description.—Large for species; tail relatively short (averaging 36% of length of head and body); hind foot short. Averages and extremes of 13 females and measurements of one male, respectively, from the valley of the Río Salado are as follows: Length of head and body, 203 (195-211), 205; length of tail, 74 (64-83), 75; length of hind foot, 36 (35-39), 37.

Color: Pelage of upper parts Dark Mouse Gray basally and from bright Salmon-Buff to rich Apricot-Buff apically, mixed with Bay-tipped hairs on back and top of head, but pure reddish buff on sides and face; pelage of underparts Light Mouse Gray basally overlaid with Light Ochraceous-Buff; hind foot whitish.

Skull: Large for species; palate and nasals long; broad across zygomata and squamosals; rostrum broad and long.

Averages and extremes of 13 females and measurements of one male, respectively, are as follows: Condylobasal length, 51.2 (50.0-52.1), 54.6; zygomatic breadth, 33.0 (31.5-34.1), 37.3; palatofrontal depth, 20.2 (19.0-21.3), 21.2; length of palate, 35.3 (34.5-36.5), 38.2; length of nasals, 18.3 (16.9-19.2), 20.6; breadth of brain case, 21.9 (20.7-23.6), 21.4; squamosal breadth, 29.8 (28.5-31.3), 31.8; breadth of rostrum, 11.7 (11.0-12.5), 13.8; length of rostrum, 21.5 (20.3-22.7), 24.1; alveolar length of maxillary tooth-row, 9.9 (9.3-10.6), 10.3.

Comparisons.—For *P. c. tamaulipensis*, see account of that subspecies. From *Pappogeomys castanops jucundus, P. c. ustulatus* differs as follows: Tail relatively shorter (36 *versus* 40% of length of head and body); upper parts darker and brighter, more rufous and less buffy; skull and palate longer; braincase slightly narrower.

From *Pappogeomys castanops subsimus, P. c. ustulatus* differs as follows: Tail relatively shorter (36 *versus* 45% of length of head and body); upper parts brighter, more rufous and less ochraceous-buff; underparts darker, more ochraceous and less whitish or buffy; skull and palate shorter; rostrum relatively broader (averaging 54.4 *versus* 51.4% of its length).

From *Pappogeomys castanops bullatus, ustulatus* differs, as follows: Larger; tail relatively shorter (36 *versus* 43% of length of head and body); upper parts more bright rufous and less ochraceous; underparts more buffy and less whitish; skull averaging smaller in all dimensions, without overlap in condylobasal length, zygomatic breadth, and length of palate.

Remarks.—Next to *P. c. subsimus, P. c. ustulatus* has the longest skull and palate in the species. The relatively short tail and intensity of rufous color of the upper parts readily distinguish *ustulatus* from other closely related subspecies. The intensity of red color in *ustulatus* is maximal for the species. Of the large subspecies, *ustulatus* most closely resembles *P. c. subsimus,* but the geographic ranges of the two do not meet at present.

P. c. ustulatus occurs on the Gulf Coastal Plain with *Pappogeomys castanops bullatus* and *Pappogeomys castanops tamaulipenses,* but does not closely resemble either of them morphologically. *P. c. ustulatus* on three sides of its range meets *P. c. bullatus* (see remarks in account of *bullatus*) but intergradation between the two has not been demonstrated. Evidently, *ustulatus* differentiated from a stock of large gophers that immigrated out onto the Coastal Plain from the high plateau to the west. The route of dispersal was most likely along the Río Salado. Anyhow, *ustulatus* today occurs only in the valley of that river. Optimum habitat is afforded by the deep, sandy soils. The thin, rocky soils of the desert plains on either side of the valley are inhabited by *P. c. bullatus.*

Even though *ustulatus* may occur farther to the southeast than present record of occurrence show, its geographic range is small. As expected, considering the small size of the geographic range, the samples of *ustulatus* are homogeneous.

Specimens examined.—Total of 17, as follows: Coahuila: Don Martín, 800 ft., 6; * base of Don Martín Dam, 2; * 2 mi. SE Don Martín Dam, along Río Salado, 2; * 5 mi. SE Don Martín, 1. Nuevo León: * 9 mi. N and 2 mi. W Anahuac (= Rodríques), 1; 4 mi. N and 1 mi. W Anahuac (= Rodríques), 5.

subnubilus subspecies-group

Pappogeomys castanops consitus (Nelson and Goldman)

Cratogeomys castanops consitus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:140, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:529 June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:364, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:465, March 31, 1959 (part).

Cratogeomys castanops, Merriam, N. Amer. Fauna, 8:160, January 31, 1895 (part).

[*Cratogeomys*] castanops, Elliot, Field Columb. Publ. 45, Zool. Ser., 2:220, April 10, 1901 (part).

[*Cratogeomys castanops*] *castanops,* Trouessart, Cat. Mamm., 1:573, 1898 (part).

Cratogeomys castanops castanops, Miller, Bull. U. S. Nat. Mus., 79:247, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924 (part).

Type.—Male, young adult, skull and skin; No. 50924 U. S. National Museum; Gallego, 5500 ft., Chihuahua; December 16, 1892; obtained by Clark P. Streator, original number 2416.

Range.—Eastern Chihuahua from Samalayuca and Ojinaga south at least as far as Camargo [= Santa Rosaliá]. See Fig. 3. Altitudinal range 2750 to 5500 feet.

Description.—Small for species (moderate for *subnubilus*-group); tail relatively long (averaging 44% of length head and body); hind foot short. Average and extreme external measurements of seven females and four males, respectively, from northeastern Chihuahua (localities labeled with reference to Samalayuca, Station Arados, Gallegos, Rancho La Campana, Santa Rosaliá, and Ojinaga) are as follows: Length of head and body, 168 (156-178), 202 (190-207); length of tail, 74 (64-82), 91 (80-98); length of hind foot, 34 (32-35), 38 (35-39). Two adult males from Rancho La Campana weighed 348 and 334 grams.

Color: Pelage of upper parts Mouse Gray basally and Light Ochraceous-Buff apically, moderately mixed with Bay-tipped hairs on back, but sides and face pure Light Ochraceous-Buff; underparts Light Mouse Gray overlaid with Pale Ochraceous-Buff; hind feet whitish.

Skull: Small for species; skull, palate, and nasals short; narrow across zygomata, braincase, and squamosals; rostrum narrow and short.

Average and extreme cranial measurements of seven females and four males from northeastern Chihuahua (for localities, see externals measurements above) are, respectively, as follows: Condylobasal length, 44.5 (43.5-45.5), 52.8 (49.9-57.2); zygomatic breadth, 27.8 (27.1-29.4), 36.3 (33.2-40.2); palatofrontal depth, 17.5 (17.1-18.0), 21.2 (19.5-23.5); length of palate, 30.0 (29.3-30.0), 37.0 (34.4-40.1); length of nasals, 15.6 (14.3-16.4), 19.3 (17.0-21.9); breadth of braincase, 19.7 (18.8-20.5), 22.7 (20.7-25.3); squamosal breadth, 25.8 (25.2-26.5), 31.2 (29.2-34.3); breadth of rostrum, 10.0 (9.3-10.7), 12.2 (11.0-13.8); length of rostrum, 18.6 (17.5-19.7), 23.3 (21.9-25.1); alveolar length of maxillary tooth-row, 9.1 (8.6-9.4), 9.5 (9.0-9.6).

Comparisons.—For comparisons with *P. c. surculus* and *P. c. perexiguus,* see accounts of those subspecies.

From *Pappogeomys castanops clarkii* of the *excelsus*-group, *consitus* differs as follows: Smaller; hind foot shorter; upper parts paler, more buffy and less ochraceous, back having fewer Bay-tipped hairs imparting an overall appearance of more buff and less brown on dorsum; underparts paler, more dull buff and less bright ochraceous-buff; skull averaging shorter in all dimensions, without overlap in condylobasal length, zygomatic breadth, palatofrontal depth, length of palate, length of nasals, squamosal breadth, and length of rostrum.

From *Pappogeomys castanops hirtus* of the *excelsus*-group, *P. c. consitus* differs as follows: Smaller; hind foot shorter; upper parts paler, owing to fewer dark-tipped hairs on back; underparts paler, more buffy and less ochraceous; skull averaging significantly shorter in all dimensions except length of maxillary tooth-row; without overlap in condylobasal length, palatofrontal depth, length of palate, length of nasals; squamosal breadth, and length of rostrum.

From *Pappogeomys castanops parviceps* of the *subnubilus*-group, *P. c. consitus* differs as follows: Upper parts darker, less pale buffy; skull shorter; zygomata less widely spreading; nasals and rostrum shorter.

From *Pappogeomys castanops torridus* of the *excelsus*-group, *consitus* differs as follows: Smaller; hind foot shorter; upper parts and underparts paler, more buffy and less ochraceous; skull averaging shorter in all dimensions, without overlap in condylobasal length and squamosal breadth, and with only slight overap in palatofrontal depth and length of palate.

Remarks.—Recent attempts to obtain additional specimens of *P. c. consitus* from the south-central part of its range have not been successful. Extensive trapping in the area around Ciudad Chihuahua, Rosales, Ciudad Delicias, Camargo, Jiménez, Valle de Allende, Hidalgo del Parral, and Escalón failed to reveal the presence of this species, although *Thomomys* was abundant at these localities. Specimens of *P. c. consitus* were taken at Camargo [= Santa Rosalia] in 1895, but the species may not occur there today. The scarcity or absence of *Pappogeomys castanops* in this part of Chihuahua may be due to the extreme degree of aridity that presently characterizes this area. *P. c. consitus* is common north and east of Ciudad Chihuahua, except in the northeasternmost part of the state from Samalayuca and Banderas (on the Río Grande) north to Ciudad Juarez. This area now is occupied by *Geomys arenarius.* Recent trapping near Samalayuca yielded *Geomys arenarius* and not *P. c. consitus. G. arenarius* is abundant in the cultivated areas of the Río Grande Valley of northeastern Chihuahua, south-central New Mexico, and in Texas from Fort Hancock north to El Paso.

P. c. consitus is a small subspecies, and is distinguished from adjacent subspecies of the *subnubilus*-group by the combination of dark color, short skull, relatively broad rostrum, long hind foot, and relatively long tail. External and cranial dimensions closely approximate those of *Pappogeomys castanops perexiguus,* but the darker upper parts of *consitus* distinguish it at once from the significantly paler *perexiguus. P. c. consitus* is also readily distinguished from adjacent subspecies of the *excelsus*-group, *P. c. clarkii, P. c. torridus, and P. c. hirtus,* by its remarkably smaller skull. Most of the cranial dimensions of *consitus* do not overlap those of the larger subspecies; condylobasal length and squamosal breadth are especially different.

P. c. consitus and *P. c. clarkii* are evidently sympatric in the Valley of the Río Grande around the town of Ojinaga in Chihuahua. *P. c. consitus* was obtained in thin, stony soil 1 mi. S Ojinaga. *P. c. clarkii* was trapped at several localities in and near Ojinaga (for exact localities, see account of *clarkii* above), mostly in deep, sandy alluvium. In Chihuahua, *clarkii* occurs only in the Río Grande Valley around Ojinaga; therefore, the population of *clarkii* west of the Río Grande probably represents a relatively recent invasion from populations east of the river.

The larger *clarkii* has replaced *consitus* in the well-developed soils of the flood plain and cultivated areas. Whether *clarkii* extends westward in the Valley of the Río Conchos has not been determined. In this area, *consitus* is probably restricted to the thinner, upland soils for the most part, as is the case elsewhere in areas where subspecies of the *subnubilus* and *excelsus* groups appear to be sympatric.

Pappogeomys castanops parviceps is comparable in size to the subspecies of the *subnubilus*-group, but is isolated from other small subspecies and from *consitus* by the ranges of large subspecies of the *excelsus*-group and the range of *Geomys arenarius* in the Río Grande Valley. *P. c. parviceps* occurs in the Tularosa Basin of New Mexico northeast of the present range occupied by *consitus.* There is no evidence indicating present contact between *consitus* and *parviceps,* but the possibility of contact in the past cannot be ruled out in view of their close geographic proximity.

Specimens examined.—Total of 23, all from Chihuahua, as follows: Samalayuca, 2 (USNM); 3½ mi. ESE Los Lamentos, 1420 mts., 1; 3 km. E El Sueco, 1 (AMNH); Gallego, 5500 ft., 1 (USNM); 40 mi. E Gallego, 5000 ft., 5 (PA); Rancho La Campana, 1470 mts., 2 (AMNH); *12 km. W Encinilla, 5000 ft., 1 (AMNH); Station Arados, about 5000 ft., 1; 1 mi. S Ojinaga, about 2750 ft., 5; Santa Rosalía [= Camargo], 4025 ft., 4 (USNM).

Pappogeomys castanops elibatus new subspecies

Type.—Female, adult, skull and skin; No. 58092 University of Kansas Museum of Natural History; 12 mi. W San Antonio de las Alazanas, about 7500 ft., Coahuila; January 10, 1954; obtained by Robert W. Dickerman, original number 2268.

Range.—High intermontane valleys of Sierra Madre Oriental in southeastern Coahuila. See Fig. 3. Altitudinal range 7200 to 8700 feet.

Diagnosis.—Small for species; tail relatively short (averaging 38% of length of head and body); hind foot short. Average and extreme external measurements of eight females and seven males, respectively, from localities labeled with reference to San Antonio, Bella Unión, Arteaga, and Saltillo, are as follows: Length of head and body, 177 (153-182), 183 (171-193); length of tail, 67 (62-70), 74 (67-85); length of hind foot, 33 (31-34), 34 (31-38).

Color: Upper parts Mouse Gray basally and Ochraceous-Buff apically, back with mixture of black-tipped hairs on back but sides and face pure Ochraceous-Buff; underparts Light Mouse Gray basally overlaid with Pale Ochraceous-Buff, brighter Light Ochraceous-Buff along mid-ventral line, basal color shows through imparting overall blackish-gray appearance to underparts; hind feet dark brown, except for whitish hairs at base of toes.

Skull: Small for species; narrow across zygomata; palate long; relatively broad across braincase and squamosals; rostrum broad and relatively long (averaging 42% of condylobasal length); nasals and maxillary tooth-row short.

Average and extreme cranial measurements for 10 females and seven males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 43.4 (42.0-44.5), 47.3 (46.4-48.8); zygomatic breadth, 27.7 (26.4-28.6), 31.7 (30.7-33.2); palatofrontal depth, 17.1 (16.6-17.9), 18.8 (17.7-19.8); length of palate, 28.8 (27.5-30.1), 32.0 (31.2-34.1); length of nasals, 14.5 (13.6-15.3), 16.3 (15.5-17.5); breadth of braincase, 21.2 (20.6-22.0), 21.9 (20.5-22.7); squamosal breadth, 26.2 (25.1-26.8), 28.4 (27.5-29.9); breadth of rostrum, 9.2 (8.6-10.1), 9.9 (9.1-10.5); length of rostrum, 18.3 (17.2-19.0), 20.2 (19.7-20.8); alveolar length of maxillary tooth-row, 8.4 (7.5-8.9), 9.0 (8.3-9.7).

Comparisons.—From *Pappogeomys castanops subnubilus, elibatus* differs as follows: Larger; tail relatively shorter (averaging 38 *versus* 44% of length of head and body); hind foot longer; underparts darker, more ochraceous and less buffy; skull longer; zygomata more widely spreading; palate longer; narrower across braincase and squamosals; rostrum longer.

From *Pappogeomys castanops planifrons, elibatus* differs as follows: Slightly larger; tail relatively shorter (averaging 38 *versus* 45% of length of head and body); hind foot shorter; upper parts paler, more ochraceous-buff and less cinnamon; underparts brighter, more ochraceous and less buffy; skull shorter; zygomata less widely spreading; palate shorter.

From *Pappogeomys castanops subsimus, elibatus* differs as follows: Smaller; tail and hind foot shorter; upper parts decidedly darker, apically more ochracous nad less yellowish-buff, back more heavily overlaid with black; underparts darker, more ochraceous and less buffy; hind foot darker, more brownish and less whitish; skull remarkably smaller in all respects, without overlap in any dimension except breadth of braincase.

Remarks.—*Pappogeomys castanops* of the northeastern part of the Sierra Madre Oriental in Coahuila clearly is one of the *subnubilus*-group of small subspecies, and previously has been referred to *Pappogeomys castanops planifrons* by Russell and Baker (1955: 607), Baker (1956:228) and Hall and Kelson (1959:466) on the basis of dark coloration and large size (for the *subnubilus*-group). Detailed comparisons with large series of *planifrons* from southwestern Tamaulipas disclose that the Coahuila population differs significantly from *planifrons* in smaller skull, especially in length, but is decidedly larger, both externally and cranially, and darker than *Pappogeomys castanops subnubilus,* the other subspecies that occupies adjacent range.

Intergradation with *planifrons* is not demonstrated in any of the available samples; nevertheless, I judge *elibatus* to be more closely allied to *planifrons* than to *subnubilus.* Specimens of *subnubilus* from Laguna, Nuevo León, average slightly larger than typical *subnubilus* from southeastern Coahuila, and may reflect intergradation bentween *subnubilus* and *elibatus.* The specimens are more nearly like *subnubilus* to which they are referred. The disparity in size between *elibatus* and the large subspecies of the *excelsus*-group to the north, especially *Pappogeomys castanops subsimus,* is so great that intergradation probably does not occur. But, no specimens are known, in the area where intergradation might occur, from localities that are close together geographically.

This subspecies is common in the wide grass-covered valleys west and southwest of San Antonio de las Alazanas, Coahuila. Burrows there can be found between those of the prairie dog, *Cynomys mexicanus,* but the burrows of *elibatus* are more abundant in the thinner, rocky soils on the valley slopes near the edge of the pine forest zone and prairie dog burrows are more abundant in the deeper soils on the valley floor. The dark color of the pelage closely matches the dark color of the soils of volcanic origin that furnish the substrate in this area.

Specimens examined.—Total of 51, all from Coahuila, as follows: 4 mi. S and 6 mi. E Saltillo, 7500 ft., 7; * 12 mi. S and 2 mi. E Arteaga [=Artegia], 7500 ft., 11; * 7 mi. S and 4 mi. E Bella Unión, 7200 ft., 15; * 12 mi. W San Antonio de las Alazanas, 16; 2 mi. E and 2 mi. N San Antonio de las Alazanas, 8700 ft., 2.

Pappogeomys castanops parviceps new subspecies

Type.—Female, adult, skull and skin; No. 87152 University of Kansas Museum of Natural History; 18 mi. SW Alamogordo, 4400 feet, Otero Co., New Mexico; June 30, 1961; obtained by M. Raymond Lee, original number 4067.

Range—Tularosa Basin of south-central New Mexico, northward into Estancia Valley, eastward, through high pass between Sacramento and Guadalupe mountain ranges into western fringe of high plains east of Sacramento mountains, and southward along western foothills of Guadalupe mountains into north-central part of Trans-Pecos area of Texas. See Fig. 3. Altitudinal range 4030 to 6000 feet.

Diagnosis.—Small for species; hind food short. Averages and extremes of seven females and measurements of one male respectively, from south-central New Mexico (localities labeled in reference to Carasal, Tularosa, Alamogordo, and Picacho) are as follows: Length of head and body, 169 (160-177), 178; length of tail, 72 (69-84), 70; length of hind foot, 33 (29-35), 34. Holotype (adult female), and an adult male paratype weighed 188 and 255 grams, respectively.

Color: Ground color of dorsum light reddish brown, hairs Cinnamon-Buff apically, back appearing darker than sides owing to mixture of black-tipped hairs, basally hairs of upper parts Mouse Gray; underparts Light Mouse Gray overlaid with creamy-white to Pinkish-Buff; hind feet whitish dorsally; hairs of tail pale buffy.

Skull: Small; rostrum narrow and short; maxillary tooth-row long relative to length of skull.

Averages and extremes of seven females and measurements of one male, respectively (see localities with external measurements), are as follows: Condylobasal length, 45.5 (44.1-46.4), 47.9; zygomatic breadth, 28.3 (26.6-29.2), 31.0; palatofrontal depth, 18.0 (17.5-18.7), 18.9; length of palate, 30.6 (29.4-31.2), 32.2; length of nasals, 16.3 (15.5-16.9), 17.6; breadth of braincase, 19.8 (19.4-20.3), 21.1; squamosal breadth, 26.2 (25.4-26.8), 28.9; breadth of rostrum, 9.9 (9.5-10.3), 10.6; length of rostrum, 19.7 (19.2-20.5), 21.2; alveolar length of maxillary tooth-row, 9.1 (8.6-9.6), 9.4.

Comparisons.—For comparison with *P. c. consitus,* see account of that subspecies.

From *P. c. hirtus, P. c. parviceps* differs as follows: Smaller; hind foot shorter; paler; underparts more whitish and less ochraceous-buff; skull averaging significantly less in all dimensions except in breadth of braincase and length of maxillary toothrow (which are only slightly less), and without overlap in condylobasal length, length of palate, and breadth across squamosals; nasals shorter and rostrum especially narrower and shorter.

From *P. c. torridus, P. c. parviceps* differs as follows: Smaller; hind foot shorter; slightly paler (uper parts more buffy and less brownish); skull shorter; narrower across zygomata and squamosals; palate decidedly shorter; rostrum slightly narrower.

From *P. c. perplanus, P. c. parviceps* differs as follows: Smaller; shorter tail and especially hind foot; paler (upper parts more light brownish and less dark reddish-brown; underparts more light buffy and less ochraceous); skull averaging smaller in all dimensions, especially condylobasal length, length of palate and nasals, palatofrontal depth, and breadth across zygomata, squamosals, and rostrum, and without overlap in all dimensions except length of maxillary tooth-row.

From *P. c. pratensis, P. c. parviceps* differs as follows: Smaller; hind foot shorter; skull averaging smaller in all dimensions, especially in condylobasal length, palatofrontal depth, length of palate, and breadth across zygomata and squamosals.

Remarks.—Bailey (1932:242), the first to investigate these pocket gophers in this part of New Mexico, referred two females from 9 mi. S Tularosa, two females from a branch of Panasco Creek, and a subadult male from Ancho, all in New Mexico, to *Cratogeomys castanops* [= *C. c. castanops*]. Benson (1933:26), following Bailey, assigned a female from the White Sands of New Mexico to *C. c. castanops.* The next year, Nelson and Goldman (1934:242) allocated the specimens examined by Bailey (*loc. cit.*) to their new subspecies *Cratogeomys castanops lacrimalis.* Subsequent authors followed Nelson and Goldman (*loc. cit.*).

My study of the above mentioned specimens and additional materials from Carasal (Bernalillo County); 5 mi. and 18 mi. SW Alamogordo; 3 mi. S Picacho, all in New Mexico; and Pine Springs Canyon, Texas (in the Guadalupe Mountains of Texas), reveals that they pertain to an undescribed subspecies, characterized by a remarkably small skull, for which I propose the name *P. c. parviceps.* It resembles the larger *P. c. torridus.* Most of the geographic range of *parviceps* is separated from that of *hirtus* by the high, and almost continuous, range of mountains that begins in the north with the Sandia Mountains and terminates in the south with the Organ Mountains. Several low passes, such as San Augustin pass, probably permit limited contact between the two subspecies.

An adult (PA 17212), if sexed correctly as a female, from the foot of Pine Canyon, a low east-west pass through the Guadalupe Mountains, approximates *perplanus* of the large *excelsus* group in condylobasal length (48.2), length of palate (32.4), length of nasals (17.2), and squamosal breadth (27.0). Another adult female (PA 17211) from the same place is typical in all respects of *parviceps* of the small *subnubilus* group. Specimens from Pine Springs Canyon and 7 mi. N Pine Springs (but not specimens from the collection of the Academy of Natural Sciences at Philadelphia) were referred to *lacrimalis* by Davis (1940:79) and Davis and Robinson (1944:267). Examination of these specimens proves them also to be referable to *parviceps.* Both *parviceps* and *perplanus* occur sympatrically in the canyon; however, there is no indication of intergradation here.

An adult female (MCZ 10554) from Carasal, New Mexico, is identified as *parviceps.* I have not been able to locate Carasal on any map, nor has James S. Findley (*in litt.*) of the University of New Mexico, but he informs me that specimens of *Thomomys,* labeled as from the same locality in the same year (1901), are referable to a subspecies that occurs to the east of the Sandia Mountains. Therefore, Carasal is presumed to be in eastern Bernalillo County.

Specimens examined.—Total of 21, as follows: New Mexico: *Bernalillo County:* Carasal, 1 (MCZ); *Lincoln County:* Ancho, 1 (USNM); 3 mi. S Picacho, 5300 ft., 4 (PA); *Otero County:* 9 mi. S Tularosa, 2 (USNM); 5 mi. SW Alamogordo, 1; 18 mi. SW Alamogordo, 4400 ft., 3; * White Sands, 18 mi. SW Alamogordo, 4030 ft., 1 (MVZ); branch of Penasco Creek, 15 mi. S Weed (east slope of Sacramento Mts.), 6000 ft., 2 (USNM).

Texas: *Culberson County:* 7 mi. N Pine Springs, 1 (TCWC); * mouth of Pine Springs Canyon, Guadalupe Mts., 1 (TCWC); * foot of Pine Canyon (= Pine Springs Canyon), Guadalupe Mts., 5740 ft., 4, (PA, Nos. 17211, 17213-17215).

Pappogeomys castanops perexiguus new subspecies

Type.—Female, adult, skull and skin; No. 55584 University of Kansas Museum of Natural History; 6 mi. E Jaco, Chihuahua, 4500 ft., *in* Coahuila; March 18, 1953; obtained by Gerd H. Heinrich, original number 6262.

Range.—Northwestern and west-central Coahuila and probably adjacent parts of southeastern Chihuahua. See Fig. 3. Altitudinal range 4000 to 4500 feet.

Diagnosis.—Small for species; tail relatively long (averaging 44% of length of head and body); hind foot short. Average and extreme external measurements of seven females and four males, respectively, from western Coahuila (localities labeled with reference to Jaco, Australia, Hundido, Tanque Alvarez, and Ocampo) are, as follows: Length of head and body, 165 (151-183), 198 (177-212); length of tail, 73 (68-78), 87 (80-94); length of hind foot, 33 (31-36), 36 (34-36).

Color: Upper parts Light Mouse Gray basally and Light Ochraceous-Buff (summer pelage) to Pinkish Buff (winter pelage) apically, with some Bay-tipped hairs on back and top of head, but sides and face pure Light Ochraceous-Buff or Pinkish Buff; underparts Pale Mouse Gray overlaid with white or Light Buff; hind feet white.

Skull: Small for species; zygomata not widely spreading; nasals relatively long; palate and maxillary tooth-row short; narrow across braincase and squamosals; rostrum narrow and short.

Average and extreme cranial measurements of seven females and four males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 44.4 (42.6-45.8), 51.6 (50.1-53.8); zygomatic breadth, 28.2 (27.3-28.8), 32.0 (29.6-33.8); palatofrontal depth, 17.8 (17.1-18.3), 19.7 (18.6-20.4); length of palate, 30.2 (29.4-31.0), 35.6 (34.3-37.1); length of nasals, 15.9 (15.3-16.2), 18.9 (18.2-19.6); breadth of braincase, 20.2 (19.7-21.0), 21.1 (19.9-22.7); squamosal breadth, 26.5 (25.7-27.0), 30.4 (28.3-32.8); breadth of rostrum, 9.9 (9.4-10.3), 12.0 (10.3-12.9); length of rostrum, 18.5 (17.9-19.2), 22.5 (20.9-23.8); alveolar length of maxillary tooth-row, 8.9 (8.1-9.4), 9.3 (9.1-9.6).

Comparisons.—From *Pappogeomys castanops consitus, perexiguus* differs as follows: Hind foot shorter; upper parts decidedly paler, more buffy and less ochraceous; zygomata more widely spreading; broader across braincase and especially squamosals.

From *Pappogeomys castanops surculus, P. c. perexiguus* differs as follows: Smaller; hind foot relatively longer (averaging 44 *versus* 36% of length of head and body); upper parts decidedly paler, more light buff and less ochraceous, back less densely set with dark-tipped hairs imparting an overall paler appearance to dorsum; hind foot paler, whitish rather than buffy; skull shorter and shallower; palate slightly shorter; maxillary tooth-row relatively longer.

From *Pappogeomys castanops excelsus* of the *excelsus*-group, *P. c. perexiguus* differs as follows: Decidedly smaller; tail and especially hind foot shorter; upper parts slightly paler, more light buffy and less yellowish-buff; skull decidedly smaller, averaging smaller in all dimensions and without overlap in condylobasal length, zygomatic breadth, palatofrontal depth, length of palate, length of nasals, squamosal breadth, and length of rostrum.

From *Pappogeomys castanops sordidulus* of the *excelsus*-group, *perexiguus* differs as follows: Decidedly smaller; tail relatively longer (averaging 44 *versus* 39% of length of head and body); hind foot shorter:; upper parts paler, more light buff and less bright ochraceous; skull remarkably smaller, averaging decidedly less in all dimensions, without overlap in condylobasal length, zygomatic breadth, palatofrontal depth, length of palate, length of nasals, squamosal breadth and length of rostrum.

From *Pappogeomys castanops jucundus* and *Pappogeomys castanops clarkii*, both of the *excelsus*-group, *P. c. perexiguus* differs in the same way that it does from *sordidulus.*

From *Pappogeomys castanops subsimus* of the *excelsus*-group, *perexiguus* differs in the same way that it does from *P. c. excelsus*.

Remarks.—The basis for recognition of *perexiguus* is the combination of short and broad cranium, relatively long tail, long hind foot, and especially remarkably pale color. *P. c. perexiguus* is the palest subspecies of *Pappogeomys castanops* being matched in pallor only by some of the palest individuals of *P. c. excelsus* of the large subspecies group. *P. c. perexiguus* is decidedly paler than its two neighbors of the small (*subnubilus*) group of subspecies, *consitus* and *surculus,* and color alone separates *perexiguus* from both of its close relatives. Of the two, *perexiguus* more closely resembles *consitus* in external and cranial dimensions.

Specimens of *perexiguus* from 3 mi. N and 9 mi. E El Pino, 6 mi. E Jaco, and 3 mi. NE Sierra Mojada formerly were referred to *Cratogeomys castanops consitus* by Russell and Baker (1955:602), Baker (1956:226), and Hall and Kelson (1959:465). Specimens from 50 mi. N and 20 mi. W Ocampo, 18 mi. S and 14 mi. E Tanque Alvarez, were previously allocated to *Cratogeomys castanops sordidulus* by Russell and Baker (*op. cit.*:602), Baker (*op. cit.*:229), and Hall and Kelson (*op. cit.*:468). A specimen of *perexiguus* from 20. S El Hundido was assigned to *Cratogeomys castanops excelsus* by Russell and Baker (*op. cit.*:603) and Baker (*op. cit.*:227).

The range of *P. c. perexiguus,* a member of the *subnubilus*-group, interdigitates with, or perhaps overlaps in part, the ranges of two of the large subspecies of the *excelsus*-group, *P. c. excelsus* and *P. c. sordidulus* (See Fig. 3). *P. c. perexiguus* is remarkably smaller than its two large neighbors, and there is no indication of intergradation with either of them in any of the samples available from the areas of contact. Because reproductive incompatability occurs elsewhere at places where the small and large forms have been trapped together, intergradation of *perexiguus* with either *excelsus* or *sordidulus* is not expected.

The continuous chain of mountains formed by the north-south oriented Sierra del Pino-Sierra de la Madera-Sierra de San Marcos ranges separates most populations of *perexiguus* from those of the *excelsus*-group to the east; however open desert flats in northwestern Coahuila, north of the Sierra del Pino and south of the Río Grande, provides a corridor for the movement of pocket gophers between the Llano de Ocampo on the eastern side of the mountain range and the desert plains to the west. *P. c. perexiguus* has evidently extended its range eastward through this pass, and it now occurs on the Llano de Ocampo with *sordidulus.* Whether the two have mutually exclusive ranges on the Llano or overlap in distribution but with niche exclusion (that is to say, the general ranges overlap without the two occurring in the same local habitat) is not certain; at least the two have not been trapped at the same place and *sordidulus* seems to occur exclusively in the southern part of the Llano south of the town of Ocampo. If their ranges are sympatric, they would be so in the northern part of the Llano. Mountains close off the Llano to the east and south, probably preventing further eastward movement of the small *subnubilus*-group in this area.

In the Bolsón de Mapimí in west-central Coahuila and adjacent parts of Chihuahua, *P. c. excelsus* seems to be more common in the deep, sandy soils in the lower parts of the basin, in areas formerly covered by the large Pleistocene lake that occupied most of the basin. Records of *perexiguus* are mainly from the desert uplands were the soils are thinner and the vegetation more sparse. Colonies of *perexiguus* are widely scattered over the arid desert flats, and individuals are only locally abundant. The sample from 21 mi. S and 11 mi. E Australia, on the western slope of the Sierra de Alameda, is well within the range of *excelsus* suggesting that the ranges of the two may also overlap in this area.

Intergradation between *perexiguus* and adjacent subspecies of the *subnubilus* group can not be demonstrated with present examples. Specimens of *Pappogeomys* from southeastern Chihuahua are not available, although intergradation with *consitus* and possibly *surculus* would be expected in this area. Efforts to secure specimens from this extremely arid desert have not been successful. Vegetation is sparse and the soils are thin and rocky in most places. Since no evidence of pocket gophers has been noted, *Pappogeomys* probably does not occur in this area at present, but these subspecies probably were joined by continuous distributions in the past. Extremes of aridity developed in the post-Wisconsin and may have resulted in their separation in the immediate past.

Specimens examined.—Total of 20, all from western Coahuila, as follows: 3 mi. N and 9 mi. E El Pino, 1; 50 mi. N and 20 mi. W Ocampo, 4150 ft., 1; 18 mi. S and 14 mi. E Tanque Alvarez, 4000 ft., 4; 6 mi. E Jaco, Chihuaua, *in* Coahuila, 4500 ft., 6; 3 mi. NE Sierra Majada, 1; 20 mi. S Hundido, 1; 21 mi. S and 11 mi. E Australia, 4400 ft., 6.

Pappogeomys castanops peridoneus (Nelson and Goldman)

Cratogeomys castanops peridoneus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:148, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:365, March 6, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Dalquest, Louisiana State Univ. Studies, Biol. Sci. Ser., 1:102, December 28, 1953; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959.

Type.—Male, adult, skull and skin; No. 82049 U. S. National Museum; Río Verde, 3000 ft., San Luis Potosí; January 10, 1897; obtained by E. W. Nelson and E. A. Goldman, original number 10,423.

Range.—Eastern San Luis Potosí, 2 mi. NW Tepeyac south to Río Verde. See Fig. 3. Known from altitudes of 3000 and 3400 feet.

Description.—Decidedly small for species; tail moderately long (averaging 42% of length of head and body in females); hind foot short. Average and extreme external measurements of six females from Río Verde and 2 mi. NW Tepeyac, and the measurements of one male from the latter place, are, respectively, as follows: Length of head and body, 162 (148-172), 175; length of tail, 69 (62-74), 78; length of hind foot, 31 (30-32), 35.

Color: Upper parts Mouse Gray basally and Cinnamon Buff apically, back heavily overlaid with black-tipped hairs imparting an overall blackish-brown appearance, sides and face pure Cinnamon Buff; underparts Light Mouse Gray overlaid with Pale Ochraceous-Buff; dorsal surface of hind feet dusky.

Skull: Smallest of species, especially well expressed in condylobasal length, length of palate, and breadth across squamosals; braincase and rostrum narrow; nasals, maxillary tooth-row, and rostrum short; narrow across zygomata.

Average and extreme cranial measurements of six females and the measurements of one male (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 39.9 (38.9-41.3), 45.4; zygomatic breadth, 26.3 (25.0-27.5), 31.9; palatofrontal depth, 16.4 (15.7-17.2), 18.3; length of palate, 26.7 (25.9-27.7), 30.2; length of nasals, 13.4 (12.3-14.6), 15.2; breadth of braincase, 19.5 (18.9-21.3), 21.1; squamosal breadth, 23.7 (22.3-25.4), 26.1; breadth of rostrum, 8.9 (8.1-9.6) 10.2; length of rostrum, 17.1 (16.4-18.2), 20.9; alveolar length of maxillary tooth-row, 8.3 (7.5-9.0), 8.6.

Comparisons.—For comparisons with *P. c. rubellus,* see account of that subspecies.

From *Pappogeomys castanops planifrons, peridoneus* differ as follows: Smaller; tail relatively shorter (averaging 42 *versus* 45% of length of head and body); hind foot decidedly shorter; underparts brighter, more ochraceous and less buffy; skull averaging smaller in all dimensions, without overlap in condylobasal length and length of palate.

From *Pappogeomys castanops subnubilus, peridoneus* differs, as follows: Slightly larger; tail relatively shorter (averaging 42 *versus* 44% of length of head and body); upper parts darker, more heavily overlaid with blackish; underparts brighter, more ochraceous and less buffy; hind feet darker, more brownish and less whitish; skull decidedly shorter, as expressed in condylobasal length and length of palate; narrower across squamosals.

Remarks.—*P. c. peridoneus* is characterized by having the smallest skull in the species. In this respect, *peridoneus* is approached only by *P. c. subnubilus,* but the skull of *peridoneus* is signficantly shorter and the two subspecies differ markedly in color. Moreover the ranges of the two are separated geographically by the ranges of *P. c. rubellus* and *P. c. planifrons. P. c. peridoneus* is readily distinguished by numerous cranial and external features from both *rubellus* and *planifrons,* although *peridoneus* closely resembles *planifrons* in coloration of the dorsum.

P. c. peridoneus seems to be restricted to the interior basin immediately west of the Sierra Madre Oriental in south-central San Luis Potosí. *P. c. rubellus* occupies the higher plateau to the west of the Río Verde Basin and *planifrons* occurs in the high country to the north. Intergradation has not been demonstrated with either of these larger neighbors.

Specimens examined.—Total of 16, all from San Luis Potosí, as follows: 2 mi. NW Tepeyac, 3400 ft. (14 mi. N and 29 mi. W Cudiad del Maíz), 6; Río Verde, about 3000 ft., 10 (USNM).

Pappogeomys castanops planifrons (Nelson and Goldman)

Cratogeomys castanops planifrons Nelson and Goldman, Proc. Biol. Soc. Washington, 47:146, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 29, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959; Alvarez, Univ. Kansas Publ. Mus. Nat. Hist., 14:428, May 20, 1963 (part).

Cratogeomys castanops tamaulipensis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:141, June 13, 1934 (part); Miller and Kellogg, Bull. U. S. Nat. Mus., 205:342, March 3, 1955 (part); Hall and Kelson, The Mamamls of North America, 1:468, March 31, 1959 (part).

Type.—Male, adult, skull and skin; No. 93942 U. S. National Museum; Miquihuana, Tamaulipas; June 9, 1898; obtained by E. W. Nelson and E. A. Goldman, original number 12527.

Range.—Intermontane valleys of Sierra Madre Oriental and eastern edge of Central Plateau in southwestern Tamaulipas northward into southeastern Nuevo León. See Fig. 3. Altitudinal range 2500 to 6500 feet.

Description.—Small for species; tail relatively long (averaging 45% of length of head and body); hind foot short. Average and extreme external measurements of eight females and three males, respectively, from the type locality, Jaumave, and Tula, Tamaulipas, are as follows: Length of head and body, 174 (163-185), 181 (149-199); length of tail, 78 (65-91), 81 (76-85); length of hind foot, 34 (32-36), 36 (35-38).

Color: Upper parts Mouse Gray basally and Cinnamon apically, back heavily overlaid with black-tipped hairs imparting an overall brownish-black appearance, sides and face pure Cinnamon Buff; underparts Light Mouse Gray overlaid with Light Buff; hind feet dusky.

Skull: Small for species; palate, nasals, and entire skull short; narrow across zygomata and squamosals; rostrum narrow and short; maxillary tooth-row moderately long.

Average and extreme cranial measurements for eight females and three males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 44.7 (43.6-45.9), 49.2 (48.6-49.2); zygomatic breadth, 28.3 (27.3-29.7), 33.7 (32.6-35.0); palatofrontal depth, 17.7 (17.2-18.5), 19.6 (19.2-20.0); length of palate, 29.6 (28.5-30.1), 33.1 (32.7-33.9); length of nasals, 15.1 (14.4-16.3), 17.0 (15.6-18.2); breadth of braincase, 21.3 (20.3-22.4), 22.9 (22.7-23.2); squamosal breadth, 26.2 (25.1-27.0), 29.9 (29.6-39.5); breadth of rostrum, 9.5 (8.8-10.2), 11.1 (10.6-11.9); length of rostrum, 18.5 (17.2-19.6), 20.8 (20.2-21.6); alveolar length of maxillary tooth-row, 8.9 (8.2-9.5), 9.7 (9.5-10.0).

Comparisons.—For comparisons with *P. c. peridoneus*, *P. c. rubellus*, *P. c. subsimus*, and *P. c. elibatus*, see accounts of those subspecies.

From *Pappogeomys castanops tamaulipensis* of the *excelsus*-group, *planifrons* differs as follows: Smaller; tail relatively longer (averaging 45 *versus* 42% of length of head and body); hind foot shorter; upper parts darker, more cinnamon and less buffy apically and back more heavily overlaid with blackish; skull decidedly smaller in all dimensions, respective ranges of variation without overlap in condylobasal length, length of palate and rostrum, and breadth across zygomata and squamosals.

Remarks.—*P. c. planifrons* is a small, dark subspecies occurring primarily in the intermontane valleys of the Sierra Madre Oriental. The markedly dark pigmentation of the upper parts, especially the back, and hind foot may be a response to the more mesic environments of the mountains compared with the more arid environment of the plateau to the west. Both *Pappogeomys castanops* *elibatus* and *Pappogeomys castanops peridoneous* approximate *planifrons* in their dark coloration, but differ from *planifrons* in other features. Also, both *elibatus* and *peridoneus* live in mesic environments in or along the fringe of the Sierra Madre Oriental.

The skull of *planifrons* is small, and, in general, resembles that of other subspecies of the *subnubilus* group, but is distinguished by a relatively short palate, broad braincase, long tooth-row, and narrowness across the zygomata. Some of these features are shared with *P. c. elibatus, P. c. rubellus,* and *P. c. subnubilus,* but the combination of them is diagnostic for *planifrons.*

Specimens from 15 mi. W Montemorelos, in the foothills about six miles from the front range of the Sierra Madre Oriental according to Goldman (1951:206-207), have been previously referred to *P. c. tamaulipensis.* The specimens are small and dark and typical in all respects of *planifrons.*

The range of *planifrons* evidently does not meet that of any of the large subspecies of the *excelsus*-group. The range of *P. c. tamaulipensis* in the valley of the Río Grande is separated from that of *planifrons* by the thorn-forest desert plains of northern Tamaulipas and eastern Nuevo León. No pocket gophers are known from that region.

Specimens examined.—Total of 35, as follows: **Nuevo León:** 15 mi. W Montemorelos (labeled only as "Montemorelos," see Goldman, 1951:206), 2500 ft., 5 (USNM); Dr. Arroyo, 1 (USNM). **Tamaulipas:** Miquihuana, 6400 ft., 22 (6 USNM, 7 MCZ, 9 KU); 4 mi. N Jaumave, 2500 ft., 5; 8 mi. N Tula, 4500 ft., 1; * 9 mi. SW Tula, 3900 ft., 1.

Pappogeomys castanops rubellus (Nelson and Goldman)

Cratogeomys castanops rubellus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:147, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Hooper, Jour. Mamm., 29:302, August 31, 1948; Dalquest, Louisiana State Univ. Studies, Biol. Sci. Ser. No. 1: 101, December 29, 1953; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959.

Cratogeomys castanops planifrons, Alvarez, Univ. Kansas Publ. Mus. Nat. Hist., 14:428, May 20, 1963 (part).

Type.—Male, adult, skull, and skin; No. 20507 Mus. Comp. Zool. (Sanford Collection); Soledad, near San Luis Potosí 6400 ft., San Luis Potosí; August 1, 1923; obtained by W. W. Brown, original number unknown.

Range.—High, arid plateau of extreme east-central Zacatecas across central San Luis Potosí to extreme western Tamaulipas. See Fig. 3. Altitudinal distribution 5500 to 7200 feet.

Description.—Size medium for species; tail moderately long (averaging 40% of length of head and body); hind foot short to moderately long. Average and extreme external measurements for six females and six males, respectively, from southwestern Tamaulipas and southwestern San Luis Potosí (specimens labeled with reference to Nicolás, Tamaulipas, and Soledad, Herradura, Matehuala, city of San Luis Potosí, and Presa de Guadalupe, San Luis Potosí) are as follows: Length of head and body, 184 (175-191), 211 (200-244); length of tail, 73 (66-80), 80 (67-94); length of hind foot, 34 (32-35), 37 (33-40). Two females from Nicolás, Tamaulipas, weighed 189 and 214 grams.

Color: Upper parts Mouse Gray basally and Ochraceous-Buff to Ochraceous-Orange apically, with some Bay-tipped hairs on back and top of head, but pure Ochraceous-Orange on sides and face; underparts Mouse Gray overlaid with Light Ochraceous-Buff; hind foot whitish.

Skull: Small for species; palate, rostrum, and nasals short (nasals averaging 84.7% of palatofrontal depth); narrow across zygomata and squamosals; rostrum relatively broad (averaging 55.8% of length); maxillary tooth-row long.

Average and extreme cranial measurements of six females and six males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 46.3 (45.5-47.2), 52.5 (50.5-54.3); zygomatic breadth, 29.8 (28.6-30.8), 36.2 (34.8-38.1); palatofrontal depth, 18.3 (17.9-18.8), 20.5 (19.3-21.5); length of palate, 31.0 (29.8-32.1), 35.7 (34.2-37.0); length of nasals, 15.4 (14.4-16.3), 18.1 (17.4-18.7); breadth of braincase, 21.0 (20.2-21.8), 22.4 (20.9-24.4); squamosal breadth, 26.8 (25.5-27.5), 31.2 (29.1-34.7); breadth of rostrum, 10.6 (9.5-11.4), 12.5 (12.0-12.9); length of rostrum, 19.0 (17.9-19.3), 23.0 (22.3-24.0); alveolar length of maxillary tooth-row, 9.2 (8.9-9.8), 9.5 (8.9-10.4).

Comparisons.—For comparisons with *P. c. subnubilus* and *P. c. surculus,* see accounts of those subspecies.

From *Pappogeomys castanops goldmani, rubellus* differs as follows: Slightly smaller; tail relatively longer (40 *versus* 38% of length of head and body); upper parts brighter, more ochraceous-orange and less ochraceous-buff; skull decidedly shorter; narrower across zygomata and especially squamosals; nasals especially shorter (averaging 85 *versus* 94% of palatofrontal depth); palate and rostrum shorter; rostrum relatively broader (averaging 56 *versus* 52% of its length).

From *Pappogeomys castanops planifrons, rubellus* differs, as follows: Larger; tail relatively shorter (averaging 40 *versus* 45% of length of head and body); upper parts brighter, more ochraceous-orange and less buffy, back less heavily overlaid with blackish giving pelage an overall paler appearance; underparts darker, more ochraceous and less buffy; hind foot paler, more whitish and less dusky; skull longer; broader across zygomata; palate longer; braincase slightly narrower; rostrum broader and slightly longer; maxillary tooth-row slightly longer.

From *Pappogeomys castanops peridoneus, rubellus* differs as follows: Larger; tail and especially hind foot longer; upper parts paler, less heavily overlaid with blackish; underparts paler, more ochraceous and less buffy; skull smaller in all dimensions, especially in condylobasal length, zygomatic breadth, palatofrontal depth, length of palate, squamosal breadth, and length of maxillary tooth-row.

Remarks.—*P. c. rubellus* is one of the small subspecies of the *subnubilus*-group. In geographic range it is contiguous with four of the other seven subspecies of the group, namely *P. c. peridoneus, P. c. planifrons, P. c. subnubilus,* and *P. c. surculus,* and, also, with *P. c. goldmani,* one of the large subspecies of the *excelsus*-group. Like other subspecies of the *subnubilus*-group, *rubellus* has a small skull that is especially short and relatively broad. In females, the parietal impressions meet at the midline but usually do not fuse or produce a bladelike crest, but instead unite into a thickened, elevated ridge. These features clearly identify *rubellus* as a member of the *subnubilus*-group.

P. c. rubellus differs from all other subspecies of the *subnubilus*-group in its distinctly larger body. In this feature, *rubellus* more closely resembles its large neighbor, *P. c. goldmani* to the west than it does other members of the *subnubilus*-group. In fact, *rubellus* provides a link in a graded series beginning with *P. c. excelsus* and followed by *P. c. goldmani,* both large subspecies of the *excelsus*-group. *P. c. rubellus* comes next in the sequence that terminates with *P. c. planifrons.* Length of head and body in *P. c. excelsus* averages 197 (184-209), a length characteristic of the group of large subspecies; in *P. c. goldmani* the average is 189 (178-199), in *P. c. rubellus,* 184 (175-191), and in *P. c. planifrons* 174 (163-185). The measurements of *planifrons* are representative of the other subspecies of the *subnubilus*-group. The intermediate sizes of *goldmani* and *rubellus* suggest the leveling influence of gene flow between these two subspecies—a decrease in size of *goldmani* and an increase in size of *rubellus. P. c. goldmani* and *P. c. rubellus* are connecting links between what would otherwise be two species.

Interbreeding between *rubellus* and *goldmani* is demonstrated in the series of *rubellus* from Villa de Cos in southeastern Zacatecas by an adult female (KU 58146) that is notably larger than *rubellus* in cranial dimensions, especially condylobasal length, zygomatic breadth and length of rostrum. In these respects, as well as in an intermediate squamosal breadth, the specimen agrees with *goldmani.* Length of palate and nasals of the same specimen are as in *rubellus.* Other specimens in the series do not differ from typical *rubellus;* therefore, the series is referred to that subspecies.

Cranially, *rubellus* is the largest of the *subnubilus*-group, although the skull is decidedly smaller than that of the *excelsus*-group. The large size may indicate the genetic influence of the large subspecies through *goldmani;* but, compared with *goldmani,* cranial dimensions of *rubellus* are more disparate than are external dimensions.

Intergradation of *rubellus* with *P. c. planifrons* is not evident in any of the available samples. The two subspecies closely resemble each other and no continuous barrier to unrestricted interbreeding is apparent. The two probably intergrade in a narrow zone where their ranges meet. Ridges of the Sierra Nevada Occidental may preclude geographic contact in some areas. Specimens from 4½ mi.

SW Herradura in west-central San Luis Potosí suggest intergradation with the smaller subspecies *Pappogeomys castanops surculus*, also of the *subnubilus*-group. One female (KU 58153) of this series is evidently an adult but is significantly smaller than typical *rubellus*. Cranial measurements of this one specimen agree with those of *surculus* as known from specimens from 8 mi. S Majoma, Zacatecas, about 40 miles to the northwest. Other specimens of the series are typical of *rubellus*.

As previously mentioned by Dalquest (1953:101), many specimens from this region are spotted with white. Of 36 examples taken in recent years from eastern Zacatecas and western San Luis Potosí, 32 (89%) have white spots. The spots, although varying in size, form a definite pattern on each individual. They occur either on the belly, the sides (immediately anterior to the thighs), or on the rump. In some individuals spots occur in all three regions, and those individuals are as much white as ochraceous. The incidence of spotting exceeds subspecific boundaries, and includes specimens of *rubellus* from 6 mi. S Matehuala, 4½ mi. SW Herrandura, Presa de Guadelupe, and 7 km. W Presa de Guadelupe, all in San Luis Potosí, and Villa de Cos, Zacatecas; specimens of *P. c. subnubilus* from 15 mi. S Concepción del Oro, Zacatecas; and specimens referred to *P. c. surculus* from 8 mi. SW Majoma. Of eight specimens of *P. c. surculus* from Concepción del Oro to the north only two have small spots. None of the 33 specimens of *rubellus* taken in 1923 at Morelos, the city of San Luis Potosí, and Soledad to the southeast is spotted. Elsewhere in the range of *P. castanops* an occasional individual has white spots, but the incidence of spotting is nowhere nearly so high as in this region, suggesting that the mutation that prevents normal pigmentation occurred locally and has spread. The occurrence of spotting in adjacent populations of the three subspecies that are affected by this conspicuous mutant provides unusually clear evidence of the pattern of gene flow between them.

Specimens examined.—Total of 73, as follows: **Zacatecas:** Villa de Cos, 6700 ft., 8. **San Luis Potisí:** 6 km. S Matehuala, 2 (LSU); 4½ mi. SW Herradura, 7200 ft., 8; 7 km. W Presa de Guadalupe, 4 (LSU); * Presa de Guadalupe, 2 (LSU); Morales, 31 (MCZ); City of San Luis Potosí, 1 (MCZ); Soledad, 4 (MCZ). **Tamaulipas:** Nicolás, 56 km. NM Tula, 5500 ft., 13.

Pappogeomys castanops subnubilus (Nelson and Goldman)

Cratogeomys castanops subnubilus Nelson and Goldman, Proc. Biol. Soc. Washington, 47:145, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:366, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Russell and Baker, Univ. Kansas Publ. Mus. Nat. Hist., 7:607, March 15, 1955; Baker, Univ. Kansas Publ. Mus. Nat. Hist., 9:229, June 15, 1956 (part); Hall and Kelson, The Mammals of North America, 1:466, March 31, 1959.

Type.—Male, adult, skull and skin; No. 79482 U. S. National Museum; Carneros, Coahuila; August 12, 1896; obtained by E. W. Nelson and E. A. Goldman, original number 10018.

Range.—Southeastern Coahuila, western Nuevo León, northern San Luis Potosí and northeastern Zacatecas, west of the main body of the Sierra Madre Oriental. See Fig. 3. Altitudinal range 5500 to 6900 feet.

Description.—Small for species; tail relatively long (averaging 44% of length of head and body); hind foot short. Average and extreme external measurements of 13 females and 10 males, respectively, from southeastern Coahuila, southeastern Zacatecas and western Neuvo León are as follows: Length of head and body, 162 (144-171), 177 (161-197); length of tail, 71 (64-77), 75 (62-86); length of hind foot, 31 (29-34), 33 (30-36). An adult female from 7 mi. NW Providencia, Neuvo León, weighed 133.6 grams.

Color: Hairs of upper parts Mouse Gray basally and Ochraceous-Buff apically, heavily mixed with black-tipped hairs on back and top of head, but pure Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with Light Ochraceous-Buff along mid-ventral line and Pale Ochraceous-Buff elsewhere; hind feet reddish-brown.

Skull: Small for species, short and shallow; zygomata not widely spreading; palate, nasals, and maxillary tooth-row short; narrow across braincase and squamosals; rostrum narrow and short.

Average and extreme cranial measurements of 14 females and nine males (for localities, see externals measurements above) are, respectively, as follows: Condylobasal length, 41.3 (40.4-42.2), 45.4 (44.0-46.5); zygomatic breadth, 26.5 (24.6-27.9), 30.6 (29.2-31.8); palatofrontal depth, 16.7 (16.1-17.3), 17.8 (17.5-18.6); length of palate, 27.6 (26.5-28.7), 30.4 (28.9-31.0); length of nasals, 13.9 (12.7-15.3), 15.3 (14.0-16.4); breadth of braincase, 20.0 (18.6-21.6), 21.3 (20.3-23.1); squamosal breadth, 24.7 (23.9-26.3), 27.7 (26.4-30.2); breadth of rostrum, 8.8 (8.1-9.8), 9.9 (9.5-10.2); length of rostrum, 17.2 (16.0-18.4), 19.1 (17.8-20.2); alveolar length of maxillary tooth-row, 8.3 (7.8-8.9), 8.6 (8.3-9.4).

Comparison.—For comparisons with *P. c. elibatus, P. c. surculus,* and *P. c. peridoneus,* see accounts of those subspecies.

From *Pappogeomys castanops planifrons, subnubilus* differs as follows: Smaller; tail and especially hind foot shorter; underparts paler, more buffy and less bright ochraceous; hind foot paler, more reddish and less blackish; skull averaging smaller in all dimensions, without overlap in condylobasal length and length of palate.

From *Pappogeomys castanops rubellus, subnubilus* differs as follows: Smaller; tail relatively longer (averaging 44 *versus* 40% of length of head and body); hind foot shorter; upper parts darker, less bright ochraceous and more heavily overlaid with black on back; hind foot darker, more reddish brown and less whitish; skull averaging smaller in all dimensions, without overlap in condylobasal length, zygomatic breadth, palatofrontal depth, and length of palate and maxillary tooth-row.

From *Pappogeomys castanops goldmani, subnubilus* differs as follows: Decidedly smaller; tail relatively longer (averaging 44 *versus* 38% of length of head and body); hind foot shorter; upper parts darker, less bright ochraceous and more heavily overlaid with black on back; hind foot darker, reddish-brown rather than white; skull remarkably smaller, without overlap in dimensions except breadth of braincase and slight overlap in breadth of rostrum.

From *Pappogeomys castanops subsimus*, *subnubilus* differs as follows: Decidedly smaller; tail and especially hind foot shorter; upper parts darker, more ochraceous and less yellowish-buff, and more heavily overlaid with black on back; hind foot darker, reddish-brown instead of black; skull remarkably smaller, without overlap in all dimensions, except for slight overlap in breadth of braincase, and especially smaller in condylobasal length (averaging 41.3 *versus* 52.4 in females), palatofrontal depth (averaging 16.7 *versus* 20.8), length of palate (averaging 27.6 *versus* 37.0), and squamosal breadth (averaging 24.8 *versus* 31.7).

Remarks.—*P. c. subnubilus* and *P. c. periodoneus* are the two smallest subspecies of *Pappogeomys castanops.* Compared with other subspecies of the *subnubilus*-group, *subnubilus* is characterized by the combination of short skull, relatively broad braincase, short nasals and maxillary tooth-row, relatively broad rostrum, short hind foot, long tail, and dark coloration. *P. c. subnubilus* is remarkably smaller, both externally and cranially, than the large subspecies of the *excelsus*-group.

Intergradation with neighboring subspecies of the *subnubilus*-group is evident in several samples of *subnubilus.* Specimens from Laguna, Nuevo León, are slightly larger than more typical examples of *subnubilus* from southeastern Coahuila, suggesting intergradation with either *P. c. elibatus* or *P. c. planifrons,* both of which are larger than *subnubilus.* Specimens of *subnubilus* from 1 mi. W Dr. Arroyo, Neuvo León, are larger externally and have longer and deeper skulls indicating intergradation with *P. c. planifrons* to the east. Specimens from Lulú, Zacatecas, show approach to *P. c. rubellus* to the south in slightly broader rostrum and longer tooth-row.

Although the ranges of *subnubilus* and *subsimus* meet south of General Cepeda in the Sierra de Gudalupe, and specimens of both subspecies have been trapped less than two miles apart (for additional comments and discussion, see account of *subsimus*), there is no evidence of intergradation. *P. c. subsimus* and *subnubilus* differ greatly in size and cranial proportions, and it is doubtful that the two interbreed in those few places where their ranges are contiguous. Rather they probably behave as full species, owing to complete reproductive isolation.

P. c. subnubilus is morphologically closer to *P. c. peridoneus* than to any other subspecies. Although the ranges of the two are now separated by other subspecies, it is likely that the two shared a common gene pool in the past. Possibly in late Pleistocene all the region south of the Sierra de Gaudalupe-Sierre de Parras mountain ranges was occupied by small pocket gophers resembling modern *subnubilus* and *peridoneus.* Trends toward increase in size in some populations may account for the differentiation of the larger subspecies *elibatus, planifrons, rubellus* and *surculus* in this region, and *subnubilus* and *peridoneus* may have remained relatively unchanged.

Specimens examined.—Total of 81, as follows: **Coahuila:** Domingo Cañon, Sierra de Guadalupe, 6700 ft., 11 mi. S and 4 mi. W General Cepeda, 1; 1 mi. N Agua Nueva, 5500 ft., 1; * Carneros, 6800 ft., 6 (USNM); * 1 mi. S Carneros, 6000 ft., 4; * 2 mi. W San Miguel, 5500 ft., 3; * 8 mi. N La Ventura, 6000 ft., 10; *La Ventura, 5600 ft., 8 (6 USNM, 2 MCZ). **Zacatecas:** 3 mi. N Lulú, 13 (MVZ); * Lulú, 1 (MVZ); 15 mi. S Concepción del Oro, 6900 ft., 3. **Nuevo León:** 7 mi. NW Providencia, 6800 ft., 6; Laguna, 6; * 5 mi. W Ascensión, 15; 1 mi. W Dr. Arroyo, 5800 ft., 4.

Pappogeomys castanops surculus new subspecies

Type.—Female, adult, skull and skin; No. 62470 University of Kansas Museum of Natural History; La Zarca, Durango; May 29, 1954; obtained by Robert W. Dickerman, original number 3361.

Range.—Eastern Durango and northern Zacatecas. See Fig. 3. Altitudinal range 3800 to 7600 feet.

Diagnosis.—Small for species; tail relatively short (averaging 36% of length of head and body); hind foot short. Average and extreme external measurements of six females from localities labeled with reference to La Zarca, Durango, and four males from Concepción del Oro and 8 mi. S Majoma, Zacatecas, are, respectively, as follows: Length of head and body, 178 (165-188), 195 (177-212); length of tail, 64 (60-69), 76 (71-85); length of hind foot, 30 (27-32), 36 (34-39). Two adult females from 7 mi. NW La Zarca weighed 195 and 168 grams.

Color: Upper parts Mouse Gray basally and Ochraceous-Buff apically, back with scattered black-tipped hairs imparting an overall dark brownish appearance to dorsum, but sides and face pure Ochraceous-Buff; underparts Light Mouse Gray overlaid with Light Buff or white; hind feet buffy or whitish.

Skull: Small for species, but moderately large for *subnubilus*-group; skull, palate, and nasals short; zygomata widely spreading relative to length of skull; cranium deep and broad, especially across braincase, relative to length of skull; rostrum narrow and short.

Average and extreme cranial measurements of six females and four males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 45.2 (44.0-46.1), 48.3 (47.3-50.3); zygomatic breadth, 28.9 (28.1-29.7), 33.7 (31.7-35.4); palatofrontal depth, 18.4 (17.7-18.9), 19.0 (17.6-20.3); length of palate, 30.8 (29.7-31.9), 32.5 (31.7-34.3); length of nasals, 15.9 (14.4-17.3), 17.3 (16.0-18.9); breadth of braincase, 20.1 (19.5-20.5), 21.6 (20.3-23.0); squamosal breadth, 26.4 (25.7-27.9), 28.6 (26.2-30.2); breadth of rostrum, 9.5 (8.9-9.9), 11.0 (10.3-11.7); length of rostrum, 18.5 (17.1-19.1), 20.9 (19.9-22.6); alveolar length of maxillary tooth-row, 8.7 (8.5-9.0), 9.0 (8.6-9.4).

Comparisons.—For comparison with *P. c. perexiguus,* see account of that subspecies.

From *Pappogeomys castanops subnubilus, surculus* differs as follows: Larger; tail relatively shorter (averaging 36 *versus* 44% of length of head and body); hind foot shorter; back less heavily overlaid with black; hind foot paler, more buffy and less reddish-brown; skull longer and deeper; zygomata more widely spreading; palate and nasals longer; breadth across squamosals greater; rostrum broader and longer.

From *Pappogeomys castanops rubellus, surculus* differs as follows: Slightly smaller; tail relatively shorter (averaging 36 *versus* 40% of length of head and body); hind foot shorter; upper parts and underparts paler, more dull buffy and less bright ochraceous; skull shorter; zygomata less widely spreading; braincase narrower; rostrum narrower and slightly shorter; maxillary tooth-row shorter.

From *Pappogeomys castanops goldmani, surculus* differs as follows: Smaller; tail and hind foot shorter; skull decidedly shorter; zygomata less widely spreading; palate and especially nasals shorter; breadth across braincase and squamosals less; rostrum narrower and decidedly shorter; maxillary tooth-row shorter.

From *Pappogeomys castanops excelsus, surculus* differs as follows: Decidedly smaller; tail and especially hind foot shorter; upper parts darker, more brownish and less yellowish-buff; underparts darker, more buffy and less whitish; skull decidedly shorter and shallower; breadth across zygomata less; palate and nasals especially shorter; narrower across braincase and squamosals; rostrum markedly narrower and shorter; maxillary tooth-row shorter; cranial dimensions without overlap in condylobasal length, zygomatic breadth, length of palate, squamosal breadth, and breadth and length of rostrum.

From *Pappogeomys castanops consitus, surculus* differs as follows: Smaller; tail relatively shorter (averaging 36 *versus* 44% of length of head and body); hind foot shorter; upper parts darker, more ochraceous and less buffy, and back more heavily set with black hairs imparting an overall dark brownish rather than pale buffy appearance to dorsum; underparts darker, more buffy and less whitish; skull slightly longer and deeper; zygomata more widely spreading; palate longer; breadth across squamosals slightly greater; rostrum narrower (averaging 51 *versus* 54% of length); maxillary tooth-row slightly shorter.

Remarks.—*P. c. surculus* applies to the population inhabiting the plateau uplands of northern Zacatecas and north-central Durango. The combination of long and deep skull, widespread zygomata, long plate and nasals, broad crainium, relatively short tail, and long hind foot distinguish *surculus* from neighboring subspecies of the *subnubilus*-group. The geographic range of *surculus* is contiguous with that of *Pappogeomys castanops excelsus* where the elevated plateau of Durango slopes down into the Bolsón de Mapimí. The contrast in size, especially in cranial features, between *surculus* and *excelsus* is as great as between small and large species of other geomyids. Specimens of *surculus* from 12 mi. W Lerdo and specimens of *excelsus* from 4 mi. WSW Lerdo show no sign of gene exchange. No evidence of intergradation elsewhere between the two is known, and it is doubtful that they interbreed.

The range of *surculus* broadly overlaps that of *Pappogeomys castanops goldmani* (see Fig. 3), one of the large, or *excelsus*, group of subspecies, without interbreeding. *P. c. goldmani* is intermediate in size between the large subspecies *excelsus* and the small subspecies *rubellus*, and *goldmani* interbreeds with both. It should be pointed out that *rubellus* is the largest subspecies of the *subnubilus*-group, and itself forms part of the reproductive link between the *excelsus*-group and *subnubilus*-group. In north-central Durango where *surculus* and *goldmani* are sympatric, the two act toward each other as full species. In the area of sympatry, *goldmani* seems to be restricted to the valleys of the Río Nazas and Río Aguanaval, and their larger tributaries, and *surculus* occurs most commonly in the uplands and on the elevated desert flats. Both *goldmani* and *surculus* have been taken in the valley of the Río Nazas, 6 mi. NW Rodeo, Durango. At this locality *goldmani* was the more common, and only two of the females of the twelve specimens are referable to *surculus*. Identification of two young individuals of this sample is uncertain, but both are tentatively referred to *goldmani*. The two females are fully adult but are remarkably smaller than adult females of *goldmani* from the same locality. Noteworthy cranial dimensions of the two females of *surculus* (KU 62472 and 62475) and three adult females of *goldmani* (KU 62477, 62479, and 62480), all from the Río Nazas Valley, 6 mi. NW Rodeo, are compared in Table 2. The metric characters listed are those that readily separate *surculus* from *goldmani* (see Table 2).

Specimens of *surculus* from Concepción del Oro and 8 mi. S Majoma, Zacatecas, are not typical of *surculus* in all respects. These samples are characterized by shorter skulls than typical

TABLE 2.

	P. c. surculus		*P. c. goldmani*		
	62472	62475	62477	62479	62480
Condylobasal length..........	45.9	45.4	49.0	48.1	48.1
Length of palate.............	30.8	30.4	32.8	32.7	32.3
Squamosal breadth...........	26.7	27.4	29.3	28.0	29.0

surculus from Durango (six females averaging 44.4 rather than 45.2), longer rostra (averaging 19.2 compared with 18.5), and longer hind foot (averaging 34 instead of 30). The longer hind foot and rostrum of these gophers suggests intergradation with *P. c. rubbellus* to the southeast and the shorter skull suggests intergradation with *P. c. subnubilus* to the east. Although other dimensions vary, as is to be expected on geographic grounds, none of the other features differs significantly from the condition in *surculus* from north-central Durango. These specimens resemble *surculus* more than they do any of the other adjacent subspecies.

Intergradation with *P. c. rubellus* is further suggested in the sample of *rubellus* from 4½ mi. SW Herradura, San Luis Potosí. One adult (KU 58153) of this sample is markedly smaller than typical *rubellus;* the dimensions of that individual closely approximate those of *surculus* as known from specimens from eastern Zacatecas. The specimens from 7 mi. NW La Zarca referred by Baker and Greer (1962:96) to *P. c. consitus* are here referred to *surculus.*

Specimens examined.—Total of 30, as follows: **Durango:** 7 mi. NW La Zarca, 6000 ft., 5 (MSU); * La Zarca, 6050 ft., 2; 12 mi. E La Zarca, 6000 ft., 2; San Juan, 12 mi. W Lerdo, 3800 ft., 2 (UMMZ); Río Nazas, 4200 ft., 6 mi. NW Rodeo, 2 (Nos. 62472 and 62475). **Zacatecas:** Concepción del Oro, 7680 ft., 8; 8 mi. S Majoma, 7700 ft., 9.

Pappogeomys merriami

(Synonymy under subspecies)

Range.—Southeastern part of Central Plateau of México, southern end of Sierra Madre Oriental, and eastern part of Neovolcanic Range. See Fig. 5. Known altitudinal range from 5400 feet in Atlixco Basin in southwestern Puebla to 13,500 feet, above timber line, on Mount Popocatépetl, but most specimens have been taken at places between 7300 and 10,500 feet elevation.

Diagnosis.—Medium to large for subgenus, both externally and cranially; rostrum massive; incisors huge, diameter more anteroposteriorly than transversely; squamosals extending medially with age over lateral part of parietals, completely covering parietals, at least in old males; broader across zygomata than across squamosals; angular processes short; occlusal surface of M3 obcordate, its posterior loph elongated, forming conspicuous heel in all subspecies except *peraltus.*

Description.—Size medium to large; extreme measurements of adult females and males are, respectively: Length of head and body, 180-253, 200-285; length of tail, 71-119, 74-126; length of hind foot, 36-49, 38-53.

Color: Pelage of upper parts varying in overall tones from pale yellowish-buff to glossy black, back and top of head with some reddish-brown or black-tipped hairs imparting darker tone than on sides and face; underparts paler than dorsum, varying from pale buff to bright ochraceous or rufous, but usually

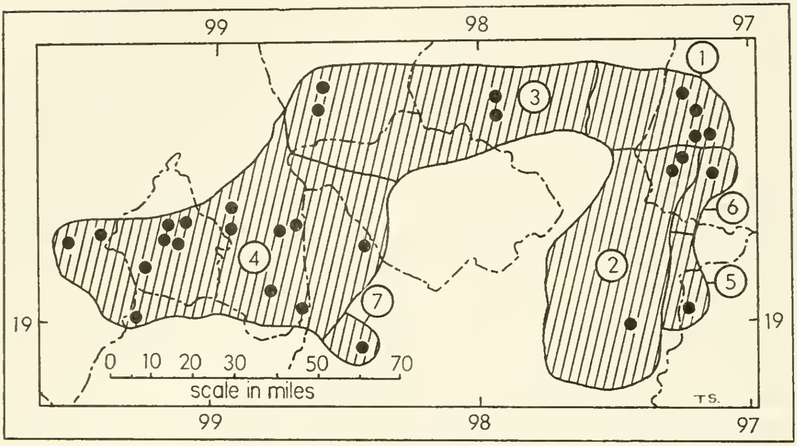

FIG. 5. *Pappogeomys merriami.*

Guide to subspecies:
1. *P. m. estor*
2. *P. m. fulvescens*
3. *P. m. irolonis*
4. *P. m. merriami*
5. *P. m. peraltus*
6. *P. m. perotensis*
7. *P. m. saccharalis*

black like dorsum in melanistic individuals; all hairs grayish basally; dorsal surface of hind feet whitish, except in melanistic individuals; auricular patch small, usually blackish.

Skull: Medium sized to large (condylobasal length 51.3 to 62.6 in females and 57.4-74.5 in males); broader across zygomata than across squamosals; angular process short; length of mandible more than breadth across mandibles (over angular processes); squamosals expanded medially in adults, covering at least lateral part of parietals (completely covering parietals in males); postglenoid notch well developed; incisors and rostrum massive; basioccipital wedge-shaped, broader posteriorly than anteriorly; paroccipital processes relatively small; M3 usually elongated (except in *peraltus*), posterior loph enlarged posteriorly forming conspicuous heel that is inclined labially producing obcordate occlusal surface; labial re-entrant fold usually deep, and lateral enamel plates long, persisting throughout life.

Relationships.—Diagnostic features of the subgenus *Cratogeomys* are well developed in *Pappogeomys merriami,* the type species of the subgenus. Of living species, *merriami* is closely allied to *Pappogeomys castanops* but is more specialized. Specializations in *merriami* include larger size, more massive rostrum and incisors, medial expansion of squamosal, and elongation of posterior loph of M3. Each of these features is a modification of the more generalized stock of the subgenus, best expressed, among living species of *Cratogeomys,* by *Pappogeomys castanops.* But, *merriami* and *castanops* resemble each other in basic cranial morphology and, due to their close relationship are arranged in the same species-group.

Compared with species of the *gymnurus*-group, *merriami*, like *castanops*, is more generalized and lacks the highly specialized cranial features that characterize the extreme condition of platycephaly developed in the *gymnurus*-group. Judging from their morphology, *merriami* and *castanops* are only distantly related to the *gymnurus*-group. For example, the skull of *merriami* is deeper and narrower; the breadth across the zygomatic arches exceeds the breadth across the squamosals; the incisors are more massive; the squamosal expands medially, not laterally; the lambdoidal crest is convex, rather than sinuous (in dorsal outline); the angular processes are distinctly shorter; M3 is elongate rather than subtriangular; and the paroccipital processes are distinctly smaller, and not developed into a flangelike projection. Evidently, *merriami* is less divergent from the ancestral stock of the subgenus than are the species of the *gymnurus*-group. But, M3 in *P. merriami* is more specialized than in the *gymnurus*-group. Elongation of the heel on M3, and rotation of its apex to the labial side producing an obcordate surface, are specializations not developed in the *gymnurus*-group.

Habitat.—Pappogeomys merriami is an upland species. The lower limits of its range are on the elevated Central Plateau rarely below 7000 feet, and the species ranges to higher elevations in adjacent mountains, especially the eastern part of the Neovolcanic massif and the southern part of the Sierra Madre Oriental. Some of the highest peaks on the North American continent are within the borders of its range. As would be expected in a region having such a highly diversified physiography, there is a wide range of climatic conditions, soil types, and vegetation zones. Moreover, environmental conditions usually change over relatively short distances. *Pappogeomys merriami* is adapted to most of the major environmental situations within its range excepting those in the tropical and nival areas. As in other species of geomyids, the factor determining local occurrence, in most instances, is edaphic.

In broad view, the species occurs in two generalized habitats: the plateau characterized by arid conditions, sandy soils, and xerophytic vegetation, and the mountains characterized by mesic conditions, volcanic soils, and boreal forests. During the pluvial cycles of the late Pleistocene the boreal forest zone occurred at lower elevations than it does today, and much of the plateau was probably wooded. Evidently, *Pappogeomys merriami* is primarily adapted to forest associations, and has secondarily become adapted to the more arid environments of the plateau in post-Wisconsin time.

In the boreal forest, this species lives as much in the woods as in the more open, montaine meadows. Probably, the woody shrubs and forbs that grow beneath the forest canopy offer a source of food. Large numbers of these gophers were found in a mesic pine-fir-sacatón grass association west of Monte Rió Frió. The black volcanic earth at this locality was so saturated with moisture as to be slushy underfoot. The species also occurs in drier situations, especially in mixed forest associations of pine and oak at lower elevations. It is a common inhabitant of open, grassy intermontane meadows everywhere in the mountains, and Davis (1944:386) obtained specimens from above timber line, but below the snow fields, on the northern slope of Popocatépetl. Musser (1964:8) trapped specimens in northern Puebla in fallow fields adjoining mixed forest of pine, oak, and fir and from a grazed meadow and open, cultivated fields at slightly lower elevations in the same area. Davis (*op. cit.*:387-388) also found this species to be common in open, cultivated fields in the pine-oak zone on the north slope of Cofre de Perote and the lower hills to the north.

On the plateau, *Pappogeomys merriami* is common on the southern rim of the Valley of México in the lowlands along the base of the Sierra Ajusco, Ixtaccíhuatl, and Popocatépetl. This area is mantled in deep, sandy soils and supports a semiarid grassland, much of which is now under cultivation. The valley populations of *Pappogeomys merriami* are continuous with those in the adjoining mountains. To the north the species occurs on the Plain of Apam in southwestern Hidalgo, an agricultural district on the arid tableland northeast of the Valley of México. Colonies of this species occupy areas in the basin where dark reddish sandy loam soils are developed. The populations in the Apam Basin and the Valley of México are probably discontinuous at present. The less elevated Atlixco Basin, an arid valley at the southern edge of the Central Plateau in southwestern Puebla, also supports a population of *Pappogeomys merriami.* The basin, mantled in sandy soils, is now extensively cultivated.

The soils in most of south-central Puebla and eastern Tlaxcala are black clays, unsuitable for *Pappogeomys merriami;* no sign of these gophers was found in such soils. But, the species is common in the light-colored sands on the arid desert plain in eastern Puebla and west-central Veracruz, west of the Sierra Madre Oriental.

Evidently those areas of clay soils in central Puebla and eastern Tlaxcala function as a barrier to gene flow between western and eastern populations on the plateau.

Geographic variation.—Relative to the size of its geographic range, *Pappogeomys merriami* is characterized by a wide range of geographic variation. Seven subspecies are here recognized, and with two exceptions, each is sharply distinguished from the others. The degree of differentiation of the subspecies suggests that *Pappogeomys merriami* is an old species with a long evolutionary history. Perhaps much of the divergence within the species preceded the time of Wisconsin glaciation; however, environmental changes due to moist conditions in Wisconsin time in central México may have accelerated the final stages of differentiation.

Earlier authors, considering the degree of distinction among the subspecies and the abruptness of their geographic boundaries, assigned specific status to most of the named kinds. For example, *perotensis, estor, fulvescens, oreocetes, peregrinus,* and *merriami* were considered to be species by Merriam (1895), and Nelson and Goldman (1934) recognized *perotensis, fulvenscens,* and *merriami,* but reduced the other named kinds to subspecific rank. Nelson and Goldman also described several new subspecies one of which was *C. m. irolonis,* later elevated by Davis (1944:387) to specific rank. However, Davis (*op. cit.*:386) synonymized *oreocetes* and *perigrinus* with *merriami.* Subsequent authors, therefore, have recognized four species, *merriami, irolonis, perotensis,* and *fulvescens.* Even though the taxa under consideration are sharply defined, in my opinion they are referable to one polytypic species.

Pappogeomys merriami is predominantly reddish-brown, although melanism is common in populations of *P. m. merriami* living in the mountains around the southern end of the Valley of México (for detailed discussion, see account of that subspecies). Melanism is unknown in *perotensis, estor,* and *peraltus* living at equally high elevations and in dark volcanic soils in the Sierra Madre Oriental at the eastern limits of the range of the species. Only *P. m. fulvescens* departs markedly from the usual coloration, being characterized by tones of pale yellowish-buff. The pale color of *fulvescens* closely approximates the pale color of the sands, the most common soil type on the desert plain. The most arid part of the range of *Pappogeomys merriami* in this desert region is in the rain shadow of the Sierra Madre Oriental. The pallor of *fulvescens* indicates prolonged evolutionary adaptation to arid conditions in eastern Puebla and west-central Veracruz during the late Pleistocene.

The configuration of M3 is especially variable in *Pappogeomys merriami*. The occlusal surface of M3 is obcordate with a short posterior loph. Moreover, the posterior loph is so twisted to the side that its posterior apex forms the labial border of the loph and its lingual plate lies transversely along the posterior border of the tooth. The anterior and posterior lophs are separated by a labial re-entrant fold, imparting a heart-shaped occlusal configuration to the tooth. In *merriami, saccharalis,* and *fulvescens,* occurring in the western part of the range of the species, the posterior loph of M3 is decidedly more elongated than in *perotensis, estor,* and *peraltus,* at the eastern margin of the range. But, the length of the heel varies individually and geographically. Maximum elongation occurs in *fulvescens* and especially *merriami,* but the posterior loph in *irolonis,* especially in the mountains of northern Puebla, is intermediate in length between the shorter heel of the eastern and the longer heel of the western subspecies. Individual variation in length of the posterior loph is greatest in *fulvescens* and *merriami.* In *fulvescens,* in which the posterior loph is smallest, the shape of the occlusal surface closely resembles that in *perotensis, estor,* and *peraltus* except that the posterior loph is less inclined labially in *fulvescens.* This somewhat intermediate condition suggests gene exchange between *fulvescens* and *estor.*

The lower incisor is characterized by a distinct bevel behind the labial edge of the enamel plate. The bevel separates a narrow shelf or bead from the bulk of the tooth. The bevel is especially deep and the bead well-developed in *merriami, irolonis,* and *saccharalis.* Although present, the bevel is shallow and the bead indistinct in *perotensis, estor,* and *peraltus.* Neither bevel nor bead is evident in *fulvescens.*

P. m. fulvescens differs from other kinds of *Pappogeomys merriami* in several other cranial features. For instance, the dorsal profile of the skull is convex rather than straight (also convex in some specimens of *estor*), the incisors are less massive, the rostrum is not so robust, and the posterior part of the skull is remarkably narrower. The breadth across squamosals averages only 56.1 per cent of condylobasal length in *fulvescens* instead of 62.2 in *merriami,* 63.2 in *irolonis,* 62.7 in *saccharalis,* 61.1 in *estor,* and 61.0 in *perotensis.* In *perotensis, estor,* and especially *fulvescens* the zygomata are broadest across their anterior angles. In *merriami* and *irolonis,* the zygomata are nearly parallel-sided, and in *saccharalis* the zygomata are bowed at their middle rather than at their anterior end. *P. m. perotensis* is unique in the construction of the jugal. Usually the anterior end of the jugal is expanded into a broad plate, but in *perotensis* it is remarkably slender.

Maximum size is attained in the western part of the range of the species. Condylobasal length and squamosal breadth reach their maximum in *P. m. merriami,* especially in populations from the Popocatépetl-Iztacíhuatl massif. *P. m. irolonis* is also large, surpassing *merriami* in palatofrontal depth and length of nasals. The trend toward larger size in the western part of the range is probably in response to interspecific competition with *Pappogeomys tylorhinus,* a specialized species of the advanced *gymnurus*-group. The ranges of the two species are in contact in the Valley of México. Evidently, both species prefer similar habitat, especially on the Central Plateau, and are in direct competition for the available space. Selection patterns in *merriami* would tend to favor increase in size due to the advantage of larger size in the competition for local territory, especially in view of the aggressive behavior of these rodents. Although other factors also may be involved, none seems so important as interspecific competition in explaining the remarkably large size of the western subspecies as compared with eastern subspecies that are remote from the range of *tylorhinus.*

Minimum size characterizes *estor* and *fulvescens,* both of which occur in the eastern part of the range occupied by *Pappogeomys merriami.* Neither has contact with a closely competing species. Differences in cranial dimensions between the two are not appreciable except in breadth of the cranium. The breadth across the squamosals and braincase are decidedly less in *fulvescens,* as mentioned above, both dimensions being minimal for the species. The degree of difference in cranial dimensions between *estor* and *fulvescens* on the one hand and the much larger *merriami* and *irolonis* on the other hand is so great that it would seem to preclude their allocation to the same species, but gophers of intermediate size, such as *perotensis* and *saccharalis,* at least partially bridge the morphological gap.

Of the seven subspecies, *fulvescens* is most divergent. It is not only small, but its paler coloration and distinctive cranial features are unique. On the other hand, the weakest subspecies are *irolonis,* which closely resembles *merriami,* and *peraltus,* which evidently is closely allied to *perotensis.* Although *estor* and *fulvescens* closely resemble each other in size, they differ sharply in color and cranial details. If these two subspecies were to be considered as only one, the taxonomist might synonymize *irolonis* with *merriami* and *peraltus* with *perotensis.* Proceeding further, he might synonymize *saccharalis* with *merriami* and *estor* with *perotensis.* If color and cranial morphology were ignored, *fulvescens* might also be assigned to *perotensis,* and thus only two subspecies, *merriami* and *perotensis,* would be recognized. Ultimate lumping, by synonymizing the subspecies *perotensis* and *merriami* (as conceived above), would result in the recognition of but one monotypic and highly polymorphic species. In my opinion seven subspecies should be recognized.

Pappogeomys merriami estor (Merriam)

Cratogeomys estor Merriam, N. Amer. Fauna, 8:155, January 31, 1895; Allen and Chapman, Bull. Amer. Mus. Nat. Hist., 9:28, June 16, 1897; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:265, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:73, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:247, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:367, April 9, 1942.

[*Cratogeomys*] *estor*, Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:314, 1904.

Cratogeomys perotensis estor, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:151, June 13, 1934; Davis, Jour. Mamm., 25:388, December 12, 1944; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:344, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959; Hall and Dalquest, Univ. Kansas Publ. Mus. Nat. Hist., 14:280, May 20, 1963.

Type.—Male, adult, skull and skin; No. 54308 U. S. National Museum; Las Vigas, 8000 ft., Veracruz; June 12, 1893; obtained by E. W. Nelson, original number 5005.

Range.—Pine forest zone in west-central Veracruz. See Fig. 5. Altitudinal range 8000 to 9100 feet.

Description.—Small for species; tail relatively long (averaging 46% of length of head and body); hind foot short. Average and extreme external measurements of eight females and five males from the lower slopes of Cofre de Perote (elevations of 8500 ft. and lower) and the low hills to the north (specimens labeled with reference to Las Vigas, Altotonga, and Jalacingo), respectively by sex, are 201 (186-212), 226 (200-242); length of tail, 92 (85-101), 87 (74-102); length of hind foot, 37 (36-38), 40 (38-43).

Color: Upper parts Dark Mouse Gray basally, apically bright Ochraceous-Tawny blending to paler Ochraceous-Buff on sides and face, with some black-tipped hairs on back and top of head but pure Ochraceous-Buff on sides; underparts Mouse Gray overlaid with Light Buff; auricular patch black, small; hind feet whitish.

Skull: Small for species, especially shallow and short; palate, nasals, rostrum, and maxillary tooth-row short; narrow across zygomata, braincase, and squamosals; rostrum relatively broad (averaging 53.8% of its length); mesopterygoid fossa V-shaped anteriorly; jugal slender, anterior end never enlarged; posterior loph of M3 not elongated into a conspicuous heel.

Average and extreme cranial measurement of eight females and four males (for localities, see external measurements above) are, respectively, as follows: Condylobasal length, 52.9 (51.8-54.7), 59.2 (57.7-60.4); zygomatic breadth, 35.4 (32.6-38.5), 40.2 (39.2-41.3); palatofrontal depth, 20.9 (20.3-21.6), 23.1 (22.1-23.5); length of palate, 35.3 (34.4-36.6), 40.0 (38.9-41.6); length of nasals, 19.7 (18.8-20.4), 22.6 (22.3-23.0); breadth of braincase, 25.1 (23.9-26.7), 27.5 (26.8-28.0); squamosal breadth, 32.3 (31.5-34.3), 36.2 (34.9-37.3); breadth of rostrum, 12.7 (11.9-13.2); 15.1 (13.9-15.8); length of rostrum, 23.6 (22.5-24.2), 27.6 (26.7-28.4); alveolar length of maxillary tooth-row, 10.9 (10.4-11.5), 12.1 (11.2-13.5).

Comparisons.—For comparisons with *P. m. perotensis* and *P. m. peraltus*, see accounts of those subspecies.

From *Pappogeomys merriami fulvescens, P. m. estor* differs as follows: Tail actually and relatively shorter (averaging 46 *versus* 51% of length of head and body); hind foot shorter; upper parts decidedly darker, reddish-brown instead of yellowish-buff; underparts paler, more buffy and less ochraceous; broader across zygomata, braincase, and especially squamosals; skull slightly shallower; rostrum shorter; posterior loph of M3 shorter.

From *Pappogeomys merriami irolonis, estor* differs as follows: Smaller; tail actually shorter but relatively longer (averaging 46 *versus* 42% of length of head and body); hind foot shorter; upper parts darker, more tawny and less ochraceous; underparts paler, more buffy and less ochraceous; skull decidedly smaller, averaging less in all dimensions and with no overlap in condylobasal length, palatofrontal depth, length of palate, breadth of braincase, squamosal breadth, breadth of rostrum, length of rostrum, and length of maxillary toothrow.

Remarks.—*P. m. estor* closely resembles *perotensis* in color, although slightly paler (more rufous) on the average than its darker relative. On the other hand, *estor* resembles *fulvescens* in cranial dimensions. Other cranial features such as the structure of M3, the jugal bone, and the shape of the mesopterygoid fossa are as in *perotensis*, but the skull is convex in dorsal outline in some individuals, a feature characteristic of *fulvescens*. The males of *estor* and *perotensis* are only slightly different (see remarks in the account of *perotensis*) but the females are strongly differentiated, the females of *estor* being significantly smaller than those of *perotensis* in most cranial dimensions. The combination of characters that is the basis for recognition of *estor* links *fulvescens* and *perotensis*. The former has been arranged as a species by previous authors.

Characters mentioned by Merriam (1895:155-156) as indicating specific distinction of *estor* and *perotensis* are, as pointed out before, subject to considerable individual variation. *P. m. estor* is smaller as Merriam points out, but the distinction in size suggests only subspecific status to me as it did to Nelson and Goldman (1934:151).

The geographic ranges of *estor* and *perotensis* interdigitate on the lower slopes of the Cofre de Perote. *P. m. estor* occurs below 9000 feet elevation on Perote, and its range extends northward in the pine forest zone that dominates the leeward slope of the relatively low ridges and peaks bordering the interior desert of the Central Plateau. *P. m. estor* is replaced by pocket gophers of the genus *Orthogeomys* in the tropical rain forest developed on the windward side of this range of mountains.

An adult female (KU 19328) from 7 km. SE Jalacingo is broader across the zygomata, braincase, and squamosals than are topotypes and near topotypes of *estor,* and suggests intergradation with the larger subspecies *irolonis* that occurs less than 50 miles to the west in Puebla.

Specimens examined.—Total, 39, all from **Veracruz,** as follows: 7 km. SE Jalacingo, 8000 ft., 1; 6 km. SE Altotonga, 9100 ft., 1; * 6 km. SSE Altatonga, 9000 ft., 1; 2 km. S Sierra de Agua, 8500 ft., 1; 2 km. W Las Vigas, 8000 ft., 2; *Las Vigas, 8500 ft., 17; *Las Vigas, 8000 ft., 9 (USNM); *3 km. E Las Vigas, 8000 ft., 4; *5 km. E Las Vigas, 8000 ft., 3 (TCWC).

Pappogeomys merriami fulvescens (Merriam)

Cratogeomys fulvescens Merriam, N. Amer. Fauna, 8:161, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:266, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:73, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924; Poole and Schantz, Bull. U. S. Nat. Mus., 178:367, April 9, 1942.

[*Cratogeomys*] *fulvescens,* Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:316, 1904.

Cratogeomys fulvescens fulvescens, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:152, July 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:469, March 31, 1959.

Cratogeomys fulvescens subluteus, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:152, June 13, 1934, type from Perote, 7800 ft., Veracruz, Republic of México; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Davis, Jour. Mamm., 25:388, December 12, 1944; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:469, March 31, 1959; Hall and Dalquest, Univ. Kansas Publ. Mus. Nat. Hist., 14:280, May 20, 1963.

Type.—Male, adult, skull and skin; No. 58168 U. S. National Museum; Chalchicomulco, 8200 ft., Puebla; January 15, 1894; obtained by E. W. Nelson and E. A. Goldman, original number 5651.

Range.—High, arid and sandy plain of eastern Puebla from type locality northward to 2 km. N Perote in eastern Veracruz. See Fig. 5. Altitudinal range 7500 feet W of Limón to 8300 feet 6 mi. SW Perote.

Description.—Small for species; tail relatively long (averaging 51% of length of head and body in females); hind foot short. Average and extreme external and cranial measurements of six females and nine males, respectively, from the desert plains of eastern Puebla and west-central Veracruz (specimens labeled with reference to Perote, Gaudalupe Victoria, and Chalchicomulco) are as follows: Length of head and body, 201 (180-211), 240 (205-284); length of tail, 103 (96-110), 96 (87-104); length of hind foot, 40 (38-42), 43 (40-45).

Color: Upper parts pale, Mouse Gray basally and Antimony Yellow apically, with strong mixture of black-tipped hairs on back and top of head imparting general "salt and pepper" appearance, sides and face bright Ochraceous-Buff apically; underparts light Mouse Gray basally overlaid with light Ochraceous-Buff; no discernible auricular patch; hind foot whitish, in a few specimens buffy.

Skull: Small for species; skull, palate, and maxillary tooth-row short; narrow across zygomata, braincase and squamosals; rostrum short and narrow; nasals long, relative to depth of skull; zygomata broadest at anterior angles; dorsal outline of skull convex or arched; posterior loph of M3 elongated into a distinct heel.

Average and extreme measurements of six females and nine males, respectively, from the desert plains of eastern Puebla and west-central Veracruz (see external measurements above) are as follows: Condylobasal length, 52.9 (51.3-54.2), 58.6 (57.7-61.2); zygomatic breadth, 34.6 (32.4-37.7), 41.2 (39.8-43.4); palatofrontal depth, 21.1 (20.4-22.2), 23.8 (23.5-24.6); length of palate, 34.9 (33.8-35.9), 39.8 (38.5-41.4); length of nasals, 19.2 (17.6-21.5), 22.5 (21.1-23.5); breadth of braincase, 23.0 (22.3-23.9), 25.3 (24.0-27.2); squamosal breadth, 29.7 (27.8-32.0), 33.9 (32.0-36.3); breadth of rostrum, 12.9 (12.4-13.2), 15.7 (14.0-17.0); length of rostrum, 24.2 (23.3-26.0), 27.3 (26.2-28.5); alveolar length of maxillary tooth-row, 10.6 (9.8-11.3), 11.3 (10.7-11.9).

Comparisons.—For comparisons with *P. m. estor, P. m. peraltus,* and *P. m. perotensis,* see accounts of those subspecies.

From *Pappogeomys merriami merriami, fulvescens* differs as follows: Smaller; tail relatively longer (averaging 51 *versus* 42% of length of head and body); hind foot shorter; upper parts and underparts decidedly paler, more pale yellowish-buffy and less bright rufous than brown phases of *merriami* (melanism unknown in *fulvescens*); auricular patch lacking; skull averaging smaller in all dimensions, with no overlap in condylobasal length, palatofrontal depth, length of palate, breadth of braincase, and squamosal breadth; dorsal outline of skull arched rather than straight; mesopterygoid fossa V-shaped instead of truncate anteriorly; heel of M3 relatively longer.

From *Pappogeomys merriami saccharalis, fulvescens* differs as follows: Smaller; tail relatively longer (averaging 51 *versus* 40% of length of head and body); hind foot shorter; upper parts and underparts decidedly paler, more dull yellowish-buff and less bright ochraceous, more drab and less glossy; back with more black-tipped hairs; auricular patch absent; skull averaging smaller in all dimensions, with no overlap in condylobasal length, palatofrontal depth, length of palate, length of nasals, breadth of braincase, squamosal breadth, length of rostrum, and length of maxillary tooth-row; dorsal outline of skull convex rather than straight; heel of M3 relatively longer; mesopterygoid fossa V-shaped anteriorly instead of truncate.

Remarks.—Merriam (1895:161-162) described several features as unique in *fulvescens,* and suggested that they were discontinuous differences. For example, he stated that height of cranium in *fulvescens,* owing to the convexity of the dorsal border of the skull, exceeds that in any other species. Actually the palatofrontal depth expressed as a percentage of the condylobasal length averages 39.9 and is only slightly more than that in *merriami* and *saccharalis* (38.3% and 39.1%, respectively); the corresponding percentages in *estor* and *perotensis* are 39.7 and 39.8 per cent, respectively. The position of the palatofrontal suture and the heavy maxillary arm of the zygomata, features also mentioned by Merriam, are matched in individuals referable to other subspecies of *Pappogeomys merriami.* M3 of *fulvescens* is obcordate and resembles that of *merriami,* *saccharalis*, and *irolonis*. Although variable, the tooth is partially bilophodont with a well-developed lateral re-entrant fold and has the posterior loph elongated into a distinct heel that, owing to lateral compression, is relatively narrower than in other subspecies. The length of the heel varies, as in the aforementioned subspecies. No distinctly elongated heel is developed in *estor, perotensis* and *peraltus*. On the other hand, the V-shaped mesopterygoid fossa resembles that of *estor, perotensis,* and *peraltus* and is unlike the truncate fossa developed in *merriami, saccharalis,* and *irolonis*. All of these differences seem to be of the sort that distinguish subspecies rather than species. Clearly none is discontinuous and unique to *fulvescens*. Therefore, I consider *fulvescens* to be a subspecies of *Pappogeomys merriami*.

Comparison of topotypes of *Cratogeomys fulvescens subluteus* Nelson and Goldman (1934:152) from Perote and examples from Guadalupe Victoria with topotypes of *Cratogeomys fulvescens fulvescens* Merriam (1895:161) from Chalchicomula reveals no difference of taxonomic importance. The only character of consequence mentioned in the description of *subluteus* was more yellowish-buff on the upper parts, but I fail to appreciate the existence of any difference in coloration. Additional specimens from Perote and from Guadelupe Victoria, only a short distance southwest of Perote, are apparently no different in color. Contrary to the original description, no difference in cranial features can be ascertained. I find no good morphological reason for retaining *subluteus* as a subspecies distinct from *fulvescens*.

In pale coloration, small external dimensions and relatively long tail, short skull, especially narrowness across the zygomata and squamosals, short maxillary tooth-row, and relatively long rostrum, *fulvescens* is a well-defined subspecies. Its pale pelage differs much from the rufous, ochraceous, and melanistic pelage of other subspecies of *Pappogeomys merriami*. But, natural selection in pocket gophers usually tends to produce close resemblance between color of pelage and color of substrate, and the pallid pelage of *fulvescens* matches well the pale-colored sands in which it lives. The narrower cranium is perhaps the most distinctive feature of the skull (see discussion in species account).

Trouessart (1898:572) and Elliot (1904:316), probably only quoting from Merriam (see below), mentioned specimens from the base of Mount Malinche in Tlaxcala. Merriam (1895:162) related that E.W. Nelson found *fulvescens* about the northeastern base of Malinche, although he noted no specimen from there. I assume that Nelson saved none as prepared specimens, and I have seen no example of the subspecies from Tlaxcala. Since the sandy soils in which *fulvescens* occurs elsewhere do extend westward to the eastern base of Mount Malinche (in the vicinity of the town of Huamantla, Tlaxcala), *fulvescens* would be expected to occur there on geographic grounds.

Specimens examined.—Total, 30, as follows: **Puebla:** Chalchicomulco (= San Andres), 8200 ft., 7 (USNM). **Veracruz:** 2 km. N Perote, 8000 ft., 2; * Perote, 7800 ft., 1 (USNM); * 2 km. E Perote, 8300 ft., 10; * 3 km. W Limón, 7500 ft., 3; * 2 km. W Limón, 7500 ft., 2; Guadalupe Victoria (= Aguatepec), 6 mi. SW Perote, 8300 ft., 5 (TCWC).

Pappogeomys merriami irolonis (Nelson and Goldman)

Cratogeomys merriami irolonis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:150, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:528, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:367, April 9, 1942; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955.

Cratogeomys merriami, Merriam, N. Amer. Fauna, 8:152, January 31, 1895 (part); Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:265, July 1, 1905 (part); Miller, Bull. U. S. Nat. Mus., 79:246, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:258, April 29, 1924 (part); Musser, Occas. Papers Mus. Zool., Univ. Michigan, 636:8, June 17, 1964.

[*Cratogeomys*] *merriami,* Elliot, Field. Columb. Mus. Publ. 95, Zool. Ser., 4:313, 1904 (part).

Cratogeomys irolonis, Davis, Jour. Mamm., 25:387, December 12, 1944 (part); Hooper, Jour. Mamm., 29:302, August 31, 1948; Villa, Anales del Instituto de Biologia, 23:396, May 20, 1953 (part); Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959 (part).

Type.—Female, adult, skin and skull; No. 53494 U. S. National Museum; Irolo, 7600 ft., Hidalgo; March 30, 1893; obtained by E. W. Nelson and E. A. Goldman, original number 4520.

Range.—Plain of Apam in southern Hidalgo eastward into the mountains of northern Puebla. See Fig. 5. Altitudinal range from 7600 feet on desert plain at type locality to 9000 feet in pine-oak-fir forest of northern Puebla.

Description.—Large for species; tail relatively short (averaging 42% of length of head and body); hind foot short. Average and extreme external measurements of six females and three males, respectively, from the type locality and northern Puebla are as follows: Length of head and body, 235 (225-245), 241 (230-258); length of tail, 98 (90-110), 104 (100-107); length of hind foot, 42 (39-44), 43 (42-45).

Color: Upper parts bright rufous in overall appearance, Mouse Gray basally and Ochraceous-Buff apically, with mixture of black-tipped hairs on back but sides and face pure Ochraceous-Buff; underparts Light Mouse Gray overlaid with Ochraceous-Buff; hairs about mouth Light Buff; auricular patch blackish; dorsal surface of hind foot whitish.

Skull: Large, long and deep; nasals actually and relatively long (averaging 38.2% of condylobasal length); broad across zygomata, braincase, and squamosals; palate and maxillary tooth-row long; rostrum broad and long; posterior loph of M3 short; incisors massive, lower incisor having lateral bevel or shelf; sides of basioccipital nearly parallel.

Average and extreme cranial measurements of six females and three males from the type locality and northern Puebla are, respectively, as follows: Condylobasal length, 58.9 (57.2-59.8), 62.3 (61.0-64.5); zygomatic breadth 39.1 (38.2-40.4), 42.4 (41.0-45.1); palatofrontal depth, 24.1 (22.8-25.9), 25.0 (23.8-26.2); length of palate, 40.3 (39.3-41.0), 42.8 (41.5-44.5); length of nasals, 22.5 (20.5-23.5), 24.4 (23.9-25.0); breadth of braincase, 28.7 (27.3-30.5), 29.5 (27.9-31.7); squamosal breadth, 37.2 (36.2-38.2), 40.8 (38.9-44.1); breadth of rostrum, 14.0 (13.4-14.7), 15.9 (15.6-16.2); length of rostrum, 26.4 (25.5-27.4), 29.4 (29.0-30.2); alveolar length of maxillary tooth-row, 12.1 (11.8-12.4), 13.1 (12.7-13.6).

Comparisons.—For comparisons with *P. m. estor* and *P. m. perotensis*, see accounts of those subspecies.

From *Pappogeomys merriami merriami, irolonis* differs as follows: Hind foot shorter, upper parts slightly more rufescent than light brown phase of *merriami;* skull shorter and deeper; nasals actually and relatively longer (averaging 38.2 *versus* 35.4% of condylobasal length); zygomatic breadth averaging 66.4 *versus* 63.9% of condylobasal length; squamosal breadth less; palate decidedly shorter; posterior loph of M3 shorter.

From *Pappogeomys merriami saccharalis, irolonis* differs as follows: Larger; tail actually and relatively longer (averaging 42 *versus* 40% of length of head and body); hind foot shorter; upper parts darked, more rufescent and less ochraceous; underparts darker, more ochraceous and less buffy; skull longer and deeper; broader across zygomata, braincase, and squamosals; palate and especially nasals longer; rostrum broader and longer.

From *Pappogeomys merriami fulvescens, irolonis* differs as follows: Larger; tail actually and relatively shorter (averaging 42 *versus* 51% of length of head and body); hind foot longer; upperparts darker, more bright rufous and less yellowish-buff; underparts darker, more ochraceous and less buffy; skull averaging larger in all dimensions, with no overlap in condylobasal length, zygomatic breadth, palatofrontal depth, length of palate, breadth of braincase, squamosal breadth, and maxillary tooth-row; squamosal breadth averaging 63.2 *versus* 56.1% of condylobasal length; posterior loph of M3 shorter.

Remarks.—In the original description, Nelson and Goldman (1934:150) distinguished *P. m. irolonis* by large size, reddish brown upper parts resembling the light brown phase of *P. m. merriami* (but more rufescent), shorter and broader skull, more inflated mastoids and auditory bullae, and shorter maxillary tooth-row. Other features mentioned in the original description are subject to a high degree of individual variation, and, therefore, cannot be depended upon as diagnostic. The description of *irolonis* was based on the three specimens from Irolo, Hidalgo, that had been discussed earlier by Merriam (1895:152). He pointed out that the specimens from Irolo differed from what he considered to be typical *merriami* from the Valley of Mexico.

Until recently no additional specimens of *irolonis* had been obtained. Study of new material from near Apam in Hidalgo and from northern Puebla as well as topotypes, substantiates the subspecific validity of *irolonis* and reveals several distinguishing features not previously described in *irolonis.* The heel of the M3 in *irolonis* is shorter than in *merriami, saccharalis,* and *fulvescens* and longer than in *estor* and *perotensis,* therefore providing a condition intermediate between the two extremes of development in the two groups mentioned above. Also, in *irolonis* the length of nasals and the depth of skull are maximal for the species. Color of the dorsum is not appreciably different in *irolonis* and the light brown phase of *merriami.* In *P. m. irolonis* the auditory bullae and mastoids appear not to be significantly inflated. However, the frontals extend farther forward along the midline than at their lateral margins. In *merriami* and *saccharalis,* the frontals extend as far forward at their lateral margins as they do medially. The jugal is large as in *merriami* (Merriam, 1895:154, considered the difference in the size of the jugal in *perotensis* and *merriami* to be diagnostic on the species level).

P. m. irolonis is clearly more closely related to *merriami* than to other subspecies of the species. Like *P. m. merriami, irolonis* is characterized by large external size and massive skull. Maximum dimensions for the species are seen in condylobasal length, length of palate, and squamosal breadth in *merriami* and in palatofrontal depth, length of nasals, and breadth of braincase in *irolonis.* Both subspecies have a remarkably long and broad rostrum, long maxillary tooth-row, widely spreading zygomatic arches, heavy upper incisors, and laterally beveled lower incisors.

P. m. irolonis forms a link both geographically and morphologically between *merriami* and the *perotensis* group of subspecies to the east. Although intergradation cannot be demonstrated in known series, it is expected in the mountains of extreme northeastern Puebla.

Considerable confusion has existed concerning the morphological characteristics and taxonomic status of *irolonis* since 1944 when Davis (p. 387) misidentified as *irolonis* 10 specimens of *P. t. tylorhinus.* By comparing these specimens—8 from 5 mi. NW Texcoco and 2 from 85 km. N Mexico City—with specimens of *P. m. merriami* he concluded that *irolonis* merited specific instead of subspecific rank. The diagnostic features listed for *irolonis* by Davis (*loc. cit.*) of course were those of the *gymnurus* species-group of the present paper and more particularly of *P. tylorhinus tylorhinus,* which until 1947 was regarded as a member of the genus *Platygeomys.*

Villa (1953:396-398) followed Davis in regarding *irolonis* as a full species, and proposed that Lake Texcoco, which inundated much of the southern part of the Valley of Mexico during the late

Pleistocene, was a major factor in the speciation of *merriami, irolonis,* and *tylorhinus,* owing to its effectiveness as a barrier to their distribution. According to Villa, populations of the three species have come in contact only recently, in the post-Wisconsin after Texcoco receded to near its present boundary.

Specimens from northern Puebla have slightly narrower braincases and longer rostra than topotypes.

Specimens examined.—Total, 14, as follows: **Hidalgo:** 10 mi. NW Apam, 7750 ft., 1; Irolo, 7600 ft., 2; (USNM): **Puebla:** Crus Alta, 4-5 mi. S Aquixtla, 9000 ft., 4 (UMMZ); Rancho Ocotal Colorado, 2 mi. E Crus Alta, 8800 ft., 7 (UMMZ).

Pappogeomys merriami merriami (Thomas)

Geomys merriami Thomas, Ann. Mag. Nat. Hist., ser. 6, 12:271, October, 1893.

Cratogeomys merriami, Merriam, N. Amer. Fauna, 8:152, January 31, 1895 (part); Elliot, Field Colum. Mus. Publ. 105, Zool. Ser., 6:265, July 1, 1905 (part); Miller, Bull. U. S. Nat. Mus. 79:246, December 31, 1912 (part); Miller, Bull U. S. Nat. Mus. 128:258, April 29, 1924 (part).

[*Cratogeomys*] *merriami,* Trouessart, Cat. Mamm., 1:573, 1898 (part); Elliot, Field Columb. Mus. Publ. 95. Zool. Ser., 4:313, 1904 (part).

Cratogeomys merriami merriami, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:149, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:528, June 8, 1940; Davis, Jour. Mamm., 25:386, December 12, 1944; Hooper, Jour. Mamm., 29:302, August 31, 1948, Villa, Anales del Instituto de Biologia, 23:391, May 20, 1953; Davis and Russell, Jour. Mamm., 35:72, February 10, 1954; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:343, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:469, March 31, 1959.

Cratogeomys oreocetes Merriam, N. Amer. Fauna, 8:156, January 31, 1895, type from Mount Popocatépetl, 11,000 ft., México; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser. 6:265, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:73, January 15, 1909; Miller, Bull. U. S. Nat. Mus. 79:247, December 31, 1912; Miller, U. S. Nat. Mus., 128:259, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:368, April 9, 1942; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:344, March 3, 1955.

[*Cratogeomys*] *oreocetes,* Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:314, 1904.

Cratogeomys peregrinus Merriam, N. Amer. Fauna, 8:158, January 31, 1895, type from Mount Iztaccíhuatl, 11,500 ft., México; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:265, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus. 62:73, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:247, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:259, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:368, April 9, 1942; Miller and Kellogg, Bull. U. S. Nat. Mus. 205:344, March 3, 1955.

[*Cratogeomys*] *peregrinus,* Troussart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:314, 1904.

Cratogeomys merriami oreocetes, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:149, June 13, 1934.

Cratogeomys merriami peregrinus, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:149, June 13, 1934.

Geomys mexicanus, Alston, Biologia Centrali-Americana, 1:159, October, 1880 (part, the holotype of *Geomys merriami,* see Thomas, 1893:272).

Type.—Sex and age unknown, skull and skin; No. 70.6.20.2 British Museum; southern México, exact locality, date, and original number, if any, unknown; holotype was purchased for the British Museum by Geale from A. Bouchard, a collector, who obtained also the type of *Oryzomys fulgens*, probably from the same locality (see Thomas, 1893:272); "probably the Valley of Mexico" (see Merriam, 1895:152).

Range.—Southern part of the Valley of Mexico and Sierra de Las Cruces, Sierra de Ajusco, Mount Popocatépetl, and Mount Iztaccíhutl bordering the Valley. From Lerma at eastern end of Valley of Toluca eastward into western Puebla. See Fig. 5. Altitudinal range 7350 to 13,500 feet.

Description.—Large for species; tail moderately long (averaging 42% of length of head and body); hind foot long. Average and extreme external measurements of 14 females and 12 males, respectively, from the Valley of Mexico and adjacent mountains are as follows: Length of head and body 238 (219-253), 266 (250-283); length of tail, 99 (83-119), 108 (92-124); length of hind foot, 45 (41-49), 49 (43-53). An adult female and male from Monte Río Frío weighed 634.0 and 846.5 grams, recpectively.

Color: Three color phases in adults of both sexes: Dark brown, light brown, and black. Hind feet whitish in all phases. Black phase: Overall appearance of upper parts metallic glossy greenish-black, hairs of back and sides dull black basally and glossy Mummy Brown apically; underparts resembling back and sides, dull Mummy Brown to roots; hairs about mouth Light Buff. Dark brown phase: Hairs of upper parts Dark Mouse Gray basally, apically glossy Cinnamon-Brown with some Bay-tipped hairs on back and top of head and pure Cinnamon-Buff on sides and face; underparts Mouse Gray basally overlaid with Cinnamon-Buff; hairs bordering mouth Light Buff; blackish auricular spots small and inconspicuous. Light brown phase (obviously unworn pelage in examples in hand): Upper parts Mouse Gray basally and Ochraceous-Buff apically, with some black-tipped hairs on back and top of head but pure Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with Ochraceous-Buff, gray base of hair conspicuous on chest and inside of legs; hairs on lips and around opening of check pouches Light Buff; blackish auricular patch small but conspicuous.

Skull: Large for species; zygomata parallel, zygomatic breadth exceeding breadth across squamosals but less narrow relative to length of skull (averaging 63.6% of condylobasal length); average dimensions more than in other subspecies in palatofrontal depth; length of palate, nasals, and rostrum; and breadth across braincase, squamosals, and rostrum; maxillary tooth-row both actually and relatively long (averaging 53.0% of palatofrontal depth); incisors massive, lower tooth with well-developed lateral shelf behind enamel face, outer edge of enamel thus forming well defined bead; auditory bulla inflated; occulsal surface of M3 obcordate with lateral re-entrant fold well-developed, tooth distinctly biprismatic, having posterior loph elongated into conspicuous heel; sides of basioccipital nearly parallel.

Average and extreme cranial measurements of 14 females and 13 males, respectively, from the Valley of México and adjacent mountains are as follows: Condylobasal length, 61.3 (49.2-63.5), 69.6 (67.4-74.5); zygomatic breadth, 39.2 (36.7-42.0), 46.0 (41.9-49.3); palatofrontal depth, 23.5 (22.6-25.0), 27.3 (25.2-29.8); length of palate, 41.7 (40.1-44.2), 48.3 (46.5-51.4); length of nasals, 21.7 (20.0-23.2), 25.4 (23.7-27.7); breadth of braincase, 28.5 (27.1-31.0), 31.3 (29.0-33.6); squamosal breadth, 38.1 (35.7-40.5), 43.0 (39.3-48.4); breadth of rostrum, 14.0 (13.2-15.2), 15.9 (14.9-19.0); length of rostrum, 26.9 (25.3-29.1), 31.3 (29-7-34.1); alveolar length of maxillary toothrow, 12.5 (11.4-14.0), 13.5 (12.4-15.4).

Comparisons.—For comparisons with *P. m. irolonis, P. m. saccharalis,* and *P. m. fulvescens,* see accounts of those subspecies.

Remarks.—*Pappogeomys merriami merriami* is the largest and most widely distributed subspecies of the species. The skull is especially distinguished by its great length, massive rostrum, and heavy incisors. The rostrum is actually, but not relative to its length, broader than in other subspecies; it is especially broad along its ventral border and heavily crested for muscle attachments. Length of hind foot, tail and body are maximal for the species.

As in the species of the *gymnurus*-group to the west, many individuals of *P. m. merriami* are melanistic. In adult pelage, 24 (42%) are black, 25 (44%) dark brown, and 8 (14%) light brown. The brown phases are more common at lower elevations and tend to be replaced by the black phase at higher altitudes. For instance, of 26 specimens examined from the Valley of México, 22 (85%) are brown (17 dark brown and 5 light brown), and only 4 (15% black). Of 31 specimens examined from the mountains 20 (65%) are melanistic, and 11 (35%) brown (8 dark brown and 3 light brown). The montane soils are volcanic in origin and characteristically black. Selection probably favors genes producing deposition of melanin in the pelage. The melanistic individuals closely match the color of the soil. The Valley of México, on the other hand, is mantled with brownish lacustren soils, evidently deposited by the retreating Lake Texcoco. Selection there probably favors the brown color phases and they are more frequent in the Valley than is the black phase. The occasional melanistic individual in the Valley probably is due to gene flow frow the adjacent highlands. The incidence of melanism is rare in other subspecies of *Pappogeomys merriami.*

Merriam (1895:156 and 158) described *Cratogeomys oreocetes* on the basis of a single specimen and did the same thing when naming *Cratogeomys peregrinus.* The type locality of *oreocetes* is at an elevation of 11,000 feet on Mount Popocatépetl, and that of *peregrinus* at 11,500 feet on Mount Iztaccíhuatl. Both species were reduced to subspecies of *Cratogeomys merriami* by Nelson and Goldman (1934:149). Both of the holotypes are subadult females. Subsequently, Davis (1944:386) secured adults from timber line (13,500 ft.) on the north slope of Mount Popocatépetl, and he and other persons collected numerous adults at 10,500 feet on the north slopes of Mount Iztaccíhuatl (from, or near, the crest of the pass west of Monte Río Frío and from the ridge east of the pass between Ixtacíhuatl and Popocatépetl). I have examined most of this material. As Davis pointed out (*op. cit.*), none of these examples differs significantly from specimens of *merriami* taken in the Valley of México or in the mountains to the south and west of the Valley. Consequently, *oreocetes* and *peregrinus* are here arranged as synonyms of *P. m. merriami.*

P. m. merriami in the southern part of the Valley of México averages slightly smaller in length of skull, zygomatic breadth, and squamosal breadth than in the adjacent mountains. Specimens from Texmelucan to the east of Mount Ixtaccíhuatl are characterized by shorter tail, slightly longer skull, longer nasals, and greater zygomatic breadth than are animals from elsewhere in the range of the subspecies (especially those in the Valley of México). These minor differences in local populations are to be expected in a subspecies occurring in several environments over a relatively extensive geographical range.

Males are more variable than females in *P. m. merriami.* An adult male (USNM 50112) from Tlálpam has a deciderly narrower braincase than any other specimens of the species. Two large males (TCWC 2004 and 2005) are incorrectly sexed as females on the field tags.

Specimens examined.—Total, 62, as follows:

Puebla: Sn. Martín Texmelucan, 3.

México: 6 mi. S and 1 mi. W Texcoco, 7350 ft., 1; Monte Rió Frió, 45 km. ESE México City (N slope Ixtacíhuatl), 10,500 ft., 13 (9 TCWC, 4 FMNH); *5 km. W Río Frío, 10,000 ft., 2; 1 mi. SSW Río Frío, 1; Salazar, 11,000 ft., 1 (USNM); Lerma, 8,650 ft., 1 (USNM); 10 km. ESE México City, 1 (TCWC); *17 km. ESE México City, 1 (TCWC); Amecameca, 8 (USNM); *5 mi. E Amecameca, 9,600 ft., 1 (MVZ); 55 km. SE México City (near Paso de Cortez, between Mt. Ixtacíhuatl and Popocatépetl), 10,500 ft., 2 (TCWC); *N slope Mt. Popocatépetl, 13,500 ft., 2 (TCWC).

Distrito Federal: Coyoacan-Churubusco, 1; *Falda SW Cerro Zacatepec, 3.9 mi. SW Monumento a Obregón, 1; *1.8 mi. E San Gregorio Altapulco, 2,270 m., 2; Ixtapalapa, 7,500 ft., 2; *½ mi. S Rancho del Llano, 4 mi. S, 8 mi. E Churubusco, 2; Tlálpam, 7,600 ft., 4 (USNM); Rancho La Noria, 4 km. W Xochimilco, 2,270 m., 2; 1 km. W Xochimilco, 2,270 m., 1; *Santa Cruz Acalpixca, 2,270 m., 2; Ajusco, 10,500 ft., 1 (USNM); *Ajusco, 11,500 ft., 1 (USNM).

Morelos: 2 mi. W Huitzilac, 10,000 ft., 1 (TCWC); * Huitzilac, 8,500 ft., 3 (USNM); * 1½ mi. SE Huitzilac, 8,000 ft., 2 (TCWC).

Pappogeomys merriami peraltus (Goldman)

Cratogeomys perotensis peraltus Goldman, Jour. Washington Acad. Sci., 27:403, September 15, 1937; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959.

Cratogeomys perotensis, Elliot, Field Columb. Mus. Publ. 115, Zool. Ser., 8:310, 1907.

Type.—Male, adult skin and skull; No. 13831 Field Museum Natural History; Mount Orizaba, about 12,500 ft., Puebla; July 5, 1904; obtained by Edmund Heller, original number 4141.

Range.—Known only from the type locality. See Fig. 5.

Description.—Size medium for species (based on males only); tail short; hind foot short. Measurements of a topotype are: Length of head and body, 223; length of tail, 82; length of hind foot, 41.

Color: Upper parts Light Mouse Gray basally and Ochraceous-Orange apically, mixed with hairs tipped with reddish-brown on back but pure bright Ochraceous-Buff on sides and face; underparts Light Mouse Gray overlaid with Light Buff; throat pale brownish; auricular patch reddish-brown; hind feet whitish.

Skull: Moderately short and shallow (based on males only); narrow across zygomata and squamosals; palate, nasals, and maxillary tooth-row short; rostrum narrow and decidedly short; auditory bullae small; posterior loph of M3 without elongation; jugal slender; dorsal outline of skull straight; mesopterygoid fossa V-shaped anteriorly.

Measurements of a topotype are: Condylobasal length, 57.4; zygomatic breadth, 39.9; palatofrontal depth, 22.4; length of palate, 39.1; length of nasals, 21.0; breadth of braincase, 27.8; squamosal breadth, 35.6; breadth of rostrum, 13.7; length of rostrum, 25.1; alveolar length of maxillary tooth-row, 11.1.

Comparisons.—From males of *Pappogeomys merriami perotensis* males of *peraltus* differ as follows: Upper parts paler both basally, Light Mouse Gray rather than Dark Mouse Gray, and apically, more ochraceous and less rufous; back paler in overall appearance owing to admixture of hairs tipped with reddish-brown rather than black; throat reddish-brown rather than buffy; underparts paler owing to paler bases of hairs that show through buffy overlay; auricular patch reddish-brown instead of blackish; skull slightly shorter; rostrum and especially nasals shorter; narrower across braincase and squamosals; maxillary tooth-row slightly shorter; M3 lacking heel; sides of basioccipital straight rather than bowed out laterally; auditory bullae smaller; mesopterygoid fossa wider.

From males of *Pappogeomys merriami estor*, males of *peraltus* differ as follows: Upper parts paler both basally, (Light Mouse Gray rather than Dark Mouse Gray), and apically, (brighter ochraceous and less rufous); back paler in overall appearance owing to admixture of hairs tipped with reddish-brown rather than black; underparts appear lighter owing to paler bases of hairs that show through overlay; auricular patch reddish-brown rather than blackish; skull slightly shorter; rostrum and especially nasals shorter; maxillary tooth-row slightly shorter; M3 lacking heel; auditory bullae smaller; mesopterygoid fossa wider.

From males of *Pappogeomys merriami fulvescens*, males of *peraltus* differ as follows: Smaller; tail and hind foot shorter; upper parts darker apically, more ochraceous and less yellowish-buff; underparts paler, more buffy and less ochraceous; zygomata less widely spreading; nasals shorter; decidedly broader across braincase and squamosals; rostrum narrower and shorter; M3 shorter, heel lacking.

Remarks.—*P. m. peraltus* is not so well known as the other subspecies of *Pappogeomys merriami* because the few males upon which the original description was based are the only specimens known. Even so, *peraltus* clearly is closely allied to *perotensis* and *estor*, although the degree of relationship is uncertain. Present material indicates that *peraltus* is paler than either *peraltus* or *estor*, and has decidedly shorter nasals (a characteristic considered to be diagnostic in the original description) and rostrum. Also, the skull and maxillary tooth-row of *peraltus* may prove to be shorter than in *perotensis* and *estor*. Other than size, diagnostic features of the skull in *peraltus* include a wider mesopterygoid fossa and shorter M3. The character of the M3 is especially variable in this species, and *peraltus* is characterized by one of the extremes in the observed range of variability. In *peraltus*, the posterior loph on the M3 is not enough projected posteriorly to form a distinct heel as it is in *irolonis*, *fulvescens*, *saccharalis*, and *merriami*. M3 of *P. m. perotensis* and *P. m. estor* most closely resembles that of *peraltus*, but even in these subspecies the posterior loph is projected slightly posteriorly, thus forming an indistinct heel; and, even though the heel is not strongly developed in *perotensis* and *estor*, it is more elongated than in *peraltus*. Conclusions concerning the taxonomic status and relationships of *peraltus* can be more firmly based when an adequate sample of females is available for analysis. An adequate sample of *peraltus* may show that it cannot be distinguished from either *perotensis* or *estor*, but it seems best to retain *peraltus* as a subspecies until its status can be determined with certainty.

P. m. peraltus is evidently restricted to higher elevations on Mount Orizaba, the highest peak in México. In the original description, Goldman (1937:403) listed the type locality as being at about 12,500 feet on the Veracruz slope of Orizaba, but Hall and Dalquest (1963:280) pointed out that the labels and collector's field catalogue indicate that the specimens came from Puebla instead. The state boundary of Puebla and Veracruz passes through the peak of Orizaba; the eastern side of the mountain is in Veracruz and the western side in Puebla. *P. m. peraltus* probably occurs on both sides and in both states; no major difference in habitat is evident on the east and west slopes at higher elevations. Only the genus *Thomomys* has been taken from lower elevations (up to 9500 ft.) on the western slope. To the east, *Orthogeomys hispidus* occurs in tropical associations in the foothills at the base of Orizaba.

Specimens examined.—Total, 2, both from **Veracruz** (see preceding paragraph), as follows: Mount Orizaba (at timber line), about 12,500 ft., 2 (FMNH).

Pappogeomys merriami perotensis (Merriam)

Cratogeomys perotensis Merriam, N. Amer. Fauna, 8:154, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:265, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:73, January 15, 1909; Miller, Bull. U. S Nat. Mus., 79:246, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:258, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:529, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:368, April 9, 1942.

[*Cratogeomys*] *perotensis*, Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:313, 1904.

Cratogeomys perotensis perotensis, Nelson and Goldman, Proc. Biol. Soc. Washington, 47:151, June 13, 1934; Davis, Jour. Mamm., 25:387, December 12, 1944; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:344, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:468, March 31, 1959; Hall and Dalquest, Univ. Kansas Publ. Mus. Nat. Hist., 14:280, May 20, 1963.

Type.—Female, adult, skull and skin; No. 54299 U. S. National Museum; Cofre de Perote, 9500 ft., Veracruz; May 28, 1893; obtained by E. W. Nelson, original number 4889.

Range.—Cofre de Perote in west-central Veracruz. See Fig. 5. Altitudinal range 9500 feet to 12,500 feet.

Description.—Size medium for species; tail relatively short (averaging 40% of length of head and body); hind foot moderately long. Average and extreme external measurements of eight females and three males are, respectively, as follows: Length of head and body, 222 (210-213), 230 (210-246); length of tail 89 (80-104), 89 (76-114); length of hind foot, 42 (39-43), 41 (39-42).

Color: Upper parts Dark Mouse Gray basally, apically bright Ochraceous-Tawny on back blending to paler Ochraceous-Buff on sides and face, some black-tipped hairs on back and top of head but pure Ochraceous-Buff on sides; underparts Mouse Gray overlaid with Light Buff, hardly concealing Mouse Gray bases; auricular patch black, and relatively small; hind feet whitish.

Skull: Size medium for species; broad relative to length, especially across zygomata; nasals, rostrum, and maxillary tooth-row moderately long; rostrum relatively narrow (averaging 53.8% of its length); mesopterygoid fossa V-shaped anteriorly; jugal slender, anterior end never enlarged; posterior loph of M3 not elongated into conspicuous heel.

Average and extreme cranial measurements of eight females and four males are, respectively, as follows: Condylobasal length, 57.3 (55.8-58.3), 59.2 (59.0-59.5); zygomatic breadth, 38.7 (37.9-39.2), 40.6 (39.5-42.0); palatofrontal depth, 22.8 (22.2-23.3), 23.5 (22.7-24.1); length of palate, 38.8 (37.7-39.8), 40.2 (39.7-40.7); length of nasals, 21.3 (21.0-22.1), 22.7 (22.2-23.2); breadth of braincase, 26.5 (25.3-28.5), 28.5 (27.5-29.2); squamosal breadth, 35.0 (33.5-36.1), 37.7 (36.4-38.6); breadth of rostrum 13.1 (12.6-13.7), 14.6 (14.2-15.0); length of rostrum, 25.1 (24.1-26.6), 27.2 (26.8-27.4); alveolar length of maxillary tooth-row, 11.7 (11.1-12.2), 12.0 (11.5-12.4).

Comparisons.—For comparison with *P. m. peraltus*, see account of that subspecies.

From *Pappogeomys merriami estor*, *perotensis* differs as follows: Larger; tail relatively shorter (averaging 40 *versus* 46% of length of head and body); hind foot longer; upper parts slightly darker tone of Ochraceous-Tawny and back more heavily overlaid with black-tipped hairs; skull averaging larger in all dimensions, with no overlap in condylobasal length, palatofrontal depth, length of palate, and length of nasals.

From *Pappogeomys merriami fulvescens*, *perotensis* differs as follows: Larger; tail relatively shorter (averaging 40 *versus* 51% of length of head and body); hind foot longer; upper parts decidedly darker, reddish-brown rather than yellowish-buff; underparts paler, more buffy and less ochraceous; skull averaging larger in all dimensions, with no overlap in condylobasal length, length of palate, breadth of braincase, and squamosal breadth; dorsal outline of skull straight rather than convex; M3 remarkably shorter, posterior loph without conspicuous elongation.

From *Pappogeomys merriami irolonis*, *perotensis* differs as follows: Slightly smaller, tail relatively shorter (averaging 40 *versus* 42% of head and body); upper parts darker, more tawny and less ochraceous; underparts paler, more buffy and less ochraceous; skull shorter and shallower; palate and nasals shorter; breadth across braincase and squamosals decidedly less; rostrum shorter and narrower; posterior loph of M3 shorter; upper incisor narrower; lower incisor less distinctly leveled laterally, shelf inconspicuous; jugal slenderer, without anterior expansion.

Remarks.—Ever since it was named in 1895, *perotensis* has been treated as a species (see synonymy). Merriam (1895:154-155) indirectly suggested that the affinities of *perotensis* lie more with *merriami* than with any other described species. Such is certainly the case. However, the morphological features selected by Merriam (*loc. cit.*) as distinctive and thus indicative of specific status for *perotensis* are the sort subject to a high degree of individual variation. For example, the degree to which the squamosal overlaps the parietal bone (often completely overlapping in adults of *merriami*), the slenderness of the jugal (especially at its anterior end), the posterior extension of the nasals (ending at or near plane of front of zygomata), and the lack of the extreme melanism are features of the magnitude usually denoting differences between subspecies; also, each feature is duplicated in other subspecies of *Pappogeomys merriami*. Davis (1944:387) noted that the squamosal completely overlapped the parietal in an adult female, from N slope of Cofre de Perote at 10,500 ft., and correctly suggested that the overlap probably develops with extreme age as in *merriami*. Inasmuch as no taxonomic feature of *perotensis* is unique in comparison with *Pappogeomys merriami*, *perotensis* here is arranged as a subspecies of *Pappogeomys merriami*. The difference in size between males and females in *perotensis* is less than in other subspecies of *Pappogeomys merriami*.

P. m. perotensis seems to occur only at higher elevations on the Cofre de Perote. No specimen has been taken from the highlands intervening between the Cofre de Perote and Mount Orizaba, the type locality of *Pappogeomys merriami peraltus*. Examples from this area, if any occur there, may demonstrate that the range of *perotensis* extends southward or that *perotensis* and *peraltus* are subspecifically inseparable. *P. m. perotensis* and *P. m. estor* also are closely related. Although males resemble each other so closely that they cannot be separated with confidence, females are remarkably distinct (see comparisons). On the basis of the small samples available for study, males of *perotensis* average larger than those of *estor* in breadth of braincase (28.5 and 27.5) and squamosal breadth (37.7 and 36.2) with a broad range of overlap. Otherwise, no significant difference can be ascertained. Seemingly, *perotensis* has only recently diverged from *estor*-like ancestors, by selection having favored in *perotensis* an increase in size in the females. The differences between females is well above the level of differentiation that usually distinguishes most subspecies in *Pappogeomys*.

P. m. perotensis evidently is common in the dark volcanic soils that mantle the Cofre de Perote. However, no melanistic individual is known. Melanism is commonly developed in *P. m. merriami* that occurs in the dark volcanic soils in the mountains around México City.

Specimens examined.—Total, 25, all from Veracruz, as follows: N slope Cofre de Perote, 10 mi. SE Perote, 10,500 ft., 6 (TCWC); *1 km. NW Pescados, 10,500 ft., 5; *N slope Cofre de Perote, 10,300 ft., 3 (UMMZ); *Cofre de Perote, 9,500 ft., 9 (USNM); *Cofre de Perote, 12,500 ft., 2 (USNM).

Pappogeomys merriami saccharalis (Nelson and Goldman)

Cratogeomys merriam saccharalis Nelson and Goldman, Proc. Biol. Soc. Washington, 47:149, June 13, 1934; Ellerman, The Families and Genera of Living Rodents, 1:528, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:367, April 9, 1942; Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:344, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:469, March 31, 1959.

Cratogeomys merriami, Merriam, N. Amer. Fauna, 8:152, January 31, 1895 (part); Elliot, Field Columb. Mus. Publ. 105, Zool. Ser. 6:265, July 1, 1905 (part); Miller, Bull. U. S. Nat. Mus., 79:246, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:258, April 29, 1924 (part).

[*Cratogeomys*] *merriami*, Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:313, 1904 (part).

Type.—Male, adult, skull and skin; no. 55347 U. S. National Museum; Atlixco, 5400 ft., Puebla; July 29, 1893; obtained by E. W. Nelson and E. A. Goldman, original number 5279.

Range.—Western Puebla on southern edge of high plateau in upper Río Balsas drainage. See Fig. 5.

Description.—Size medium for species; tail relatively short (averaging 40% of length of head and body); hind foot long. Average and extreme external measurements of five females and three males from Atlixco are, respectively, as follows: Length of head and body, 216 (200-240), 238 (230-247); length of tail, 86 (73-102), 93 (89-100); length of hind foot, 44 (41-48), 47 (47-48).

Color: Upper parts Mouse Gray basally and Ochraceous-Buff apically, with mixture of black-tipped hairs on back but sides and face pure Ochraceous-Buff; underparts Light Mouse Gray basally overlaid with Light Ochraceous-Buff, blending to Ochraceous-Buff along mid-ventral line in fresh unworn pelage; hairs about mouth Light Buff; small, reddish-brown or black auricular patch; hind foot whitish or buffy.

Skull: Size medium for species; palate relatively long (averaging 69.7% of condylobasal length); rostrum short and broad; maxillary tooth-row short.

Average and extreme cranial measurements for five females and three males are, respectively, as follows: Condylobasal length, 56.3 (53.8-57.3), 60.5 58.9-62.9); zygomatic breadth, 36.7 (36.3-37.0), 39.2 (37.3-42.3); palato-frontal depth, 22.0 (20.9-22.7), 23.8 (23.0-25.1); length of palate, 39.1 (38.7-39.3), 42.0 (40.4-44.0); length of nasals, 20.5 (19.4-21.7), 23.3 (22.1-24.2); breadth of braincase, 26.0 (24.2-27.6), 26.4 (25.1-28.8); squamosal breadth, 35.3 (32.9-37.0), 38.3 (36.0-42.2); breadth of rostrum, 13.4 (12.5-14.1), 15.4 (13.3-16.4); length of rostrum, 24.8 (23.2-26.6), 27.4 (26.8-28.5); alveolar length of maxillary tooth-row, 11.8 (11.0-12.1), 12.3 (12.1-12.4).

Comparisons.—For comparisons with *P. m. fulvescens* and *P. m. irolonis*, see accounts of those subspecies.

From *Pappogeomys merriami merriami*, *saccharalis* differs as follows: Smaller; tail actually and relatively shorter (averaging 40 *versus* 42% of length of head and body); hind foot slightly shorter; upper parts paler and brighter than dark brown phase of *merriami;* underparts decidedly paler, more buffy and less ochraceous; skull averaging less in all dimensions, with no overlap in condylobasal length, palatal length, zygomatic breadth, and squamosal breadth. Skull wider, relative to length.

Remarks.—Of contiguous subspecies, *P. m. saccharalis* most closely resembles *P. m. merriami,* differing mainly in smaller cranial dimensions, especially in measurements of length. The color of the pelage, especially the upper parts, resembles the dark brown phase of *merriami,* but the upper parts are brighter rufous and the underparts are paler buff. I have seen no example of melanism in *saccharalis,* although melanism is common in *merriami* especially in the adjacent mountains to the west. The arid environment and light colored soils in which *saccharalis* lives would not favor the selection of extremely dark pelages. Externally, its relatively short tail is diagnostic.

As now understood, the geographic range of *saccharalis* comprises a small area around Atlixco, the type locality. The town is situated in a relatively small valley at an elevation of 5,500 feet, considerably lower than the Central Plateau immediately to the north. Southward the elevation decreases abruptly to approximately 4,000 feet in the basin of the Río Balsas 15 miles away at Izucar de Matamoros. The upper drainage of the Balsas Basin is inhabited by the geomyid genus *Orthogeomys* (KU specimens not previously reported are from Tilapa, a few miles west of Izucar de Matamoros); pocket gophers of different genera tend to occupy mutually allopatric ranges, hence it is improbable that *saccharalis* occurs to the south of the Atlixco Basin.

Furthermore, *P. merriami* was taken at Texmelucán, Puebla, a locality at approximately 7,000 feet elevation on the Central Plateau less than 30 miles north of Atlixco. To the west in Morelos, several field workers including myself have explored the eastern border of the state wtihout finding sign of pocket gophers in the vicinity of Cuautla, Tlacotapec, Jonacatepec, or Santa Clara. The soils in these places are predominantly heavy clays and are thin and rocky in most places, especially east of Cuautla. Exploration eastward in the area south of Ciudad Puebla in 1952 also revealed no sign of pocket gophers. Edaphic conditions there were restrictive (mostly heavy black clays) for geomyids, and inhabitants of the area said that no pocket gophers occurred there.

Specimens examined.—Total, 13, from **Puebla**, as follows: Atlixco, 5,400 ft., 7 (USNM); * 2 mi. S Atlixco, 5,800 ft., 6.

gymnurus species-group

Diagnosis.—Skull strongly platycephalic in most species; cranium shallow and broad posteriorly relative to length of skull, squamosal breadth averaging more than 66 per cent of condylobasal length, except in *P. t. zodius* (averaging 63.4%); squamosal breadth usually equalling or exceeding zygomatic breadth; lambdoidal crest strongly sinuous in dorsal outline, except in *P. neglectus;* squamosals expanded laterally partly obscuring postglenoid fossa; rami of mandible wide-spread posteriorly and angular processes elongated, breadth across angular processes more than greatest length of lower jaw; occlusal surface of M3 subtriangular.

Remarks.—The *gymnurus* species-group includes five species, two polytypic (*P. tylorhinus* and *P. gymnurus*) and three monotypic (*P. neglectus, P. zinseri,* and *P. fumosus*). Aside from *neglectus,* the species appear to be closely related and do not differ greatly from one another, although the skulls of *P. fumosus* and *P. t. zodius* are less platycephalic than those of the other species. *P. neglectus* probably is most nearly like the ancestral morphotype. *P. fumosus* is uniquely adapted for living in the Tropical Life-zone. *P. tylorhinus, P. zinseri,* and *P. gymnurus,* listed in order of specialization, appear to be a natural group that could have diverged at about the same time from a common ancestral stock. *P. tylorhinus* and *P. gymnurus* differ primarily in size of skull, *gymnurus* being considerably the larger is most respects.

Pappogeomys neglectus (Merriam)

Platygeomys neglectus Merriam, Proc. Biol. Soc. Washington, 15:68, March 22, 1902; Miller and Rehn, Proc. Boston Soc. Nat. Hist., 31:92, August, 1903; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:268, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:74, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924; Goldman, Jour. Mamm., 20: 92, February 15, 1939; Ellerman, the Families and Genera of Living Rodents, 1:531, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:376, April 9, 1942.

[*Platygeomys*] *neglectus*, Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:319, 1904.

Cratogeomys neglectus, Hooper, Jour. Mamm., 29:303, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:347, March 3, 1955; Hall and Kelson, the Mammals of North America, 1:470, March 31, 1959.

Type.—Male, adult, skull and skin; No. 81218 U. S. National Museum; Cerro de la Calentura, 9500 ft., about 8 mi. NW Pinal de Amoles, Querétaro; September 14, 1896; obtained by E. A. Goldman, original number 10142.

Range.—Known only from the type locality. See Fig. 6.

Diagnosis.—Size small; pelage soft; skull decidedly small and relatively deep, but strongly platycephalic; broader across squamosals than across zygomata; rostrum relatively short (averaging 37.7% of condylobasal length) and remarkably broad; maxillary teeth small.

Description.—Size small for *gymnurus*-group; tail relatively long (averaging 41.2% of length of head and body); hind feet short. External measurements of two females and one male (probably not fully adult) from the type locality are, respectively, as follows: Length of head and body, 194, 194, 202; length of tail, 87, 73, 90; length of hind foot, 39, 37, 42.

Color: Hairs of upper parts Dark Mouse Gray basally and Ochraceous-Tawny apically, with some Bay-tipped hairs on back and top of head but pure Ochraceous-Tawny on sides and face; hairs of underparts Light Mouse Gray basally overlaid with Ochraceous-Buff; chin buffy; throat whitish; auricular patch small, blackish; hind foot whitish; tail sparsely clothed with ochraceous hairs.

Skull: Size small for *gymnurus*-group and subgenus *Cratogeomys*, especially in dimensions of length, and smoothly rounded; platycephalic specializations highly developed (mandible widely spreading; angular processes long; cranium relatively broad posteriorly, squamosal breadth averaging 69.5% of condylobasal length; and squamosal breadth greater than zygomatic breadth); lambdoid crest weakly developed, only slightly sinuous; skull relatively deep for *gymnurus*-group (palatofrontal depth averaging 41.1% of condylobasal length); rostrum decidedly short (averaging 37.7% of condylobasal length) and relatively broad (breadth of rostrum averaging 63.2% of length); upper incisors procumbent; maxillary teeth decidedly small.

External measurements of two females and measurements of one male (probably not fully adult) from the type locality are, respectively, as follows: Condylobasal length, 46.7, 45.6, 48.6; zygomatic breadth, 32.3, 31.1 32.5; palatofrontal depth, 19.1, 18.8, 19.8; length of palate, 33.0, 32.0, 33.8; length of nasals, 15.3, 13.8, 15.2; breadth of braincase, 24.2, 23.4, 24.8; squamosal breadth, 33.2, 31.0, 32.8; breadth of rostrum, 11.0, 10.9, 11.0; length of rostrum, 17.8, 16.9, 18.9; alveolar length of maxillary tooth-row, 10.2, 10.1, 10.7.

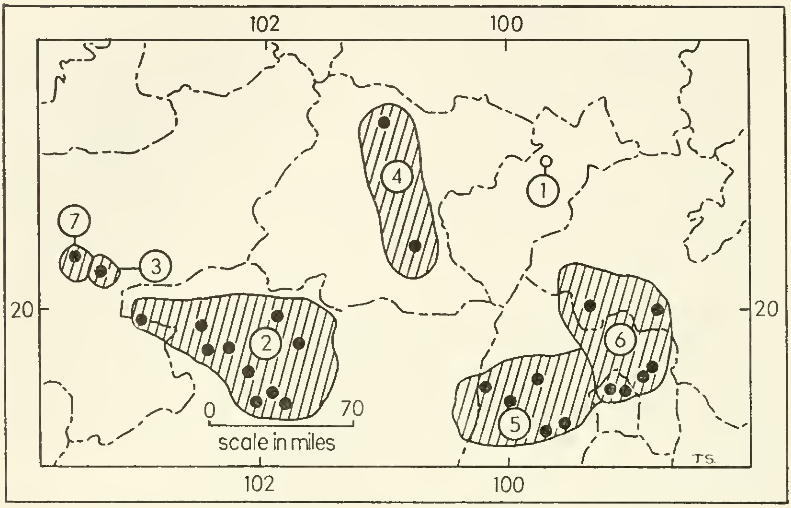

FIG. 6. *Pappogeomys neglectus* and *Pappogeomys tylorhinus.*

Guide to kinds:
1. *P. neglectus*
2. *P. t. angustirostris*
3. *P. t. atratus*
4. *P. t. brevirostris*
5. *P. t. planiceps*
6. *P. t. tylorhinus*
7. *P. t. zodius*

Relationships.—Morphologically, *Pappogeomys neglectus* is referable to the *gymnurus* species-group of *Cratogeomys.* The skull, as judged by small size, relatively deep cranium, slightly sinuous lambdoidal crest, roundness, and weakly developed processes and ridges is generalized as compared with other species in the *gymnurus*-group. Along with the generalized features, *neglectus* is characterized by the basic characters of the *gymnurus*-group, including the broad cranium (broader across squamosals than across zygomata), widely spreading mandibles, long angular process, and subtriangular M3. The shortness and relatively great breadth of the rostrum and the shortness of the nasals are extreme for the *gymnurus*-group. For example, length or rostrum averages only 37.7 per cent of condylobasal length in *neglectus* compared with 38.6 to 42.7 in *tylorhinus,* 43.2 in *zinseri,* 40.5 to 43.6 in *gymnurus,* and 41.0 in *fumosus.* *P. neglectus* closely resembles the hypothetical ancestor of advanced species of the *gymnurus*-group.

P. neglectus is monotypic, has a small geograpic range at the northern edge of the range ascribed to the *gymnurus*-group of species, and appears to be a geographic isolate, restricted to higher elevations in the mountains of northern Querétaro. Small size of skull, the generalized cranial morphology, peripheral geographic distribution, and small geographic range indicate that *neglectus* is a relict species derived from the ancestral stock that gave rise to the much larger *P. fumosus, P. tylorhinus, P. zinseri,* and *P. gymnurus.*

Habitat.—The species occurs in pine forest.

Specimens examined.—Total, 4, from **Querétaro:** Cerro de la Calentura, about 9500 ft., approximately 8 mi. NW Pinal de Amoles, 4 (USNM).

Pappogeomys fumosus (Merriam)

Geomys fumosus Merriam, Proc. Biol. Soc. Washington, 7:165, September 29, 1892; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:74, January 15, 1909; Poole and Schantz, Bull. U. S. Nat. Mus., 178:375, April 9, 1942.

Platygeomys fumosus, Merriam, N. Amer. Fauna, 8:170, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:267, July 1, 1905; Miller, Bull. U. S. Nat. Mus., 79:249, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924; Goldman, Jour. Mamm., 20:90, February 15, 1939; Ellerman, The Families and Genera of Living Rodents, 1:531, June 8, 1940.

Cratogeomys fumosus, Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:346, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:471, March 31, 1959.

Type.—Male, adult, skull and skin; No. 33202/45207 U. S. National Museum; 3 mi. W Colima, 1700 ft., Colima; March 27, 1892; obtained by E. W. Nelson original number 2338.

Range.—Plain in eastern Colima. See Fig. 8. Altitudinal range 1400 to 1700 feet.

Diagnosis.—Pelage coarse and bristly; skull of medium size for *gymnurus* group, condylobasal length 51.2-52.2; narrower across squamosals than across zygomata; rostrum relatively broad (averaging 58.0% of condylobasal length); maxillary tooth-row long.

Description.—Size moderate to large for subgenus; tail relatively short (averaging 36% of length of head and body); hind feet short (for *gymnurus* species-group). External measurements of two females and average and extreme measurements of three males from the Plain of Colima are, respectively, as follows: Length of head and body, 213 and 194, 229 (222-242); length of tail, 75 and 71, 86 (74-98); length of hind foot, 41 and 39, 42 (40-44).

Color: Pelage of upper parts, including auricular area and sides, Dark Mouse Gray basally and Mars Brown apically; pelage of underparts, including chin and throat, Gull Gray basally overlaid with Pale Ochraceous-Buff, overall appearance being grayish-brown and indistinctly paler than darker blackish-brown upper parts; hind foot sparsely haired; tail naked except for few inconspicuous colorless hairs about base. Pelage in general coarse and bristly.

Skull: Size medium for subgenus; zygomata nearly parallel, being slightly broadest across middle; rostrum relatively long (averaging 41.0% of condylobasal length) and broad (averaging 58.0% of its length). Within *gymnurus*-group, notable for squamosal breadth being less than zygomatic breadth; angular processes long (but short relative to anteroposterior length of lower jaws); mandibles not widely spread.

Average and extreme cranial measurements of three females and three males from the Plain of Colima are, respectively, as follows: Condylobasal length, 51.7 (51.1-52.2), 58.7 (56.9-60.6); zygomatic breadth, 35.7 (35.1-36.6), 39.2 (38.4-40.4); palatofrontal depth, 20.1 (19.9-20.4), 22.3 (21.5-23.8); length of palate, 35.5 (35.0-36.1), 40.6 (39.3-42.2); length of nasals, 18.4 (17.5-19.2), 21.3 (20.2-22.7); breadth of braincase, 28.2 (27.5-29.2), 29.4 (28.5-29.9); squamosal breadth, 34.7 (33.5-36.0), 39.1 (37.9-40.9); breadth of rostrum, 12.3 (12.0-12.6), 13.3 (12.7-13.6); length of rostrum, 21.2 (20.6-22.0), 24.7 (22.8-26.4); alveolar length of maxillary tooth-row, 11.8 (11.5-12.2), 12.8 (12.5-13.2).

Relationships.—In general, the morphological features of *Pappogeomys fumosus* are those of the subgenus *Cratogeomys.* Assignment to the *gymnurus* species-group is based on cranial specializations: The skull is large, shallow, and broad; viewed from above the lambdoidal crest is sinuous; the squamosals are expanded laterally over the external auditory tube obscuring the postglenoid notch; the angular processes are long; and the occlusal surface of M3 is subtriangular. The relatively broad rostrum is especially noteworthy in as much as it averages 58.0 per cent of its length in *fumosus* compared with 63.2 in *neglectus,* 50.8 to 55.9 in *tylorhinus,* 55.1 in *zinseri,* and 53.8 to 57.3 in *gymnurus.* The skull of *fumosus* is decidedly platycephalic, (a characteristic of the *gymnurus* group), although not so strongly so as in *Pappogeomys gymnurus* and *Pappogeomys tylorhinus.* In *gymnurus* and *tylorhinus* the cranium is usually so expanded laterally that its breadth (as measured across the squamosals) exceeds or equals the breadth across the zygomata; in *fumosus* the squamosal breadth is only rarely so, although it is relatively wider than in the *castanops* group. The maxillary tooth-row is relatively longer in *fumosus* than in other taxa of the *gymnurus* group.

The morphology of the skull suggests that *fumosus* diverged from early stock of the *gymnurus*-group, at a time before the trend toward increase in cranial size was initiated in *tylorhinus, zinseri,* and especially *gymnurus; fumosus* is significantly smaller than either *zinseri* or *gymnurus* in all cranial dimensions without overlap in the range of variation of most measurements taken, but it overlaps the smaller subspecies of *tylorhinus.* The pelage of *fumosus* is coarse and bristly rather than soft as in other species of the *gymnurus*-group. Evidently, *fumosus* represents an early offshoot of the ancestral stock that became isolated, on the Coastal Plain, from the main line of evolution that took place in the *tylorhinus-zinseri-gymnurus* stock to the east.

Habitat.—All known specimens have been taken in association with open, arid grasslands on the more elevated inland part of the Plain of Colima. To the west the plain slopes gradually down to sea level. Low, thorny shrubs are of common occurrence on the plain, but trees are rare. The area is considered by Goldman (1951: 135) to be Arid Lower Tropical Life-zone.

Remarks.—Pappogeomys fumosus is the only member of the subgenus *Cratogeomys* that inhabits the Tropical Life-zone and probably has done so through much of the later part of the late Pleistocene. Long residence in the tropics is reflected in the color and texture of its pelage. These same features are even better developed in many of the species of the genus *Orthogeomys,* also inhabitants of tropical environments; but, the pelage of *fumosus* is less hispid than in most species of *Orthogeomys.* The parallelism seems to be a response to similar environmental conditions. *Pappogeomys fumosus* and *Orthogeomys grandis* occupy mutually exclusive ranges on the coastal plain of western México, *grandis* occurring in more mesic habitat along the cost of western Michoacán to the south of the range of *Pappogeomys.* Possibly the two are competitors, and each restricts the other geographically.

Pappogeomys bulleri burti of the subgenus *Pappogeomys* also occurs on the Coastal Plain of Colima, but occupies the more mesic coastal belt, and apparently its range does not overlap that of *fumosus. P. b. burti,* although its pelage is scanty, has not developed the harsh texture of pelage that characterizes *fumosus* and other pocket gophers adapted to tropical conditions. *P. fumosus* and *P. b. burti* are the only two pocket gophers of the genus to have become adapted to the arid tropical environment, and both occur in the same region. At other places where the range of the genus extends down to the Tropical Life-zone, the tropical environment already is occupied by well adapted resident populations of *Orthogeomys.*

For further discussion concerning relationships, see account of geographic variation of *Pappogeomys gymnurus.*

Specimens examined.—Total of 12, all from **Colima**, as follows: 3 mi. W Colima, about 1700 ft., 9 (USNM); * Colima City, 1; * 4 mi. SW Colima, 1400 ft., 2.

Pappogeomys tylorhinus

(Synonymy under subspecies)

Range.—Neovolcanic Range and Central Plateau from arid basins of central Jalisco eastward into Valley of Mexico and from northern Guanajuato southward to southern slopes of Neovolcanic Range in western México and Michoacán. See Fig. 6. Altitudinal range from about 4500 feet in central Jalisco to 11,200 feet near top of Volcán de Toluca.

Diagnosis.—Pelage soft and lax; length of skull moderate for *gymnurus*-group, condylobasal length of skull varying from 50.4 to 58.3; breadth across squamosals usually equalling or exceeding breadth across zygomata (except in *P. t. zodius* and some specimens of *P. t. brevirostris*); rostrum long, 20.0 to 26.7; relatively broad across squamosals, averaging in six subspecies 63.4 to 71.7 per cent of condylobasal length.

Description.—Size small to large for *gymnurus*-group; tail relatively short (averaging 36 to 41% of length of head and body); hind feet small to moderately large. Extremes in external measurements of adult females and males are, respectively: Length of head and body, 193-248, 212-276; length of tail, 65-106, 79-106; length of hind foot, 37-46, 37-47.

Color: Overall tone of upper parts pale ochraceous-buff to glossy black, back and top of head having some Bay- or black-tipped hairs in brownish phases resulting in generally darker tones compared with sides and face; underparts paler than dorsum, varying from white to bright shades of ochraceous in both color phases (underparts never black in melanistic individuals); throat gray or buffy; hind feet whitish or brownish.

Skull: Size medium for species of *gymnurus*-group (condylobasal length 50.4 to 58.3 in females and 56.5 to 65.0 in males), rugose and angular, and relatively shallow and flat; squamosal breadth no less than zygomatic breadth (except in *P. t. zodius* and in some specimens of *P. t. brevirostris*); angular processes elongated; mandibles widely spread posteriorly; breadth across angular processes more than length of lower jaw; lambdoidal crest sinuous; rostrum relatively narrow and lightly constructed; zygomata broadly spreading, angles of maxillary arm enlarged into platelike expansion; jugal usually moderately large, slender in some subspecies; upper incisors relatively narrow, usually procumbent; lower incisor lacking lateral bevel behind enamel plate; occlusal surface of M3 subtriangular, apex of posterior loph forming posterior margin of tooth; enamel pattern of premolars and molars as in *Cratogeomys*.

Relationships.—Dental and cranial features of *Pappogeomys tylorhinus* are characteristic of the subgenus *Cratogeomys*. Moreover, the skull is strongly platycephalic (although variation exists as described beyond), indicating membership in the *gymnurus* species-group and distinctly separating *tylorhinus* from the *castanops* species-group. Platycephalic specializations include flat, broad cranium, especially expanded posterior to the squamosal roots of the zygomatic arches, widely spreading rami of the lower jaws and elongated angular processes, and the rugosity and angularity of the occiput, including the lambdoidal crest and enlarged paroccipital processes. The subspecies *P. t. zodius* has a narrow cranium (narrower across squamosals than across zygomata) and therefore is judged to be the least specialized subspecies.

Pappogeomys tylorhinus closely resembles *Pappogeomys zinseri* and *Pappogeomys gymnurus*. In all three the level of specialization is essentially the same and they differ mainly in cranial dimensions and proportions. Seemingly, there is no gene exchange among the three.

P. tylorhinus is the most variable and the smallest, especially in cranial dimensions; *P. gymnurus* is the largest. In condylobasal length, zygomatic breadth, squamosal breadth, and length of palate, the two species do not overlap. *P. zinseri* is intermediate in size, and in cranial measurements overlaps *tylorhinus*, except in zygomatic breadth (see account of *zinseri*). The significantly greater breadth across the zygomata and deeper skull distinguish *zinseri* from *tylorhinus* (see Fig. 7).

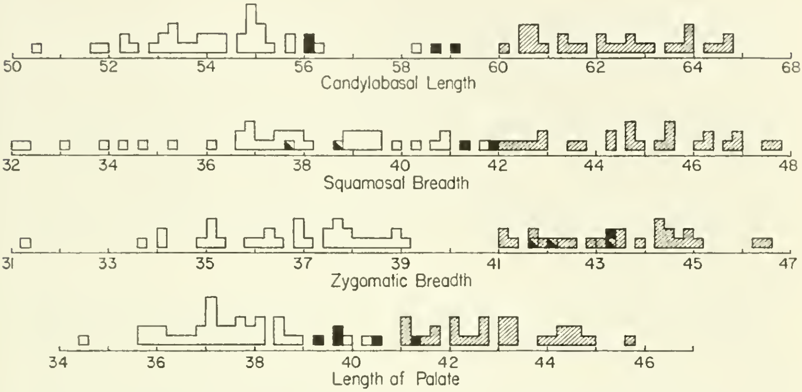

FIG. 7. *Pappogeomys tylorhinus* (unshaded), *P. zinseri* (black), and *P. gymnurus* (diagonal lines).

Among *P. tylorhinus*, *P. neglectus* and *P. fumosus* the differences are greater. *P. neglectus* is small and in many respects generalized. *P. tylorhinus* and *P. fumosus* are larger and about the same size, but differ markedly in other features. *P. fumosus* is the most specialized in type of pelage, relatively large cheek teeth, and especially in relatively broad rostrum (with respect to its length), and significant ecological specializations, but has less strongly developed platycephalic features (see account of *fumosus*).

Habitat.—*P. tylorhinus*, like *P. gymnurus* and *P. merriami*, occurs in a wide variety of ecological situations. *P. tylorhinus* ranges through parts of the Neovolcanic Range, some of the elevated southern part of the Central Plateau (sometimes referred to as the Anahuac Plateau) to the north of the high transverse mountain chain, and also into one of the lower interior basins of central Jalisco. This area of central México is characterized by a wide variety of soils, climates, and vegetation. Changes in these features occur in short distances. The mountains mostly are forested, and, although the soils are varied, extensive areas are mantled in black, highly friable soils of volcanic origin. In the mountainous areas, this species prefers volcanic soils. The densest populations, judging from trap-records, are in the pine-oak zone. But, *tylorhinus* occurs in the pine-fir zone above the pine-oak zone and, less commonly, in the desert-shrub zone below the pine-oak zone. Open areas where grasses, sedges, and forbs are abundant are preferred over heavy forests. Corn fields are especially good habitat. On the plateau to the north, volcanic soils are uncommon, and *tylorhinus* lives in sandy soils and sandy loam where the content of clay is low. The dominant vegetation on the plateau is desert grasses and shrubs.

Shallow, rocky soils and predominantly clayey soils evidently are unsuitable for *P. tylorhinus* and any kind of *Pappogeomys*. These soils cover large areas of northern Michoacán (south of the Río Lerma and north of the Neovolcanic Range), southern and southwestern Guanajuato (south of Celaya and south and west of Irapuato), and southeastern Jalisco west of the Río Grande de Santiago (see accounts of *P. zinseri, P. t. angustirostris,* and *P. t. brevirostris*) where gophers are absent. The belt of unsuitable soils probably extends eastward into southern Querétaro and extreme western Hidalgo; however, field work in this area has not been so extensive as in the area to the west (described above) and some places there may be suitable for gophers. The patchwork pattern of favorable and unfavorable soils has isolated populations of *tylorhinus* (see Fig. 6).

Geographic variation.—Pappogeomys tylorhinus is a polytypic species consisting of six subspecies. The records of occurrence suggest a discontinuous distribution with at least four and possibly five disjunct populations (see Fig. 6). As discussed elsewhere, *P. t. brevirostris* is isolated from other populations by unsuitable soils. In two other areas the range of *P. tylorhinus* is interrupted by land occupied by *P. gymnurus* (compare maps, Figs. 6 and 8). In the west, *P. g. gymnurus* occurs in the basins between the ranges of *P. t. zodius* and *P. t. angustirostris.* To the east, *P. g. imparilis* of the highlands in northeastern Michoacán occurs between the ranges of *P. t. angustirostris* of the highlands of northwestern Michoacán and *P. t. planiceps* of the highlands of western México. Areas in which elevation and habitat change abruptly seem to separate *P. t. zodius* from *P. t. atratus.* The existing pattern of distribution probably results from environmental changes in the Wisconsin glacial period and the subsequent readjustment of range in the post-Wisconsin (see discussion beyond in section on evolution of genus).

Color of the upper parts varies geographically in *P. tylorhinus,* from reddish-brown to pale ochraceous-buff. *P. t. brevirostris, P. t. tylorhinus,* and *P. t. zodius* occurring in more arid environments on the Central Plateau, and especially those individuals that live in light-colored sands, are pale whereas individuals occurring at higher elevations in the Neovolcanic Range are darker, glossy rusty-brown. As in *P. merriami* and *P. gymnurus,* melanism is common in populations occurring in the Neovolcanic Range, especially where black volcanic soils are prevalent, but the frequency of melanistic individuals varies geographically. For instance, all known specimens of *atratus* are melanistic. In *angustirostris,* the percentage of black individuals varies from 17 to 33%, with melanism occurring in all samples, and in *planiceps* 44% of the specimens examined were melanistic. Melanism seems to be correlated with color of the substrate rather than elevation; however, in this region the black volcanic soils are at high elevations, and so far as I know are not at lower elevations on the plateau north of the mountainous region. Melanism does not occur in *tylorhinus* or *brevirostris,* subspecies that occur exclusively on the plateau, and melanism is unknown in *zodius,* which is restricted to one of the arid basins of central Jalisco.

In the species *P. tylorhinus,* specimens assigned to *planiceps* are largest, cranially and in external measurements, and specimens assigned to *zodius* are smallest; specimens assigned to *tylorhinus* are almost as small as those assigned to *zodius.* In general, size increases with elevation, and the maximum size is in the Neovolcanic Range at elevations higher than 7000 feet where *planiceps* and *angustirostris* occur. Nevertheless, *atratus* from 9700 feet on the top of Cerro Viejo in central Jalisco is smaller than *angustirostris* and *planiceps* from comparable and lower elevations. Evidently factors other than elevation are important, for example, the depth of the top soil. Friable soils within the ranges of the large subspecies *planiceps* and *angustirostris* are deep, and on the other hand, the soil on Cerro Viejo, where specimens of *atratus* were obtained, was described by J. A. Alcorn (field notes, February 16-18, 1949) as shallow and rocky. Moreover, samples taken from lowland sites characterized by deep soils have, regardless of soil depth, populations with the smallest external dimensions.

P. t. zodius not only has a small skull, but has also cranial proportions different from those of other subspecies of *P. tylorhinus;* the cranium is narrow (squamosal breadth averaging 63% of condylobasal length, instead of 67 to 72% as in other subspecies), and the squamosal breadth is less (averaging 98%) than the zygomatic breadth. The zygomatic breadth itself is relatively narrower in *zodius* (averaging 65% of condylobasal length) than in the other subspecies (67 to 68%). In *brevirostris* also the breadth across the squamosals averages slightly less (99.7%) than the zygomatic breadth. The squamosal breadth averages more than 100% of the zygomatic breadth in all of the subspecies except *brevirostris* and *zodius.* The latter has also a relatively long maxillary tooth-row, being only slightly less (22.4% of condylobasal length) than that of *fumosus* (22.8% of condylobasal length), which is maximal for the *gymnurus* group.

Character gradients in cranial features that correspond to environmental gradients are not clearly discernible in *P. tylorhinus.* Lack of clines is probably due to the high incidence of geographic isolation and the concomitant restriction of gene flow. Isolation allows for the selection of phenotypes that are adapted closely to local conditions without the leveling effects of gene flow. Most subspecies of *P. tylorhinus* are distinguished by one or more unique features.

Rostrum, nasals, and maxillary tooth-row are shortest in samples of *brevirostris* from the desert plains on the Central Plateau in southeastern Guanajuato. The longest rostrum is in *planiceps* from the cool, humid pine forest in the Neovolcanic Range of the western part of the state of México. The longest nasals are in specimens from the Neovolcanic Range in México, Michoacán, and Jalisco, referred respectively to the subspecies *planiceps, angustirostris,* and *atratus,* and the longest maxillary tooth-row, relative to length of skull, is in *zodius* from the lowlands. The broadest rostrum, relative to rostral length, is in *angustirostris* of the humid Neovolcanic Range in northwestern Michoacán and in *zodius* from an arid basin in central Jalisco. The narrowest rostrum relative to rostral length is in *planiceps.* The broadest cranium (posterior to squamosal roots of zygomata) is in *tylorhinus* from the arid Valley of México, although the posterior part of the crania of *planiceps* and *angustirostris* from higher elevations in the Neovolcanic Range are also broad.

Of the six subspecies, *zodius* in general is the most different. Its skull is least platycephalic owing, perhaps, to retention of features of the ancestral stock. *P. t. zodius* is geographically isolated at the western periphery of the range of the species. *P. t. brevirostris* also is geographically isolated at the north-central periphery of the range of the species, and is characterized by several unique features. Although the posterior part of the skull is relatively broader than in *zodius*, it is not so broad as in the more specialized members of the species (*angusticeps, planiceps,* and *tylorhinus*). The geographic distribution of the platycephalic skull indicates that it developed in the main body of the species and probably when populations were contiguous. Subsequently, the main body has broken up into four more or less issolated subspecies, *tylorhinus, planiceps, angustirostris,* and *atratus. P. t. zodius* could have been cut off from the main body of the species before the platycephalic skull evolved. *P. t. brevirostris* probably has had contact with the main body of the species later than *zodius* did, and, therefore, is more specialized.

If *angustirostris, atratus, planiceps,* and *tylorhinus* were combined as one highly variable subspecies, the name *tylorhinus* would apply by reason of priority. *P. t. brevirostris* and especially *P. t. zodius* differ so much from each other and from other subspecies that they can hardly be placed in one subspecies. In fact, *zodius* might be given specific status, although it seems best to me to stress its relationship to the *tylorhinus* complex by treating *zodius* as a subspecies of *P. tylorhinus.*

Pappogeomys tylorhinus angustirostris (Merriam)

Platygeomys tylorhinus angustirostris Merriam, Proc. Biol. Soc. Washington, 16:81, May 29, 1903; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:267, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:74, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:531, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:376, April 9, 1942.

[*Platygeomys tylorhinus*] *angustirostris,* Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:319, 1904.

Platygeomys angustirostris, Goldman, Jour. Mamm., 20:90, February 15, 1939.

Cratogeomys angustirostris, Hooper, Jour. Mamm., 29:303, August 31, 1948; Hall and Villa, Univ. Kansas Publ. Mus. Nat. Hist., 1:452, December 27, 1949; Hall and Villa, Anal. Inst. Biol., 21:186, September 28, 1950; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:346, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:471, March 31, 1959.

Platygeomys varius Goldman, Jour. Mamm., 20:90, February 15, 1939, type from Uruapan, about 6000 ft., Michoacán; Poole and Schantz, Bull. U. S. Nat. Mus., 178: 376, April 9, 1942.

P. [*latygeomys*] *varius,* Hooper, Jour. Mamm., 27:398, November 25, 1946.

Cratogeomys varius, Hooper, Jour. Mamm., 29:303, August 31, 1948; Hall and Villa, Univ. Kansas Publ. Mus. Nat. Hist., 1:453, December 27, 1949; Hall and Villa, Anal. Inst. Biol., 21:186, September 28, 1950; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:346, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959.

Type.—Adult, female, skull and skin; No. 125688 U. S. National Museum; Cerro Patambán (= Patambá on some maps), 10,000 ft., Michoacán; February 3, 1903; obtained by E. W. Nelson and E. A. Goldman, original number 15,850.

Range.—Northern Michoacán in Sierra del Tigre, eastward in the Neovolcanic Range to 2 mi. SE of Zacapu, and on south-facing slopes in vicinity of Uruapan. See Fig. 6. Altitudinal range from about 5000 to 10,000 feet.

Description.—Large for species; tail moderately long (averaging 39% of length of head and body); hind foot average in length for species. Average and extreme external measurements for 12 females and six males, respectively, from the mountains of northwestern Michoacán and southeastern Jalisco are as follows: Length of head and body, 222 (211-244), 237 (222-251); length of tail, 87 (73-98), 93 (79-102); length of hind foot, 41 (39-45), 43 (42-45).

Color: Adults of both sexes exhibit two color phases—a bright reddish-brown phase and a dark brownish-black phase. Hind feet usually whitish, regardless of color phase of rest of pelage, but sometimes varing in reddish-brown phases to tones of buffy and brownish hues; tail covered with dark brownish hairs; throat usually grayish. Reddish-brown phase: Hairs of upper parts Dark Mouse Gray basally, varying apically from glossy Cinamon-Brown on back to Ochraceous-Buff on sides in paler individuals to bright Russet in darker individuals, back and top of head having also Bay or black-tipped hairs imparting a darker tone to mid-dorsal area than to sides and face; underparts Mouse Gray basally overlaid with Light Ochraceous Buff in paler individuals and bright Ochraceous-Tawny in darker, richer pelages; hairs of auricular patch black to roots. Dark brownish-black phase: Hairs of upper parts Dark Mouse Gray basally and Mummy Brown apically, with black-tipped hairs imparting an overall dark brownish-black appearance, sides and face varying from pure Mummy Brown in darker individuals to rich Ochraceous-Tawny in brighter pelages; underparts distinctly paler than dorsum, hairs Mouse Gray basally overlaid with Light Buff or Ochraceous-Buff in brighter pelages; auricular patch not distinguished from surrounding area.

Skull: Medium in size for species; zygomata widely spreading; skull relatively deep (averaging 39.4% of condylobasal length); palate, nasals and maxillary tooth-row long; broad across braincase and squamosals; rostrum long and broad (breadth averaging 55.9% of length).

Average and extreme cranial measurements of 12 females and six males from northwestern Michoacán and southeastern Jalisco are, respectively, as follows: Condylobasal length 54.5 (53.0-56.3), 58.7 (57.5-60.7); zygomatic breadth, 37.3 (35.9-38.8), 42.8 (40.5-44.2); palatofrontal depth, 21.5 (20.2-22.3), 23.0 (22.0-23.5); length of palate, 37.7 (37.0-39.9), 41.3 (40.0-43.3); length of nasals, 19.4 (17.5-20.8), 21.6 (20.5-22.4); breadth of braincase, 28.6 (27.4-30.4), 30.9 (29.3-33.5); squamosal breadth, 38.2 (36.1-40.9), 41.9 (40.1-43.4); breadth of rostrum, 12.7 (12.1-13.9), 14.5 (13.7-15-6); length of rostrum, 22.7 (22.1-23.6), 25.3 (24.2-26.4); alveolar length of maxillary tooth-row, 11.7 (10.8-12.5), 12.4 (11.6-12.9).

Comparisons.—For comparisons with *P. t. atratus, P. t. brevirostris,* and *P. t. planiceps,* see accounts of those subspecies.

Remarks.—Smaller size of skull allies *angustirostris* with *Pappogeomys tylorhinus* rather than with the significantly larger *Pappogeomys gymnurus.* The geographic range of *angustirostris* separates two of the subspecies of *Pappogeomys gymnurus* (*imparilis* to the east and *gymnurus* to the west). Populations of *angustirostris* are geographically close to those of both *P. g. gymnurus* and *P. g. imparilis,* yet there is no indication of intergradation between *angustirostris* and either of the two subspecies of *P. gymnurus.* Lack of evidence of interbreeding suggests that *angustirostris* is specifically distinct, and forms the basis for the recognition of two species, *Pappogeomys tylorhinus* and *Pappogeomys gymnurus.*

Pappogeomys varius was described by Goldman (1939a:90) on the basis of a single specimen from Uruapan, a town at about 6000 feet on the southern slope of the Neovolcanic massif in central Michoacán. Goldman (*loc. cit.*) pointed out the similarity of *varius* to *angustirostris,* but owing to the disparity in the size of the cranium, accorded *varius* specific status. His conclusions were, no doubt, influenced by the fact the only specimen of *varius,* identified by the field collector as a male, was appreciably smaller than the holotype and only known specimen of *angustirostris,* an adult female. Although the range of variation cannot be estimated on the basis of single specimens, Goldman knew, of course, that males exceed females in size. A total of 63 specimens from this area was studied by me, including topotypes of both *varius* and *angustirostris,* and examples of all age groups of both sexes. This material has provided, for the first time, an adequate sample for segregating age groups, for estimating the range of variations, and for a more reliable diagnosis of both *varius* and *angustirostris.* On the basis of its size, the holotype of *varius* is evidently a female; certainly it is not large enough cranially to be included in the range of variation ascribed to adult males of either *varius* or *angustirostris.* Also, it is evident from this material that all the specimens are referable to one species, *Pappogeomys tylorhinus.* Moreover, I find no morphological grounds for distinguishing *varius* from *angustirostris* subspecifically. Only minor differences could be ascertained of the sort usually associated with differences between local populations and not of a magnitude that would warrant taxonomic recognition. Therefore, *P. varius* is synonymized with *P. t. angustirostris,* the valid name by reason of priority.

Largest external dimensions are attained in populations from the Cerro Patambán area of northwestern Michoacán where length of head and body averages 226 compared with 218 in the Sierra del Tigre to the east and 219 in the Uruapan district in the southeastern part of the range. The length of the tail, both actually and relatively, is shortest in the population occurring in the Sierra del Tigre.

The tail in the Sierra del Tigre sample averages 37 per cent of the length of head and body compared with 42 per cent in both the Patambán and Uruapan samples. The nasals average shorter (18.8) in the Patambán series than in either the Uruapan (20.0) or Sierra del Tigre (19.5) series, and the breadth across the squamosals averages remarkably greater in the sample from the Sierra del Tigre (39.7) than in the samples from the Patambán area (38.0) or the Uruapan area (37.0). Of these differences between local populations of *angustirostris*, only squamosal breadth suggests a cline, namely an increase in breadth from southeast to northwest.

Examples in the reddish-brown color phase from the eastern part of the range including specimens labeled with reference to Uruapan, Nuevo San Juan, and Corupo (previously referred to *varius*), and also specimens from 2 mi. SE Zacapu and 8 mi. SE Carapan are slightly paler dorsally than those from the western part of the range owing to the less deeply pigmented apical coloration and less suffusion of blackish. Also, in samples from the east, the hair of the belly is overlaid with paler tones of buffy and is less brightly ochraceous. Brightest pigmentation is developed in specimens from the northwestern slope of Cerro Patambán (Jesús Diaz, Tarequato, and Tangancícuaro). Melanism occurs in all samples, but is more frequent in the series from the Sierra del Tigre where 33 per cent of the known specimens are melanistic. In the adjacent mountains to the east (the Patambán) area, only 17 per cent of the known specimens are melanistic. None of the distinctions in color is great, and, in my opinion, these differences are of the sort to be expected in a region of complex soils representing several distinct color variations, including deep black, brick red, and grayish-brown.

The most divergent population of *angustirostris* is that from the Sierra del Tigre in extreme southeastern Jalisco. This mountainous area is separated by the relatively low valley of the Río Tepalcatepec drainage from the highlands of northwestern Michoacán. These pocket gophers become less abundant at lower elevations below the pine forest zone; therefore, the intervening valley may function as a partial barrier reducing gene exchange between gophers of the Sierra del Tigre and areas to the east.

Pappogeomys tylorhinus seems not to occur along the southern shore of Lago de Chapala or on the Central Plateau in the vicinity of Jaquilpan, Zamora, Panindicuaro, Morelia, and along the southern shore of Lago de Cuitzeo. No sign of gophers was observed at these places, and the natives, most of whom knew pocket gophers, said they did not know of gophers locally but that they did occur in the mountains to the south.

Ingles (1958:391) reported a specimen identified by him as *Cratogeomys varius* (=*Pappogeomys angustirostris*) from Pontezuelas (=Mil Cumbres), 7000 ft., Michoacán. I have not examined it because, at this time (December, 1966), it is in storage while Dr. Ingles is out of the country. Mil Cumbres is approximately half-way between Cd. Hidalgo and Morelia. *Pappogeomys gymnurus imparilis* has been recorded from this area, and on geographic grounds I would suspect that the Mil Cumbres specimen is referable to that species rather than to *angustirostris*.

An adult, KU 62499, from Tangancícuaro, sexed as a female by the collector, has dimensions within the range of variation ascribed to males and beyond that of females.

Specimens examined.—Total of 63, as follows: **Jalisco:** 4 mi. W Mazamitla (Sierra del Tigre), 6600 ft., 3; *3 mi. WSW Mazamitla (Sierra del Tigre), 12. **Michoacán:** 4½ mi. NE Tarequato, 6600 ft., 3; * 2 mi. N Tarequato, 7200 ft., 3; 1 mi. N Tinquindin, 6300 ft., 4; Jesús Diaz (= Sirio), west slope Cerro Patambán (= Patambá), 7500 ft., 6; Tangancícuaro, 5500 ft., 3; 8 mi. SE Carapán, 3; * 2 mi. SW Zacapu, 6600 ft., 1; * Zacapu, 6600 ft., 2; * 2 mi. SE Zacapu, near village of Tacumbo, 6600 ft., 2; 1 mi. S Corupo, 2 (UMMZ); * 2 mi. S Corupo (= Corpua), 2350 m. (= about 7750 ft.), 2 (UMMZ); * 5 mi. NNW Uruapan, 2; Capatitzio Nat'l. Park, Uruapan, 2 (UMMZ); * airfield, 1½ mi. E Uruapan, 3 (UMMZ); * 2½ mi. E Uruapan, 1 (UMMZ); Nuevo San Juan (= Los Conejos), 7 (UMMZ); on road to Tzuraracua Falls, 1520 m. (= about 5000 ft.), 6 mi. SE Uruapan, 2 (UMMZ).

Pappogeomys tylorhinus atratus (Russell)

Cratogeomys gymnurus atratus Russell, Univ. Kansas Publ. Mus. Nat. Hist., 5:539, October 15, 1953; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Type.—Female, adult, skull and skin; No. 31880 University of Kansas Museum of National History; Top of Cerro Viejo de Cuyutlán, 9700 ft., 19 mi. S and 9 mi. W Guadalajara, Jalisco; February 17, 1949; obtained by J. R. Alcorn, original number 7902.

Range.—Known only from the type locality, north of the west end of Lago de Chapala, Jalisco; probably restricted to higher elevations on Cerro Viejo. See Fig. 6.

Description.—Size medium for species; tail relatively short (averaging 36% of length of head and body); hind foot moderately long. Average and extreme external measurements of three females and the measurements of one male from the type locality are, respectively, as follows: Length of head and body, 216 (209-222), 227; length of tail, 78 (74-83), 88; length of hind foot, 41 (40-43), 43.

Color: Hairs of upper parts Dark Mouse Gray basally and glossy Mummy Brown apically, with some black-tipped hairs on back and top of head, but pure Mummy Brown on sides and face; hairs of belly Mouse Gray basally overlaid with Warm Buff; throat grayish; auricular area as rest of dorsum, distinct patches not discernible; tail sparsely set with dark brownish hairs; hind feet whitish above.

Skull: Medium in size for species; zygomata not widely spreading; skull relatively shallow (palatofrontal depth averaging 38.2% of condylobasal length); palate and nasals moderately long; narrow across braincase and squamosals (but, on the average, squamosal breadth exceeds zygomatic breadth); rostrum relatively long.

Average and extreme cranial measurements for three females and the measurements of one male from the type locality are, respectively, as follows: Condylobasal length, 54.2 (53.3-55.3), 56.5; zygomatic breadth, 36.4 (35.0-37.8), 37.6; palatofrontal depth, 20.7 (20.0-21.5), 21.1; length of palate, 37.3 (36.1-38.8), 39.0; length of nasals, 19.5 (19.4-19.6), 20.7; breadth of braincase, 27.1 (25.9-28.4), 28.6; squamosal breadth, 36.8 (35.3-38.0), 39.5; breadth of rostrum, 12.2 (11.5-12.8), 13.2; length of rostrum, 22.6 (22.3-22.8), 24.2; alveolar length of maxillary tooth-row, 11.1 (10.6-11.5), 11.4.

Comparisons.—For comparisons with *P. t. brevirostris* and *P. t. zodius,* see accounts of those subspecies.

From *Pappogeomys tylorhinus angustirostris, atratus* differs as follows: Smaller; tail relatively shorter (averaging 36% *versus* 39% of length of head and body); upper parts darker (compared with reddish-brown phase of *angustirostris*), more glossy black and less reddish-brown (compared with dark phase of *augustirostris,* about the same); underparts paler (compared with reddish-brown phase), more buffy and less ochraceous, but a brighter shade of buffy than in black phase of *angustirostris;* skull slightly shallower; narrower across zygomata, braincase and squamosals; maxillary tooth-row slightly shorter.

Remarks.—J. R. Alcorn, who obtained the specimens of *atratus,* found these gophers at the top of Cerro Viejo, and although he searched for gophers at various lower elevations on the sides of this isolated peak, saw no sign of any below the top. Apparently, *atratus* is restricted to high elevations on Cerro Viejo and is isolated at this time from other populations of *Pappogeomys tylorhinus.*

P. t. atratus more closely resembles *angustirostris* than any other subspecies. The resemblance is especially strong in cranial features, but *atratus* is distinguished by a decidedly narrower cranium. All known specimens of *atratus* are glossy black dorsally as in the black phase of *angustirostris.* Indeed, the black phase is more common in populations of *angustirostris* that occur in the Sierra del Tigre, a mountain range about 35 miles southeast of Lago de Chapala. *P. t. zodius* occurs on the plateau a short distance to the west of the base of Cerro Viejo, but *atratus* shows no close resemblance to *zodius* despite their geographic affinity.

Melanism, especially on the upper parts, is found in all populations of *Cratogeomys* occurring in the Neovolcanic Range, but evidently it attains its highest frequency in *atratus.* The total population of this subspecies is no doubt small; therefore, selection would be more effective in establishing 100 per cent fixation of the genes that phenotypically produce melanism. Based on the sample in hand, all of which are in the extreme phase of melanism on their dorsum, a frequency of melanism of nearly 100 per cent has evolved on Cerro Viejo. However, the underparts are buffy in all specimens and show no tendency toward melanism.

Specimens examined.—Total 6, all from **Jalisco**, as follows: Top of Cerro Viejo de Cuyutlán, 9700 ft., 19 mi. S and 9 mi. W Guadalajara, 6.

Pappogeomys tylorhinus brevirostris new subspecies

Type.—Female, adult, skull and skin; No. 66151 Univ. of Kansas Museum of Natural History; 2 mi. E. Celaya, 5800 ft., Guanajuato; January 17, 1955; obtained by Robert W. Dickerman, original number 4844.

Range.—From Ceylaya in southeastern Guanajuato northward to San Diego de la Unión in north-central Guanajuato. See Fig. 6. Known from elevations of 5800 and 6000 feet.

Diagnosis.—Size medium for species; tail moderately long (averaging 38% of length of head and body); hind foot long. Average and extreme external measurements of three females and four males from 2 and 5 mi. E Celaya are, respectively, as follows: Length of head and body, 216 (211-219), 235 (215-252); length of tail, 82 (71-88), 98 (93-104); length of hind foot, 42 (40-43), 44 (43-44).

Color: Pelage of upper parts Mouse Gray basally and varying apically from Ochraceous-Orange to Ochraceous-Tawny, becoming pure Ochraceous-Buff on sides and face, but some hairs on back and top of head tipped with dark brown; auricular patch small, blackish; underparts Light Mouse Gray basally overlaid with Light Ochraceous-Buff; chin buffy; throat dark grayish; hind feet dark brownish except for few white hairs about bases of toes.

Skull: Small for species; palate, rostrum, and especially nasals short; narrow across rostrum, zygomata, braincase, and especially squamosals; maxillary tooth-row short.

Average and extreme cranial measurements of three females and four males from 2 and 5 mi. E Celaya are, respectively, as follows: Condylobasal length, 52.6 (51.9-53.4), 61.0 (60.5-61.5); zygomatic breadth, 35.3 (33.6-37.4), 42.0 (41.7-42.3); palatofrontal depth, 20.4 (19.8-21.2), 22.7 (22.0-23.2); length of palate, 36.3 (35.6-36.9), 42.2 (41.8-42.4); length of nasals, 16.8 (16.2-17.5), 20.3 (19.5-21.5); breadth of braincase, 27.4 (26.8-28.5), 30.4 (30.0-31.3); squamosal breadth, 35.2 (34.2-36.8), 42.8 (41.5-44.0); breadth of rostrum, 11.1 (10.7-11.4), 13.0 (12.2-13.6); length of rostrum, 20.3 (20.0-20.7), 24.3 (24.0-24.9); alveolar length of maxillary tooth-row, 10.7 (10.2-11.0), 12.3 (11.8-12.7).

Comparisons.—For comparisons with *P. t. planiceps* and *P. t. tylorhinus,* see accounts of those subspecies.

From *Pappogeomys tylorhinus angustirostris, brevirostris* differs as follows: Smaller; hind foot longer; upper parts (compared with reddish-brown phase of *angustirostris*) brighter, more rich ochraceous and less tawny or cinnamon; underparts paler, more buffy and less rufous; dorsal surface of hind foot brownish rather than whitish; skull averaging smaller in all dimensions, without overlap in length of palate, breadth of rostrum, and length of rostrum; also significantly smaller in palatofrontal depth, length of nasals, and squamosal breadth.

From *Pappogeomys tylorhinus atratus, P t. brevirostris* differs as follows: Tail relatively longer (averaging 38% *versus* 36% of length of head and body); hind foot slightly longer; upper parts distinctly paler, more ochraceous-buff and less brownish-black; underparts paler, with less bright buff; dorsal surface of hind foot brownish rather than whitish; skull smaller; narrower across zygomata and squamosals; palate and especially nasals shorter; slightly broader across braincase; rostrum narrower and especially shorter; maxillary tooth-row slightly shorter.

Remarks.—Next to *P. t. zodius, brevirostris* is the smallest subspecies of *Pappogeomys tylorhinus,* and the rostrum, nasals, and maxillary tooth-row each averages considerably shorter than in other subspecies, except for the maxillary tooth-row which averages only slightly shorter than in *P. t. atratus* and *P. t. tylorhinus.* The relatively short tail distinguishes *brevirostris* from all other subspecies. Although resembling *zodius* in size, *brevirostris* is geographically separated from *zodius* by a large area in southwestern Guanajuato and southeastern Jalisco from which pocket gophers are not known. Also the Río Grande de Santiago, entrenched in a steep-walled canyon, forms an impassable barrier between their ranges.

All specimens of *brevirostris* are in the pale, or reddish, phase, and it seems unlikely that the dark phase occurs in this subspecies. *P. t. brevirostris* lives in a xeric environment, on part of the elevated southern portion of the Central Plateau. Neither dark soils nor local areas of high rainfall are found within its range. Melanism usually is associated with areas of dark soil and heavy rainfall in the species *P. tylorhinus.* A high incidence of melanism, therefore, occurs in *P. t. angustirostris* and *P. t. planiceps* that inhabit the mountainous country to the south. At this time, *brevirostris* is apparently isolated from these subspecies by inhospitable habitat (for further discussion, see species account above). Also barriers to the east now separate the ranges of *brevirostris* and *P. t. tylorhinus* occurring in the Valley of México. The range of *brevirostris* is restricted to a belt of deep, pale sandy soils.

An adult (USNM, No. 13301/37776), probably a female, from San Diego de la Unión in north-central Guanajuato, was referred by Goldman (1939a:91) to *Cratogeomys zinseri*—see also Miller and Kellogg (1955:347) and Hall and Kelson (1959:470). This specimen lacks external measurements and its skull is shattered. Although the breadth across the braincase and squamosals is greater than in topotypical material from 2 and 5 mi. E Celaya, the San Diego specimen is within the range of variation of *brevirostris* in other features that can be measured. The short maxillary tooth-row (11.0) especially suggests *brevirostris* rather than *zinseri*.

Specimens examined.—Total of 9, all from **Guanajuato,** as follows: San Diego de la Unión, 1 (USNM); 2 mi. E Celaya, 5800 ft., 6; * 5 mi. E Celaya, 6000 ft., 2.

Pappogeomys tylorhinus planiceps (Merriam)

Platygeomys planiceps Merriam, N. Amer. Fauna, 8:168, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:267, July 1, 1905; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:74, January 15, 1909; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924; Goldman, Jour. Mamm., 20:91, February 15, 1939; Ellerman, The Families and Genera of Living Rodents, 1:531, June 8, 1940; Poole and Schantz, Bull. U. S. Nat. Mus., 178:376, April 9, 1942.

[*Platygeomys*] *planiceps*, Trouessart, Cat. Mamm., 1:574, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:319, 1904.

P. [*latygeomys*] *planiceps*, Hooper, Jour. Mamm., 27:398, November 25, 1946 (part).

C. [*ratogeomys*] *t.* [*ylorhinus*] *planiceps*, Hooper, Jour. Mamm., 28:46, February 15, 1947.

Cratogeomys tylorhinus planiceps, Hooper, Jour. Mamm., 29:303, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:347, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959.

Type.—Male, adult, skull and skin; No. 55906 U. S. National Museum; north slope Volcán de Toluca, 9000 ft., México; September 12, 1893; obtained by E. W. Nelson, original number 5466.

Range.—Valley of Toluca in western part of state of México and slopes of surrounding mountains. See Fig. 6. Altitudinal range from about 8500 feet on valley floor to 11,200 feet near top of Volcán de Toluca.

Description.—Large for species; tail long (averaging 40% of length of head and body); hind foot long. Average and extreme external measurements of five females and five males from Toluca Valley area are, respectively, as follows: Length of head and body, 233 (217-248), 249 (235-276); length of tail, 93 (75-102), 92 (80-106); length of hind foot, 43 (41-46), 45 (41-47).

Color: Individuals of both sexes having two color phases (reddish-brown and black); hind feet white and throat grayish in both phases. Reddish-brown phase: Hairs of upper parts Dark Mouse Gray basally and apically pure Ochraceous-Tawny on sides and face becoming bright Russet on back and top of head, mixed with black-tipped hairs; hairs of underparts Mouse Gray overlaid with Light Ochraceous-Buff varying to Ochraceous-Buff in a few individuals; chin whitish; auricular area small, hairs sooty black to roots. Black phase: Hairs of upper parts Dark Mouse Gray basally and apically dark Mummy Brown, mixed with black-tipped hairs, some specimens paler on sides than back, being pure Ochraceous-Buff rather than Mummy Brown; hairs of underparts Mouse Gray basally, slightly tinged with Ochraceous-Buff apically; chin grayish like throat.

Skull: Large for species; zygomata widely spreading; nasals, maxillary tooth-row, and especially palate long; broad across braincase and especially squamosals; rostrum long (averaging 42.7% of condylobasal length) and relatively narrow (averaging 50.8% of length of rostrum).

Average and extreme cranial measurements of four females and five males from Toluca Valley area are, respectively, as follows: Condylobasal length, 56.2 (55.1-58.3), 60.9 (59.1-65.0); zygomatic breadth, 38.1 (37.6-39.1), 43.0 (39.8-46.0); palatofrontal depth, 21.6 (20.8-22.7), 23.7 (22.6-25.2); length of palate, 38.8 (37.5-40.3), 42.4 (40.5-45.1); length of nasals, 19.5 (18.7-20.7), 20.8 (19.6-22.6); breadth of braincase, 28.4 (28.1-28.8), 31.5 (29.4-34.5); squamosal breadth, 38.8 (37.7-39.2), 42.6 (41.2-43.8); breadth of rostrum, 12.2 (11.5-12.7), 14.1 (12.7-14.8); length of rostrum, 24.0 (22.1-26.7) 25.4 (23.5-28.8); alveolar length of maxillary tooth-row, 11.6 (10.2-13.0), 12.4 (11.5-13.4).

Comparisons.—For comparison with *P. t. tylorhinus*, see account of that subspecies.

Compared with *Pappogeomys tylorhinus angustirostris*, *planiceps* differs as follows: Larger; tail slightly longer (averaging 40 *versus* 39% of length of head and body); hind foot longer; upper parts (black phase) darker, more blackish and less brownish-black (dorsum in reddish-brown phase about the same); underparts (in black phase) brighter, more ochraceous and less buffy, or (in reddish-brown phase) paler, more buffy and less ochraceous-tawny; skull decidedly longer; zygomata more widely spread; palate longer; rostrum slightly narrower and decidedly longer (relatively narrower, breadth averaging 50.8% *versus* 55.9% of length); breadth across squamosals slightly greater.

Compared with *Pappogeomys tylorhinus brevirostris*, *planiceps* differs as follows: Larger; tail relatively longer (averaging 40% *versus* 38% of length of head and body); hind foot longer; upper parts (comparison of reddish-brown phases only) darker, more dark brownish and less bright ochraceous on back, and more tawny and less buffy on sides; underparts paler owing to lighter shades of buff; chin whitish or grayish rather than buffy; dorsal surface of hind foot whitish instead of brownish; skull averaging larger in all dimensions, without overlap in condylobasal length, zygomatic breadth, length of palate, length of nasals, squamosal breadth, and length of rostrum; rostrum relatively narrower (averaging 50.8% *versus* 54.7% of its length); nasals, rostrum and maxillary tooth-row remarkably longer.

Remarks.—Previously, *planiceps* has been known only by the holotype, an adult male, and two female paratypes, one with a shattered skull, all from the upper slopes of Volcán de Toluca. Additional specimens, mostly obtained by R. W. Dickerman farther east, west, and north show that *planiceps* occurs also at lower elevations in the Neovolcanic Range of which Volcán Toluca is a part as well as in the Valley of Toluca. The range of *planiceps* lies directly between those of *Pappogeomys gymnurus imparilis* to the west in the uplands of Michoacán and *Pappogeomys merriami merriami* to the east in the Sierra de Ajusco of México and Morelos. There is no indication of interbreeding between *planiceps* and *imparilis*. Expansion of the range of *planiceps* is thought to be prevented to the south by the arid lowlands of the Balsas Basin and to the east and west by interspecific competion. *Pappogeomys merriami* occurs in the western foot hills (Salazar) of the Sierra Ajusco, and it is unlikely that *planiceps* occurs on even the lower slopes of these mountains. However, the range probably extends farther north than actual records indicate, at least throughout the Valley of Toluca. In 1952, natives told me at Acambay and Aculco that pocket gophers did not occur locally there or in the pass to the north of Aculco but were abundant to the south in the valley of the Río Lerma. We found no evidence of pocket gophers in the mountains in the northern part of the state of México nor in southern Querétaro.

Early authors, including Goldman (1939a:91) in his review of the genus *Platygeomys*, treated *planiceps* as a species. Specific characters, according to Goldman (*loc. cit.*) included: Flattened braincase; straighter, less sinuous lambdoidal crest than in *tylorhinus;* slender zygomata; narrow jugal, without anterior expansion; long nasals; procumbent upper incisors. All of these features are subject to considerable individual variation, and are matched in individuals of one or the other subspecies of *Pappogeomys tylorhinus*. For example, the nasals are no longer than those of *P. t. angustirostris* or *P. t. atratus*, both of which have smaller, shorter skulls, and the braincase is usually flattened in old individuals, especially in males. The lambdoidal crest of *zodius* is only slightly sinuous, and the jugal is slender in individuals of several subspecies. The upper incisors of *P. t. tylorhinus*, as Goldman pointed out, are decidedly procumbent, as also are those of *P. t. angustirostris*. None of these characters is peculiar to *planiceps* and although intergrades between *P. t. planiceps* and neighboring subspecies of *P. tylorhinus* are unknown, the differences are no greater than those between subspecies that do intergrade. Therefore, I follow Hooper (1947:46) in arranging *planiceps* as a subspecies of *Pappogeomys tylorhinus*.

P. t. planiceps is the largest of the subspecies assigned to *Pappogeomys tylorhinus*. It is distinguished especially by great breadth across the zygomata and long tail, skull, palate, and rostrum. Compared with other subspecies, *planiceps* most closely resembles *angustirostris*, differing only in the features mentioned above. Both have large and deep skulls, long nasals, and broad crania. The ranges of *planiceps* and *angustirostris* at present seem not to meet, the intervening mountainous country being inhabited by *Pappogeomys gymnurus imparilis*. The morphological features of *planiceps* approximate those of *tylorhinus* to the east, but the resemblance is less than between *planiceps* and *angustirostris*. Most of the geographic range of *P. t. planiceps* is separated from that of *P. t. tylorhinus* by the range of the species *Pappogeomys merriami* that occurs in the mountains between the Valley of Toluca and the Valley of

México. *P. t. tylorhinus* also inhabits the plateau in southwestern Hidalgo just north of the Neovolcanic Range, and contact between it and *P. t. planiceps* may occur in the mountains in northwestern México; but, as mentioned above, no actual specimens are known from there. *P. t. planiceps* is remarkably larger than *brevirostris*, its neighbor to the northwest, and, judging from the degree of divergence, the two have not been in contact recently. Field observations disclose a hiatus in their ranges at present.

As in other subspecies occurring in the Neovolcanic Range, both rusty and black color phases are known in *planiceps*. Of the 16 specimens in adult pelage available to me, nine (56%) are in the rusty phase and seven (44%) are in the black phase. All of the black individuals are from the southwestern part of the range of *planiceps*, an upland region of pine forests and black volcanic soils near the México-Michoacán boundary (localities labeled with respect to San José Allende and Valle de Bravo). In this region, the dorsum of all specimens is glossy black, and the intensity of pigmentation is matched only by that of *P. t. atratus* from the top of Cerro Viejo in Jalisco. Also the venter of these specimens is more richly pigmented, being bright Ochraceous-Buff rather than Light Ochraceous-Buff as in specimens from elsewhere in the range of the species. Specimens from San José Allande have paler sides than do specimens from Valle de Bravo, being Ochraceous-Buff rather than dark Mummy Brown. No specimens in the rusty color phase are known from this area. To the east, all known specimens are in the rusty phase, and none in the black phase is known. Specimens have been taken from higher elevations than in the area where melanism predominates; for example, specimens in the rusty phase have been obtained from areas of black volcanic soils at 9000 and 11,200 feet on Volcán de Toluca. Specimens from Isla have small white flecks or spots scattered over their backs.

Hooper (1957:3) reported three males, all in the black color phase, from 8200 feet in pine forests at San Cayetano, a locality in southwestern México, as "*Cratogeomys tylorhinus* subsp." Although I have not examined them, specimens listed below with reference to San José Allende and Valle de Bravo, are, respectively, 11 miles WNW and six miles ESE of Hooper's locality and are *P. t. planiceps*.

Specimens examined.—Total of 16, all from the state of México, as follows: El Río (= San Bernabe), on the Río Lerma 14 mi. NW Toluca, about 8500 ft., 4; 7 mi. W and 3 mi. N San José Allende, about 9000 ft., 3; 10 mi. N and 6 mi. E Valle de Bravo, 7460 ft., 4; NW slope Volcán de Toluca, 11,200 ft., 1; * N slope Volcán de Toluca, 9000 ft., 2 (USNM); Isla, 3 mi. NW Tenango del Valle, 8500 ft., 2.

Pappogeomys tylorhinus tylorhinus (Merriam)

Platygeomys tylorhinus Merriam, N. Amer. Fauna, 8:167, January 31, 1895 (part); Goldman, Jour. Mamm., 20:91, February 15, 1939; Poole and Schantz, Bull. U. S. Nat. Mus., 178:376, April 9, 1942.

[*Platygeomys*] *tylorhinus*, Trouessart, Cat. Mamm., 1:574, 1898 (part).

P[*latygeomys*]. *tylorhinus*, Hooper, Jour. Mamm., 27:398, November, 1946.

Platygeomys tylorhinus [=*tylorhinus*], Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:267, July 1, 1905 (part); Lyon and Osgood, Bull. U. S. Nat. Mus., 62:75, January 15, 1909.

[*Platygeomys*] *tylorhinus* [= *tylorhinus*], Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:319, 1904 (part).

Platygeomys tylorhinus tylorhinus, Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924 (part); Ellerman, The Families and Genera of Living Rodents, 1:531, June 8, 1940.

C[*ratogeomys*]. *t*[*ylorhinus*]. *tylorhinus*, Hooper, Jour. Mamm., 28:46, February 15, 1947.

Cratogeomys tylorhinus tylorhinus, Hooper, Jour. Mamm., 29:303, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:346, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959.

Cratogeomys tylorhinus arvalis Hooper, Jour. Mamm., 28:45, February 15, 1947, type from Colonia del Valle, 2275 m, México City, Distrito Federal; Villa, Anal. Inst. Biol. 23:394, May 20, 1953; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:346, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959.

Cratogeomys irolonis, Davis, Jour. Mamm., 25:387, December 12, 1944 (part); Villa Anal. Inst. Biol., 23:396, May 20, 1953 (part); Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959 (part).

Type.—Male, adult, skull and skin; No. 51883 U. S. National Museum; Tula, 6800 ft., Hidalgo; March 13, 1893; obtained by E. W. Nelson, original number 4442.

Range.—Southern Hidalgo southward across the open, sandy plain to southern edge of Valley of México in southern part of México City. See Fig. 6. Altitudinal range 6800 to 8200 feet.

Description.—Small for species; tail moderately long (averaging 39% of length of head and body); hind foot short. Average and extreme external measurements of 10 females and six males from several localities, are, respectively, as follows: Length of head and body 209 (159-230), 228 (212-240); length of tail, 86 (65-98), 94 (87-102); length of hind foot, 39 (37-42); 41 (37-42).

Color: Hairs of upper parts Mouse Gray basally and varying from Ochraceous-Orange to bright Tawny apically, with some Bay-tipped hairs on back and top of head; hairs of underparts Light Mouse Gray basally overlaid with Ochraceous-Buff in paler specimens and Ochraceous-Tawny in darker specimens; auricular patch small, hairs blackish to roots; throat ochraceous; hind feet whitish.

Skull: Moderately large for species; nasals short; broad across squamosals; rostrum narrow.

Average and extreme cranial measurements for 10 females and six males are, respectively, as follows: Condylobasal length, 54.0 (52.8-55.1), 59.5 (58.0-63.3); zygomatic breadth, 36.9 (35.0-38.9), 41.4 (40.2-42.7); palatofrontal depth, 21.2 (20.6-21.9), 23.2 (22.4-24.3); length of palate, 37.1 (35.6-38.5), 41.0 (39.7-410); length of nasals, 18.2 (16.9-19.0), 21.1 (20.5-22.2); breadth of braincase, 27.5 (26.3-29.1), 29.8 (28.4-31.5); squamosal breadth, 38.7 (36.6-40.7), 42.9 (41.0-45.1); breadth of rostrum, 11.6 (11.0-13.3), 13.1 (12.5-14.0); length of rostrum, 22.1 (21.2-23.3), 25.2 (24.2-26.8); alveolar length of maxillary tooth-row, 11.1 (10.3-12.5), 12.3 (11.2-14.4).

Comparisons.—From *Pappogeomys tylorhinus planiceps, tylorhinus* differs as follows: Smaller; tail shorter; hind foot decidedly shorter; upper parts (compared with reddish-brown phase of *planiceps*) paler and brighter, more ochraceous or tawny and less dark brownish; underparts darker and brighter, more ochraceous and less buffy; throat ochraceous rather than grayish; chin ochraceous rather than whitish; no specimens known in black color phase; skull shorter; zygomata less widely spreading; palate and nasals decidedly shorter; braincase narrower; breadth across squamosals relatively greater (averaging 72% *versus* 69% of condylobasal length); rostrum narrower and decidedly shorter; maxillary tooth-row slightly shorter.

From *Pappogeomys tylorhinus brevirostris, tylorhinus* differs as follows: Slightly smaller; hind foot decidedly shorter; chin darker and brighter, ochraceous rather than buffy; hind feet paler, whitish instead of brownish; skull longer and deeper; zygomata more widely spreading; palate and maxillary tooth-row slightly longer; nasals and rostrum decidedly longer; broader across zygomata.

Remarks.—*P. t. tylorhinus* is the easternmost subspecies of *Pappogeomys tylorhinus.* The eastern and southern boundaries of its range appear to be contiguous with that of *Pappogeomys merriami;* both species have been taken at Coyoacán, a suburb in the southern part of México City. *P. t. tylorhinus* has been taken 5 km. NW Texcoco, México, and *P. m. merriami* 6 mi. S and 1 mi. W Texcoco. To the north, *tylorhinus* has been obtained from 9 km. S Pachuca, Hidalgo, and *P. m. irolonis* from 10 km. NW Apam, about 25 miles to the southeast.

Villa (1953:397) suggests that the recession of Lago Texcoco, which in the late Pleistocene was much more extensive than now and almost filled the basin, permitted the ranges of the two species to meet. As the shore line of the large lake receded, *tylorhinus* advanced southward and eastward from the plains of southwestern Hidalgo and *merriami* northward and westward from the mountains that rise above the valley to the east and south. Hibbard (1955:52) recorded *Cratogeomys tylorhinus* from the top of the Upper Becerra, late Pleistocene beds one-half mile east of Tequixquiac in the northern part of the state of México, 11 kilometers south of the Hidalgo border. These fossils prove the occurrence of *Pappogeomys tylorhinus* in this region in late Pleistocene time, and at a point northwest of the shore line of Lago Texcoco. *P. t. tylorhinus* does not occur in the mountains that separate the Valley of México from the Valley of Toluca to the west; all known samples come from the Central Plateau.

Davis (1944:387) mistakenly identified 10 specimens of *tylorhinus* two from 9 km. S Pachuca, Hidalgo, and eight from 5 km. NW Texcoco, México, as *Cratogeomys irolonis.* These specimens have been carefully examined and are referable to *tylorhinus.* Davis, when comparing these specimens with *Pappogeomys merriami merriami,* elevated *irolonis* to a full species on the basis of differences between the two samples mentioned above, but the differences he listed actually are characters that distinguish the *gymnurus* species-group from the *castanops* species-group of *Cratogeomys* (see account of *Pappogeomys merriami irolonis* for further discussion).

P. t. tylorhinus is recognized by the combination of small size (only *P. t. zodius* is smaller), short hind feet, moderately long skull, short nasals (shorter only in *P. t. brevirostris*) and great breadth across squamosals (about as in *P. t. planiceps*). *P. t. tylorhinus* can not be distinguished from *P. t. brevirostris* by coloration (see under comparisons above). No black specimen of *P. t. tylorhinus* is known; all specimens are in the rusty color phase which matches closely the deep reddish color of the sandy soils where they occur. In the south, around México City, blackish volcanic soils are found, and the gophers occurring there have slightly darker upper parts than do others owing to a stronger suffusion of Bay-tipped hairs. The difference in color is not so great as the range of variation observed in other subspecies of *Pappogeomys tylorhinus,* and, in my opinion, has no taxonomic significance.

Hooper (1947:45) proposed the subspecific name *Cratogeomys tylorhinus arvalis* for specimens from Colonia del Valle, a suburb on the southern outskirts of México City (now, 1966, entirely residential), and a sample from Coyoacan, a small pueblo approximately 3½ miles to the east. In the original description he distinguished *arvalis* from *tylorhinus* as follows: Nasals relatively longer (39% *versus* 36% of basilar length); skull broader posteriorly (breadth across squamosals 83% *versus* 79% of basilar length), and smaller mastoid bullae. A critical analysis of the features that distinguish *arvalis* has been made with additional examples in hand of *tylorhinus* (Hooper had three, only one an adult female). The differences relied on by Hooper prove to be less distinctive than he thought. In *arvalis* the nasals are slightly longer relative to the basilar length (averaging 38.8% *versus* 37.6% in *tylorhinus* from northern México and Hidalgo); the posterior breadth of skull (across squamosals) is slightly greater relative to the basilar length (averaging 82.2% *versus* 81.0% in *tylorhinus*); and specimens of *tylorhinus* with equally small mastoid bullae are in hand. Also, the hind foot and skull of *arvalis* average slightly longer. These differences are not greater than infra-subspecific variations among local populations in other subspecies of *Pappogeomys tylorhinus*, for instance in *angustirostris*. No other feature of systematic worth was found by which *arvalis* could be distinguished from *tylorhinus*; therefore, *arvalis* is relegated to the synonomy of *P. t. tylorhinus*.

Specimens No. 2952 (TCWC) from 9 km. S Pachuca and Nos. 2944, 2946, and 2948 (TCWC) from 5 km. NW Texcoco, listed as females on the specimen labels are almost certainly a subadult male and three adult males, respectively. In external and cranial dimensions they exceed females of the subspecies *tylorhinus* and are within the size-range of males.

Specimens examined.—Total of 25, as follows: **Hidalgo:** Tula, 6800 ft., 3 (USNM); 9 km. S Pachuca (85 km. NW México City, at junction of Federal Highway 1 and road to Pachuca), 8200 ft., 2 (TCWC). **México:** Tempo del Sol, Piramida de San Juan Taotihuacán, 1; 5 km. NW Texcoco, 7600 ft., 7 (TCWC); * 5 km. N Texcoco, 7600 ft., 1 (TCWC). **Distrito Federal:** Colonia del Valle, México City, about 7500 ft., 9 (8 UMMZ, 1 KU); Coyoacan, 2380 m. (about 7850 ft.), 2. (UMMZ).

Pappogeomys tylorhinus zodius (Russell)

Cratogeomys zinseri zodius Russell, Univ. Kansas Publ. Mus. Nat. Hist., 5:540, October 15, 1953; Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959.

Type.—Male, adult, skull and skin; No. 31879 Museum of Natural History, of University Kansas; 13 mi. S and 15 mi. W Guadalajara, about 4500 ft., Jalisco; February 6, 1949; obtained by J. R. Alcorn, original number 7747.

Range.—Known only from the type locality. See Fig 6.

Description.—Small for the species; tail relatively long (averaging 41% of length of head and body); hind foot short. Average and extreme external measurements of four females and two males, from the type locality are, respectively, as follows: Length of head and body, 204 (193-211), 235 and 223; length of tail, 83 (78-92), 89 and 95; length of hind foot, 39 (38-39), 41 and 41.

Color: Hair of upper parts Dark Mouse Gray basally and Sayal Brown apically with some Bay-tipped hairs on back and top of head but pure Sayal Brown on sides and face; hairs of underparts Mouse Gray basally overlaid with Light Buff; auricular patch small, hairs sooty black to bases; throat grayish; hind foot whitish.

Skull: Remarkably small for species; zygomata not widely spreading, but breadth across zygomata averaging more than breadth across squamosals; palate and nasals short; palatofrontal region shallow; decidedly narrow across braincase and squamosals; rostrum actually and relatively broad (averaging 55.9% of length) and short; maxillary tooth-row long.

Average and extreme cranial measurements of four females and the measurements of two males from the type locality are, respectively, as follows: Condylobasal length, 51.7 (50.4-52.4), 57.8 and 58.6; zygomatic breadth, 33.5 (31.3-34.8), 38.9 and 40.4; palatofrontal breadth, 20.6 (19.9-20.9), 22.4 and 22.2; length of palate, 35.9 (34.4-36.8), 40.8 and 41.1; length of nasals, 18.7 (18.2-19.3), 21.2 and 21.5; breadth of braincase, 24.4 (23.7-25.1), 25.9 and 26.6; squamosal breadth, 32.8 (32.0-33.8), 36.7 and 37.0; breadth of rostrum, 11.9 (11.4-12.3), 13.8 and 13.2; length of rostrum, 21.3 (20.7-21.7), 24.4 and 25.4; alveolar length of maxillary tooth-row, 11.6 (11.3-12.0), 13.0 and 12.8.

Comparisons.—From *Pappogeomys tylorhinus atratus, zodius* differs as follows: Smaller; tail actually and relatively longer (averaging 41% *versus* 36% of length of head and body); hind foot shorter; both upper parts and underparts distinctly paler (lacking melanistic color phase seen in *atratus*); skull distinctly shorter, without overlap in range of variation; zygomata less widely spreading; nasals and especially palate shorter; breadth across braincase and squamosals decidedly less; squamosal breadth averaging less instead of more than zygomatic breadth; rostrum relatively broader (averaging 55.9% *versus* 54.0% of length) and decidedly shorter; maxillary tooth-row slightly longer.

From *Pappogeomys tylorhinus angustirostris, zodius* differs as follows: Smaller, tail relatively longer (averaging 41% *versus* 39% of length of head and body); hind foot shorter, upper parts (comparison only with reddish-brown phase of *angustirostris*) darker and duller, more brownish and less bright russet; underparts paler, more buffy and less bright ochraceous; skull averaging smaller in all cranial dimensions (without overlap in condylobasal length, zygomatic breadth, length of palate, breadth of braincase, squamosal breadth, and length of rostrum); squamosal breadth averaging less instead of more than zygomatic breadth; length of maxillary tooth-row slightly less.

From *Pappogeomys tylorhinus brevirostris, zodius* differs as follows: Smaller; tail relatively longer (averaging 41% *versus* 38% of length of head and body); hind foot shorter; upper parts and underparts darker and less brightly pigmented; dorsal surface of hind foot whitish rather than brownish; skull shorter and slightly deeper; zygomata less widely spreading; palate slightly shorter; nasals, rostrum, and maxillary tooth-row decidedly longer; narrower across braincase and squamosals; rostrum actually and relatively broader (averaging 55.9% *versus* 54.7% of length).

Remarks.—Geographically *P. t. zodius* is marginal in relation to the species as a whole and its geographic range is far removed from those of most of the other subspecies. See Fig. 6. *P. t. zodius* is characterized by a greater degree of distinctness morphologically than are the other subspecies of the species. Small body, short skull, relatively large cheek teeth, and less extreme specialization of the cranium toward platycephaly (breadth across squamosals less than breadth across zygomatic arches) are features of *zodius*. Although the rostrum is relatively broad with respect to its length (averaging 55.9%), the cranium is remarkably narrow posteriorly; the squamosal breadth averages only 63.4% of the condylobasal length compared with 66.9% or more (usually more than 68.0%) in other subspecies of *Pappogeomys tylorhinus*. Also, the dorsal outline of the skull is convex rather than straight.

The small size (usually associated with high elevations) in a lowland population and other unusual features strongly suggest nonselective influences or accidental sampling. Moreover, the population is small, the subspecies being restricted to a small area of suitable soils, in a low arid basin situated between the ranges of other species. The range of *Pappogeomys gymnurus gymnurus,* for example, lies to the south, the range of *Pappogeomys gymnurus tellus* to the northwest, and the range of *Pappogeomys bulleri albinasus* on the more elevated plateau immediately to the north. The steep-walled canyon of the Río Grande de Santiago blocks expansion to the east. Sharply defined shifts from normal ranges of variation usually characterize the effects of genetic drift. In *zodius,* a sharp decrease from the normal range of variation is evident, suggesting genetic drift in a small isolated population.

Some of the features of *zodius,* especially its relatively long tail and the narrowness of the posterior part of cranium relative to breadth across zygomata, suggest relationship with *Pappogeomys zinseri,* and originally (Russell, 1953:540) *zodius* was described as a subspecies of that species. But, at that time the characters of *tylorhinus, gymnurus, angustirostris, planiceps, fumosus,* and *varius* had not been satisfactorily evaluated. Now, after the characters have been re-evaluated and the taxonomic affinities of the *gymnurus* species-group have been more clearly defined, it seems that *zodius* is best referred to the species *Pappogeomys tylorhinus.* Probably *P. t. zodius,* the other subspecies of *P. tylorhinus,* and *P. zinseri* all arose from a common ancestor in the Pleistocene, but *Pappogeomys zinseri* is remarkably larger than the subspecies of *Pappogeomys tylorhinus,* especially *P. t. zodius.* Aside from the features mentioned above and the few features distinctive of *P. t. zodius,* it otherwise shows more resemblance to *Pappogeomys tylorhinus* than to any other known species. Perhaps, the features of *P. t. zodius* are primitive and little changed from those of the ancestral stock that differentiated into the modern taxa of the *gymnurus* species-group (except for *Pappogeomys neglectus*). If so, *P. t. zodius* lacks the specializations evolved in the other subspecies and species.

Specimens examined.—Total of 7, all from **Jalisco,** as follows: 13 mi. S and 15 mi. W Guadalajara, 7.

Pappogeomys zinseri (Goldman)

Platygeomys zinseri Goldman, Jour. Mamm., 20:91, February 15, 1939 (part); Poole and Schantz, Bull. U. S. Nat. Mus., 178:376, April 9, 1942.

Cratogeomys zinseri, Hooper, Jour. Mamm., 29:303, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:347, March 3, 1955 (part).

Cratogeomys zinseri zinseri, Hall and Kelson, The Mammals of North America, 1:470, March 31, 1959 (part).

Type.—Male, adult, skull and skin; No. 78971 U. S. National Museum; Lagos, 6150 ft., Jalisco; June 29, 1896; obtained by E. W. Nelson and E. A. Goldman, original number 9718.

Range.—Known only from the area of deep sandy soils on the Central Plateau in extreme northeastern Jalisco. See Fig. 8.

Diagnosis.—Moderately large for subgenus, both externally and cranially; tail long; pelage soft and lax; skull relatively deep and narrow; zygomatic arches widely spreading (relative to length of skull); lambdoidal crest sinuous; breadth across squamosals less than breadth across zygomata; mandible widely spreading posteriorly; maxillary tooth-row moderately long; upper incisors procumbent.

Description.—Moderately large; tail actually and relatively long (averaging 46% of length of head and body); hind foot moderately long. Average and extreme external measurements of five females and the measurements of one male (probably not fully adult) from northeastern Jalisco are, respectively, as follows: Length of head and body, 223 (212-236), 223; length of tail, 103 (93-106), 100; length of hind foot, 44 (44-45), 43.

Color: Hairs of upper parts Mouse Gray basally and Ochraceous-Tawny apically becoming pure bright Ochraceous-Buff on sides and face; some with Bay-tipped hairs on back and top of head; underparts Light Mouse Gray basally overlaid with Ochraceous-Buff; throat grayish; chin buffy; auricular area blackish; hind foot dark brownish above with white hairs about base of toes.

Skull: Moderately deep and long; zygomata widely spreading (averaging 73.9% of condylobasal length); palate moderately long; breadth across braincase and squamosals moderately great (squamosal breadth averaging 69.3% of condylobasal length); rostrum moderately long and relatively broad (averaging 55.1% of its length); maxillary tooth-row moderately long.

Average and extreme cranial measurements of five females and the measurements of one male (probably not fully adult) from northeastern Jalisco are, respectively, as follows: Condylobasal length, 57.5 (56.1-59.1), 59.0; zygomatic breadth, 42.5 (41.6-43.2), 40.0; palatofrontal depth, 23.1 (22.5-23.7), 22.4; length of palate, 40.2 (39.3-41.4), 40.7; length of nasals, 20.3 (19.1-21.5), 20.6; breadth of braincase, 29.5 (28.5-29.9), 27.1; squamosal breadth, 39.8 (37.7-41.6), 38.7; breadth of rostrum, 13.4 (12.9-13.9), 13.0; length of rostrum, 24.3 (23.6-25.2), 24.8; alveolar length of maxillary tooth-row, 12.6 (11.9-13.5), 12.5.

Relationships.—Cranial features clearly identify *Pappogeomys zinseri* as a member of the *gymnurus* species-group of the subgenus *Cratogeomys.* Platycephalic specializations of the skull are well developed but somewhat obscured by the great increase in the breadth of the zygomatic arches. Breadth across the zygomata averages 73.9 per cent of the condylobasal length in *zinseri* compared with an average range of from 64.8 to 68.4 per cent in *tylorhinus* (according to subspecies), from 68.1 to 69.6 per cent in *gymnurus* (according to subspecies), and 69.1 per cent in *fumosus.* As a result of the lateral expansion of the zygomata, the zygomatic breadth exceeds the squamosal breadth in *zinseri,* whereas the opposite is the case in most platycephalic skulls owing to the remarkably broad braincase. Therefore, on first consideration it would seem that the skull of *zinseri* is less strongly platycephalic than the other species of the *gymnurus*-group. Nevertheless, the breadth across the squamosal does compare favorably with that in the other species, suggesting an equally high index of platycephaly. For example, the breadth across the squamosals amounts to 69.3 per cent of the condylobasal length in *zinseri*, and averages 63.4 to 71.7 per cent in the subspecies of *P. tylorhinus*, 70.4 to 73.2 per cent in the subspecies of *P. gymnurus* and 67.1 per cent in *P. fumosus*. Therefore, the posterior part of the cranium is as broad with respect to the length of the skull in *zinseri* as it is in the other specialized species.

Pappogeomys zinseri is a monotypic species. Of the species of the *gymnurus*-group, *zinseri* seems to be most closely related to *Pappogeomys tylorhinus;* however, it is more specialized than *tylorhinus*. Specializations of *zinseri* include larger skull, especially in length and depth; remarkably broader spread of zygomatic arches, and longer tail and hind feet. *P. zinseri* is significantly smaller both in cranial and external dimensions than *Pappogeomys gymnurus; P. zinseri* is relatively narrower across the squamosals, relatively broader across the zygomata, and its tail is relatively longer. The characters that distinguish *zinseri* are extreme, especially in the lateral extension of the zygomatic arches. *P. zinseri* probably differentiated from *tylorhinus*-like stock in the late Pleistocene. The geographic range of *zinseri* is adjacent to that of *tylorhinus*, but apparently the two do not meet, being separated by soils unsuitable for either one. *P. zinseri* evidently became geographically isolated from the main population of *tylorhinus* and, during the period of isolation developed its specialized features. As judged by morphological features and geographic position *zinseri* and *Pappogeomys gymnurus* probably never were genetically continuous.

Habitat.—All known specimens of *zinseri* have been recorded from desert grassland in northeastern Jalisco. This area is mantled with deep, pale sandy soils, and supports low xerophytic shrubs widely spaced in open grassland. Most of this country is devoted to grazing, but some crops, mostly corn, are cultivated. The area is situated at the northern border of the more elevated and mesic southern part of the Central Plateau, sometimes called the Anahuac Plateau.

Remarks.—*Pappogeomys zinseri* seems to be restricted to an area of sandy soils occurring in extreme northeastern Jalisco in the vicinity of Lagos de Moreno. All known specimens are from near the town of Lagos; however, sandy soils extend northward into southern Aguascalientes and westward at least to San Juan de los Lagos in Jalisco. The habitat appears to be approximately the same in this area, and *zinseri* probably occurs in scattered colonies throughout the sandy soils of northeastern Jalisco. No more than 20 miles southeast of Lagos de Moreno, just north of the border of Guanajuato, the nearly level desert plain rises abruptly to a more elevated part of the plateau. Correlated with this increase in elevation is a change to heavy, black clays unsuitable for these gophers, and no evidence of the animals' occurrence was found at León, Silao, Guanajuato, Irapuato, or Salamanca. Evidently none of the southwestern third of Guanajuato offers suitable habitat. The

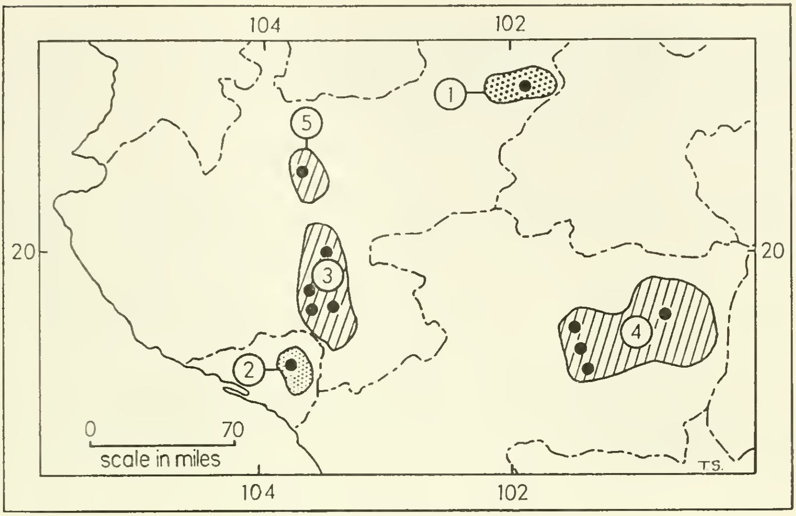

Fig. 8. Three species of *Pappogeomys*.

Guide to kinds:
1. *P. zinseri*
2. *P. fumosus*
3. *P. gymnurus gymnurus*
4. *P. gymnurus imparilis*
5. *P. gymnurus tellus*

clayey soils change to sands immediately west of Celaya in southeastern Guanajuato, where large gophers (*P. t. brevirostris*) again are found. The clayey soils in southwestern Guanajuato seem to function as an edaphic barrier separating the ranges of *P. zinseri* from *P. t. brevirostris.*

R. W. Dickerman searched unsuccessfully for pocket gophers in central and southeastern Jalisco east of the Río Grande de Santiago. Extensive collecting in the vicinities of Jalostotitlán, Tepatitlán, Zapotlanejo, Arandas, and Atotonilco failed to reveal the presence of pocket gophers. Soils seemed to be unsuitable in this area, being for the most part thin and rocky or heavy, reddish clays. Moreover, most of the natives of these localities did not know pocket gophers, and the few that did said the "topos" did not occur locally but were to be found to the south in the high mountains of Michoacán. As in adjacent parts of Guanajuato, pocket gophers evidently do not occur in southeastern Jalisco. Edaphic conditions seem to be the limiting factor.

P. zinseri seems to be isolated from other populations of the *gymnurus*-group. Contact with *P. t. brevirostris* may take place to the east between Lagos and San Diego de la Unión, Guanajuato; however, a ridge of north-south oriented mountains north of the city of Guanajuato may prevent contact. The specimen from San Diego de la Unión, previously referred to *zinseri,* is here allocated to *P. t. brevirostris.* However, identification is based on a broken skull and is tentative. The posterior part of the cranium was not damaged, and the breadth across the braincase and squamosals is greater than in typical *brevirostris* from southeastern Guanajuato. Otherwise the features that could be observed fit well with those of *brevirostris* and differ from those of *zinseri,* especially the small molariform teeth. The breadth of the posterior part of skull suggests the possibility of intergradation with *zinseri,* but the scanty evidence for interbreeding is inconclusive. If eventually intergradation is demonstrated, it will probably occur in this area.

Specimens examined.—Total of 13, all from Jalisco, as follows: ½ mi. NE Lagos de Moreno, 6370 ft., 2; * Lagos de Moreno, 6150 ft., 9 (USNM); * Lagos de Moreno, 6300 ft., 2.

Pappogeomys gymnurus

(Synonymy under subspecies)

Range.—Southwestern fringe of Central Plateau in central Jalisco and eastern Michoacán, at higher elevations in Neovolcanic Range and in adjacent lowlands of Central Jalisco both in Valle de Ameca and undrained basins between Sierra del Tigre and Sierra Nevada de Colima. Present distribution pattern disjunct, and the three known subspecies either completely or partially isolated. See Fig. 8. Altitudinal range from about 4000 to 10,000 feet.

Diagnosis.—Pelage soft and lax; skull largest of *gymnurus*-group (condylobasal length varying from 60.1 to 64.6); broad across zygomata (41.0 to 46.5), but breadth across squamosals usually equals or exceeds zygomatic breadth; squamosals relatively broad (averaging from 70.4 to 73.2% of condylobasal length; rostrum long (24.6 to 29.1).

Description.—Large for *gymnurus* species-group and for subgenus; tail short relative to length of head and body; hind foot large. Extremes in external measurements of adult females and males are, respectively: Length of head and body, 230-267, 234-279; length of tail, 75-105, 87-112; length of hind foot, 44-54, 47-54.

Color: Pelage of upper parts varying in overall tones from pale brownish-buff to glossy brownish-black, back and top of head with reddish-brown or iridescent black-tipped hairs imparting generally darker tone to back and top of head than sides and face; underparts paler than dorsum, varying from creamy-white to bright shades of ochraceous-tawny, or black like dorsum in most melanistic individuals; throat usually grayish (except in *tellus*); dorsal surface of hind foot buffy or white; dark auricular patches developed in lighter pelage phases, but lacking in melanistic pelages.

Skull: Large for *gymnurus* species-group and for subgenus (condylobasal length varying from 60.1 to 64.6 in females and from 65.1-71.3 in males); rugose and angular; relatively shallow and flat; breadth across squamosals equal or exceeds breadth across zygomata, with few exceptions; angular processes long, mandible broader than long; squamosals expanded laterally in adults, covering most of external auditory tube and obscuring postglenoid notch; dorsal outline of lambdoidal crest sinuous; paroccipital processes large and flangelike; rostrum broad and heavily constructed, but not massive relative to size of skull; zygomata broadly spreading, angle of maxillary arms enlarged into platelike expansion; jugal large; incisors not especially large relative to size of skull, lower incisors without lateral bevel behind enamel plate; occlusal surface of M3 subtriangular, its bilophate pattern weakly expressed, having shallow re-entrant angles and short posterior loph, the apex of which forms posterior margin of tooth; enamel pattern of premolars and molars as in subgenus *Cratogeomys*.

Relationships.—Dental and cranial features characteristic of the subgenus *Cratogeomys* are well developed in *Pappogeomys gymnurus*. Also, the strongly-developed platycephalic specializations of the skull distinctly separate *gymnurus* from the *castanops* species-group. The specializations include the flat, broad cranium, especially that part lying behind the posterior roots of the zygomatic arches; the widely spreading rami of the mandible and the remarkably elongated angular processes; and the rugosity and angularity of the occiput, including the lambdoid crest and paroccipital processes.

Compared with *Pappogeomys merriami,* the larger subspecies of which it approximates in size, *gymnurus* has less massive incisors and rostrum, the anteroposterior diameter of the molariform teeth is less relative to their breadth, especially in M3; the cranium is decidedly shallower and broader; the squamosal is expanded laterally but not medially and covers no significant part of the parietal as in *merriami;* the dorsal outline of the lambdoidal crest is sinuous rather than posteriorly convex; and the paroccipital processes are decidedly larger. The cranial differences are distinctly those that differentiate an extremely platycephalic skull (in *gymnurus*) from a generalized skull (in *merriami*).

Pappogeomys gymnurus differs from *Pappogeomys castanops* in the same way that it does from *merriami,* but in addition is significantly larger and M3 is less specialized.

Pappogeomys gymnurus, P. tylorhinus and *P. zinseri* probably differentiated directly from the same ancestral stock, and differ from one another primarily in size of skull and to some extent in its shape. The skull in each is strongly platycephalic, but in the two subspecies, *zodius and breverostris,* of the species *P. tylorhinus* the skull is narrow posteriorly as it may have been in the ancestral stock. *P. fumosus* and *P. neglactus,* also of the *gymnurus*-group, probably differentiated earlier.

Habitat.—Pappogeomys gymnurus occurs in both the highlands and lowlands. Highland populations occur in areas of reddish or blackish, friable soils largely of volcanic origin. Areas of thin or rocky soils are not usually occupied. The pine-oak-madrona zone and the pine-fir zone at higher elevations are preferred habitat, and the largest concentrations occurr in open sacatón grass meadows developed in the shallow basins within the mountains. Areas of dense forest in both zones lack this species but it is common in open parklike forest of pure stands of pine having a ground cover of sacatón grass and small shrubs and forbs. Such pine-grass savannas occur frequently above the oak zone at from 7800 to 8500 feet. Often the montane basins are under cultivation, usually with corn as the principal crop. These gophers are especially common in fallow and cultivated areas.

In the lowlands, especially in the series of arid basins occurring across central Jalisco from the elevated valley lying between the Sierra de Tigre to the east and the Sierra Nevada to the west, *Pappogeomys gymnurus* occurs in areas of deep sandy and sandy loam soils developed in the shallow basins. These are arid, mostly treeless, and support a natural vegetation of grasses and xerophytic shrubs. Most areas are under cultivation. Pocket gophers occur abundantly in the basins and less commonly on the surrounding foothills. Populations in the Zapotlán and Sayula basins are continuous with those on the lower slopes of the Sierra Nevada to the west.

Geographic variation.—Pappogeomys gymnurus includes three subspecies: *gymnurus, imparilis* and *tellus*. The species approaches morphological homogeneity; differences between the subspecies, especially in external dimensions and cranial feature, are slight. For example, except for the smaller hind foot in *tellus,* the subspecies do not differ appreciably in external dimensions. No significant geographic variation exists in condylobasal length, length of palate, breadth of rostrum, or length of rostrum. The principal distinction between the several subspecies is in coloration. Aside from melanistic individuals, the palest and dullest pigmentation is developed in *tellus* in the northwestern part of the range and the darkest and richest pigmentation in *imparilis* in the southeastern part of the range. The glossy, rusty-colored pelage characteristic of *gymnurus* is somewhat intermediate between the two extremes, but more closely resembles that of *tellus,* but is darker and richer. Of the three, therefore, the most distinctive is the glossy, iridescent pelage characterizing *imparilis*. Melanistic phases are developed in both *gymnurus* and *imparilis,* but melanism is more common in *gymnurus* in both lowland and highland populations. Melanistic individuals of the two subspecies are, of course, difficult to distinguish, but the black phase in *gymnurus* tends to be less glossy black and more of a dull sooty color. However, the intensity of pigmentation in some individuals of *gymnurus* matches that of *imparilis.* No example of melanism is known in *tellus.*

The greater degree of color distinction in *imparilis* may be due to its isolation. The range of *imparilis* is presently separated from the range of *gymnurus* and *tellus* by mountainous country in western Michoacán and extreme southeastern Jalisco inhabited by *Pappogeomys tylorhinus angustirostris.* Evidently the separation has been continuous throughout the post-Wisconsin, and the disjunction in range probably developed as a result of late Wisconsin shifts of environments and concomitant changes in distribution. But, considering the evolutionary plasticity of this group of rodents, the length of isolation has not been long enough to allow for profound divergence. Also, *gymnurus* and *tellus* are currently geographically separated. The separation evidently occurred recently, and the geographic hiatus in their ranges is narrow. The resemblance in cranial features between *tellus* and upland populations of *gymnurus* is close, suggesting relatively recent continuity in distribution and gene flow between these adjacent populations. Even so, divergence in cranial features is greater between *gymnurus* and *tellus* than between *gymnurus* and *imparilis.*

Pappogeomys gymnurus gymnurus (Merriam)

Geomys gymnurus Merriam, Proc. Biol. Soc. Washington, 7:166, September 29, 1892; Lyon and Osgood, Bull. U. S. Nat. Mus., 62:74, January 15, 1909; Poole and Schantz, Bull. U. S. Nat. Mus., 178:375, April 9, 1942.

Platygeomys gymnurus, Merriam, N. Amer. Fauna, 8:164, January 31, 1895; Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:266, July 1, 1905; Allen, Bull. Amer. Mus. Nat. Hist., 22:149, July 25, 1906; Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912; Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924; Ellerman, The Families and Genera of Living Rodents, 1:530, June 8, 1940; Hooper, Jour. Mamm., 27:398, November, 1946.

[Platygeomys] gymnurus, Trouessart, Cat. Mamm., 1:573, 1898; Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:318, 1904.

Platygeomys gymnurus gymnurus, Goldman, Jour. Mamm., 20:88, February 15, 1939.

Platygeomys gymnurus inclarus Goldman, Jour. Mamm., 20:88, February 15, 1939, type from north slope Sierra Nevada de Colima, 10,000 ft. Jalisco.

Cratogeomys gymnurus gymnurus, Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Cratogeomys gymnurus inclarus, Hooper, Jour. Mamm., 29:302, August 31, 1948; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Cratogeomys zinseri morulus Russell, Univ. Kansas Publ. Mus. Nat. Hist., 5:541, October 15, 1953, type from N end Lago de Sayula, 4400 ft., 9 mi. N and 2 mi. E Atoyac, Jalisco; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Type.—Female, adult, skull and skin; No. 33579/45614 U. S. National Museum; Zapotlán (=Ciudad Guzmán), 4000 ft., Jalisco; April 16, 1892; obtained by E. W. Nelson, original number 2338.

Range.—Valley and series of low basins and playas, including Zapotlán and Sayula, at eastern base of Sierra Nevada de Colima in southern Jalisco, westward into Sierra Nevada de Colima. See Fig. 8. Altitudinal range from about 4000 feet up to 10,000 feet.

Description.—Large; tail relatively short (averaging 37% of length of head and body); hind foot long. External measurements of two females, and average and extreme external measurements of four males from the Zapotlán and Sayula basins are, respectively, as follows: Length of head and body, 230 and 255, 261 (250-279); length of tail, 75 and 105, 96 (90-108); length of hind foot, 45 and 51, 51 (49-54).

Color: Adults of both sexes are of two distinct color phases—a bright rusty-brown and a sooty-black; tail naked; chin and throat grayish in both phases. Rusty phase: Hairs of upper parts Mouse Gray basally, Ochraceous-Tawny apically mixed with Bay-tipped hairs on top of head and back but pure Ochraceous-Tawny on sides and face; underparts Light Mouse Gray basally overlaid with Light Ochraceous-Buff; hair of pre- and post-auricular areas blackish to tips; top of hind foot scantily set with ochraecous hairs. Black phase: Hairs of back and top of head Fuscous-Black basally, overlaid with Walnut Brown or Mummy Brown; sides and belly Dark Mouse Gray basally, washed with Light Ochraceous-Buff in paler individuals or Cinnamon-Buff in dark individuals; top of hind foot dark brownish; auricular patches indistinct, blending with dark hairs of back.

Skull: Large; zygomata broadly spreading; palate and nasals short; broad across braincase and especially squamosals; maxillary tooth-row long.

Average and extreme measurements of 13 females and eight males from the Zapotlán and Sayula basins are, respectively, as follows: Condylobasal length, 62.6 (60.6-64.6), 67.3 (65.3-71.3); zygomatic breadth, 43.6 (41.0-44.8), 47.1 (45.2-48.5); palatofrontal depth, 23.8 (22.6-25.0), 25.3 (24.4-26.3); length of palate, 43.0 (41.1-44.5), 46.4 (44.7-49.0); length of nasals, 22.0 (21.0-23.3), 23.8 (22.1-26.1); breadth of braincase, 32.5 (30.8-34.3), 34.4 (32.5-35.9); squamosal breadth, 45.8 (44.6-47.4), 49.0 (47.0-52.3); breadth of rostrum, 14.7 (14.0-16.1), 16.0 (15.2-17.1); length of rostrum, 27.3 (26.3-28.8), 29.3 (27.6-31.7); alveolar length of maxillary tooth-row, 13.5 (12.6-14.3), 14.4 (13.7-15.8).

Comparisons.—For comparisons with *P. g. imparilis* and *P. g. tellus,* see accounts of those subspecies.

Remarks.—This is one of a group of large subspecies comparable in size to *Pappogeomys merriami merriami* of the *castanops* species-group. The several morphological features that Merriam (1895: 165) suggested were unique in *gymnurus* vary individually and are not useful in studies of geographic variation. *P. g. gymnurus* is distinguished by its broad skull, short nasals, and bright reddish-brown color (with the exception of melanistic individuals). It is more variable in color than either of the other two subspecies.

Goldman (1939a:88) described *Cratogeomys gymnurus inclarus* from the Sierra Nevada de Colima and Sierra de Colima on the basis of its dark-colored pelage. He found no significant difference in either cranial or external features between *inclarus* and its closest relative *P. g. gymnurus.* Comparative material of *gymnurus* available to Goldman (*loc. cit.*) consisted only of specimens in the brown color phase, and he considered the melanistic tones characterizing the pelage of *inclarus* to be diagnostic at the subspecific level. Additional specimens of *gymnurus* from the lowlands reveal a high incidence of melanism (see discussion beyond), matching in dark tones the pelage of *inclarus.* Therefore, color is not diagnostic in these gophers, and this character alone does not warrant subspecific separation of a lowland and highland population in this area. Since no other difference can be ascertained, I place *inclarus* as a synonym of *gymnurus.*

Russell (1953:541) described *Cratogeomys zinseri morulus* based on a type series from the north end of Lago de Sayula, 4400 ft., 9 mi. N and 2 mi. E Atoyac, Jalisco. These specimens were allocated to the species *zinseri* primarily because of their narrow crania, one of the diagnostic features of *Pappogeomys zinseri*. Re-examination of this material, and study of larger samples of both *gymnurus* and *zinseri*, convinces me that the Sayula specimens are referable to *gymnurus* and not to *zinseri*. Aside from their narrower cranium, the specimens do not differ significantly from topotypical samples from the Zopatlán Basin to the south. Moreover, analysis of a larger sample of *gymnurus* reveals that the breadth across the squamosals is subject to a higher degree of variation than was previously supposed. Although squamosal breadth does exceed the zygomatic breadth in most examples of *gymnurus*, the squamosal breadth is less than or equal to the zygomatic breadth in a few individuals. There is no morphological reason for separating *morulus* on the subspecific level from *P. g. gymnurus;* therefore, *morulus* is arranged as a synonym of *gymnurus*.

Females from the Sierra de Colima and Sierra Nevada de Colima average slightly narrower across the zygomata (42.6 *versus* 43.6), braincase (31.5 *versus* 32.5), and squamosals (42.6 *versus* 45.8), and the nasals average shorter (20.9 *versus* 22.0) than in topotypes and near topotypes of *gymnurus* from lower elevations in the Zapotlán Basin. These variations are within the lower range of variation observed in lowland populations, and, therefore, are not considered to be taxonomically significant. An adult female (KU 36678) and male (KU 36679) from the Sayula Basin in the lowlands, are characterized by a combination of maximum zygomatic breadth (44.9 and 49.3, respectively) for the subspecies and minimal breadth across the braincase (31.2 and 43.9) and squamosals (42.7 and 47.6). Although all these dimensions are within the range of variation observed in typotypes and near topotypes, their combination in single individuals is unusual. As mentioned above, the series from Sayula was at first referred to another species, *zinseri*, on the basis of this combination of features. The narrow cranium of the series from Sayula resembles that of the upland population of the subspecies.

All examples of *gymnurus* taken at higher elevations in the Sierras are uniformly melanistic, the pelage being dull blackish overlaid with a tinge of dark brownish that imparts an overall sooty appearance to the fur. The population from the low interior basin to the east is dichromatic, the individuals being of the rusty phase or the sooty phase. Of the 44 specimens from Las Canoas in the Zapotlán Basin 32 (or 73%) are in the rusty phase and 12 (or 27%) are in the sooty phase. All four of the available specimens from the Sayula Basin are melanistic.

Specimens in the sooty phase are not uniform in color, some being more heavily tinged with brownish than others. The darkest tones, considering both highland and lowland populations, are developed in the Sayula specimens from the lowlands. One specimen in the rusty phase, KU 77155, comes from near Zapoltitac at the edge of the pine zone in the foothills of the Sierras.

Specimens examined.—Total of 63, all from **Jalisco**, as follows: N end Lago de Sayula, 4400 ft., 9 mi. N and 2 mi. E Atoyac, 4; Sierra Nevada de Colima, 6500 ft., 1 (USNM); *Sierra Nevada de Colima, about 5000 ft., 1 (USNM); 2 mi. N Ciudad Guzmán, 4; * 3 mi. W Ciudad Guzmán, 1; * Zapotlán (= Ciudad Guzmán), about 4000 ft., 6 (USNM); *Las Canoas, 44 (43 AMNH, 1 FMNH); *3½ mi. WNW Zapoltitic, 5100 ft., 1; 9 mi. W and 2 mi. S Ciudad Guzmán, about 7000 ft., 1.

Pappogeomys gymnurus imparilis (Goldman)

Platygeomys gymnurus imparilis Goldman, Jour. Mamm., 20:89, February 15, 1939; Poole and Schantz, Bull. U. S. Nat. Mus., 178:375, April 9, 1942.

Platygeomys tylorhinus Merriam, N. Amer. Fauna, 8:167, January 31, 1895 (part); Elliot, Field Columb. Mus. Publ. 105, Zool. Ser., 6:267, July 1, 1905 (part); Miller, Bull. U. S. Nat. Mus., 79:248, December 31, 1912 (part); Miller, Bull. U. S. Nat. Mus., 128:260, April 29, 1924 (part).

[*Platygeomys*] *tylorhinus*, Trouessart, Cat. Mamm., 1:573, 1898 (part); Elliot, Field Columb. Mus. Publ. 95, Zool. Ser., 4:319, 1904 (part).

Cratogeomys gymnurus imparilis, Hooper, Jour. Mamm., 29:302, August 31, 1948; Hall and Villa, Univ. Kansas Publ. Mus. Nat. Hist., 1:452, December 27, 1949; Hall and Villa, Anal. Inst. Biol., 21:185, September 28, 1950; Miller and Kellogg, Bull. U. S. Nat. Mus., 205:345, March 3, 1955; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Type.—Male, adult, skull and skin; No. 34918/47183 U. S. National Museum; Pátzcuaro, Michoacán; July 23, 1892; obtained by E. W. Nelson and E. A. Goldman, original number 2918.

Range.—Central Michoacán, from lowlands around Lago Pátzuaro south to the southern flanks of the Neovolcanic range at Tacámbaro, thence eastward into high mountains to 3 mi. S Cd. Hidalgo. See Fig. 8. Altitudinal range 5700 to 9100 feet.

Description.—Large, tail relatively short (averaging 37% of length of head and body); hind foot large. Average and extreme external measurements of seven females and the measuremets of two males from the Pátzcuaro Basin and Tacámbaro, are, respectively, as follows: Length of head and body, 249 (235-267), 238 and 234; length of tail, 91 (84-99), 112 and 100; length of hind foot, 49 (45-54), 50 and 50.

Color: Adults occur in two color phases—a rich iridescent brownish-black phase and a dull sooty phase. Hairs Dark Mouse Gray basally, top of hind foot and chin whitish, and throat grayish in both color phases. Brownish-black phase: Hairs of upper parts dull Russet apically (winter pelage) or bright Argus Brown (summer pelage), with strong admixture of black-tipped iridescent hairs in both pelages, imparting glossy brownish-black appearance; auricular area, top of head, and face greenish-black; hairs of underparts Ochraceous-Tawny in both winter and summer pelage. Sooty phase: Hairs of both upper parts and underparts dark Mummy Brown with many black-tipped hairs giving pelage a dull sooty appearance; auricular patch not evident.

Skull: Large; zygomata widely spreading; nasals short; braincase broad; narrow across squamosals; maxillary tooth-row short.

Average and extreme cranial measurements of seven females and measurements of two males from the Pátzcuaro Basin and Tacámbaro are, respectively, as follows: Condylobasal length 62.5 (60.4-64.6), 65.1 and 65.2; zygomatic breadth, 43.5 (41.1-46.5), 46.8 and 42.7; palatofrontal depth, 23.8 (22.9-24.9), 24.3 and 24.6; length of palate, 43.3 (41.0-45.6), 44.3 and 45.6; length of nasals, 22.0 (20.5-24.1), 31.4 and 33.0; breadth of braincase, 32.7 (31.4-34.7), 31.4 and 33.0; squamosal breadth, 44.0 (41.6-47.8), 43.1 and 45.0; breadth of rostrum, 14.5 (13.6-16.2), 14.8 and 14.5; length of rostrum, 25.3 (24.6-29.1), 27.9 and 29.2; alveolar length of maxillary tooth-row, 12.8 (12.1-13.5), 12.8 and 14.0.

Comparisons.—From *Pappogeomys gymnurus gymnurus*, *imparilis* differs as follows: Pelage in brownish phase darker and richer, more glossy black and iridescent, and less dull reddish-brown; underparts darker, more of reddish and less of buffy tones; dark phase richer, more glossy hues of black and less of dark brownish tones; narrower across squamosals; maxillary tooth-row shorter.

Remarks.—*Pappogeomys gymnurus imparilis* is distinguished by its glossy, iridescent pelage. Its dark color is striking, having hues of dark brownish and greenish-black blended into an elegant pattern with the more iridescent tones developed on the head, shoulders, and down the back. The beauty of its pelage is not surpassed in any other geomyid. Otherwise its features, both external and cranial, closely resembles those of *P. g. gymnurus*. The morphological resemblance indicates that the two are closely related, even though they presently do not share contiguous ranges. Clearly, *imparilis* has no close relationship with the smaller *Pappogeomys tylorhinus*, which occupies adjacent areas in Michoacán, Guanajuato, and México.

Samples of *imparilis* available for study are morphologically homogeneous, and no significant geographic variation could be detected. The only noteworthy variation is in color. Although two color phases are developed, the differences between them are slight. The brownish-black color phase is the more common of the two. The samples in hand indicate less sexual dimorphism in cranial dimensions than in most members of the subgenus *Cratogeomys*. This may be due entirely to the small size of the sample of adult males, and I suspect that a larger sample will show that the range of variation is greater than presently indicated. However, it is evident that most cranial dimensions in males overlap the maximum measurements in females.

The range of *imparilis* is disjunct, and is separated from that of other subspecies of *Pappogeomys gymnurus* by territory occupied by other kinds of geomyids. The hiatus probably developed as a result of distributional changes in the late Pleistocene; now, *imparilis* is isolated from its close relatives to the west, but has not diverged much morphologically.

Specimens examined.—Total of 23, all from **Michoacán**, as follows: 15 mi. W and 3 mi. S Cd. Hidalgo, about 9100 ft., 1; 2 mi. W Pátzcuaro, 7800 ft., 2 (MVZ); *Pátzcuaro, about 7000 ft., 4 (USNM); *3 mi. S Pátzcuaro, 7800 ft., 1 (MVZ; *4 mi. S Pátzcuaro, 7800 ft., 1 (MVZ) *5 mi S Pátzcuaro, 7800 ft., 6 (MVZ); *9 mi. SE Pátzcuaro, 8000 ft., 1 (MVZ); 2 mi. E San Gregorio (10 mi. S and 2 mi. E Pátzcuaro), 2; *5 mi. SE Opopeo, 4; 1¾ mi. S Tacámbaro, about 8000 ft., 1.

Pappogeomys gymnurus tellus (Russell)

Cratogeomys gymnurus tellus Russell, Univ. Kansas Publ. Mus. Nat. Hist., 31:537, October 15, 1953; Hall and Kelson, The Mammals of North America, 1:472, March 31, 1959.

Type.—Female, adult, skull and skin; No. 33454 University of Kansas Museum of Natural History; 3 mi. W Tala, 4300 ft., Jalisco; June 2, 1949; obtained by J. R. Alcorn, original number 9379.

Range.—West-central Jalisco, in eastern part of Valle de Ameca at elevations of 4300 and 4400 feet. See Fig. 8.

Description.—Large; tail relatively short (averaging 37% of length of head and body); hind foot short. Average and extreme external measurements of four females and the measurements of one male, respectively, from localities labeled with reference to Tala and El Refugio are as follows: Length of head and body, 249 (241-257), 269; length of tail, 92 (88-99), 87; length of hind foot, 46 (44-48), 47.

Color: Pelage of upper parts Mouse Gray basally and Kaiser Brown apically, back and top of head darker than sides due to admixture of Hazel-tipped hairs; underparts, including throat and chin, Light Mouse Gray overlaid with creamy-white, tinged with pale buffy in a few specimens; throat never grayish; auricular area blackish; hind feet whitish; tail naked.

Skull: Large; narrow across zygomata, squamosals, and especially braincase; nasals and maxillary tooth-row long; rostrum short.

Average and extreme cranial measurements of four females labeled with reference to Tala and El Refugio are as follows: Condylobasal length, 62.1 (60.7-63.6); zygomatic breadth, 42.3 (41.2-43.5); palatofrontal depth, 23.1 (22.5-24.1); length of palate, 43.2 (42.3-44.9); length of nasals, 23.3 (22.9-24.1); breadth of braincase, 30.3 (29.4-31.7); squamosal breadth, 43.9 (42.5-45.2); breadth of rostrum, 14.7 (14.2-15.2); length of rostrum, 26.5 (26.0-27.1); alveolar length of maxillary tooth-row, 13.7 (13.3-14.0).

Comparisons.—From *Pappogeomys gymnurus gymnurus*, *tellus* differs as follows: Hind foot shorter; upper parts (compared with rusty phase in *gymnurus*) paler, more light brownish and less bright ochraceous; underparts distinctly paler, creamy white or pale buff rather than ochraceous; hind foot whitish instead of ochraceous-buff; hairs of throat same color as on belly, not grayish; skull slightly shorter and shallower; narrower across zygomata, braincase, and squamosals; nasals longer; rostrum slightly shorter.

Remarks.—All available specimens of *P. g. tellus* come from an area of deep sandy soils in the Ameca Basin that opens to the southeast and is connected by lowlands with the basins of south-central Jalisco, which are inhabited by *P. g. gymnurus.* So far as I know only *Pappogeomys tylorhinus* has been taken in the intervening lowland, but *tellus* and *gymnurus* possibly have contiguous ranges although intergradation between the two has not thus far been demonstrated.

P. g. tellus, compared with *gymnurus,* is more divergent in cranial features than is *imparilis;* the skull is much narrower and the nasals longer in *tellus* than in *gymnurus* and *imparilis.* Also the pelage is much paler, especially on the venter. The pallor probably is a response to the pale sands of the arid environment in which *tellus* lives. The few specimens studied are remarkably uniform.

Specimens examined.—Total of 10, all from Jalisco, as follows: 1 mi. NE Tala, 4400 ft., 3; *3 mi. W Tala, 4300 ft., 5; *1 mi. S El Refugio (2½ mi. W Tala), 2.

FACTORS INFLUENCING DISTRIBUTION AND SPECIATION

EDAPHIC FACTORS

Pocket gophers of the genus *Pappogeomys* live in sandy soil and sandy loams. A search for these gophers in areas mantled in clay or gravel is futile. *Pappogeomys* avoids clays, which become hard and cloddy when dry and sticky and cohesive when wet. Individuals of *Pappogeomys* are found occasionally in soils that contain a low percentage of gravel or stones, but are never abundant in such soils.

In the transverse Volcanic Mountain region of central México extensive accumulations of dark volcanic ash and dust have formed rich blackish soils. These exceedingly loose, friable soils offers optimum habitat for *Pappogeomys.* The species and individuals of that genus are abundant in this region. The minimum depth of suitable soil required by *Pappogeomys* is unknown. The large kinds of the genus almost certainly require deeper soils than do the small kinds.

Herman (1950:379) excavated several burrows of *P. castanops* along Independence Creek on the Stockton Plateau of Texas, and found the floor of the main tunnel to be as much as 23 inches below the surface. Pocket gophers were especially common along Independence Creek suggesting near optimum habitat. Blair and Miller (1949:13-14) dug out a burrow of *P. castanops* at the western edge of the Valentine Plain in the Trans-Pecos of Texas; the roof of the main burrow was 21 inches below ground. Villa (1953:381) recorded a depth of 0.50 meters (approximately 20 inches) for the main tunnels of *P. merriami* in loose volcanic soil in the Valley of Mexico. Hall and Villa (1949:451) recorded a depth of 16 inches for a main burrow of *P. gymnurus* near Pátzcuaro, Michoacán. Raymond Alcorn informs me that the burrows of *P. alcorni,* one of the smaller species of the genus, were only six or so inches below the surface. All of the above-mentioned recordings were in habitat where pocket gophers were abundant, and therefore inferentially in soils of adequate depth for the gophers. In suitable habitat I have found most burrows of *Pappogeomys* to be at least 12 inches below the surface, except those of the diminutive species *P. bulleri* and *P. alcorni,* which were of lesser depth.

Minimal depth of topsoil required by the larger species of *Pappogeomys* probably is seven to eight inches, and by the smaller species (*P. neglectus, P. bulleri,* and *P. alcorni*) five to six inches. I have been unsuccessful in locating *P. castanops* in areas where the topsoil was less than five inches deep. Robert Dickerman could find no burrows of *P. gymnurus* in Guanajuato south of Celeya; the topsoil there was gravelly and shallow, and natives told him that no gophers occurred there although the natives knew of "topos" to the north (at Celeya). Davis (1940:79) and Davis and Robertson (1944:267) found in western Texas that *P. castanops* did not occur in thin, rocky soils.

Some areas of favorable soils are surrounded by soils unsuitable for *Pappogeomys.* Many of such favorable areas are uninhabited. In broad aspect, the occurrence of *Pappogeomys* may be pictured as an archipelago of large and small "islands" of favorable soils surrounded by an inhospitable "sea" of uninhabitable soils. Because only the overall distribution is depicted on range-maps, they could easily lead an inexperienced biologist to underestimate the discontinuity of distribution that actually exists in nature.

BEHAVIORAL FACTORS

Most of my knowledge of behavior and population structure of *Pappogeomys* comes from field observations made incidental to collecting specimens for taxonomic study.

Interspecific Relationships

Genera as well as species of geomyids usually are allopatric in distribution, and in places where ranges of two or more kinds are contiguous the kinds commonly remain allopatric in local occurrence. Hall and Villa (1949:451-452) found that *Thomomys um-*

brinus pullus and *Cratogeomys* (*Pappogeomys*) *gymnurus imparilis* occurred at points three, four, and five miles south of Pátzcuaro, Michoacán. The burrows of *Thomomys* were smaller and shallower than those of *Pappogeomys. Thomomys* is approximately an eighth the size (weight) of *Pappogeomys gymnurus.* In the Sierra de Tigre of western Michoacán near Mazamitla, Raymond Alcorn obtained *Pappogeomys gymnurus* and *Pappogeomys alcorni* in the same intermountain meadows and noted that the burrows of the much smaller *Pappogeomys alcorni* were near the surface, whereas the burrows of the larger *Pappogeomys gymnurus* were deep and in some instances directly below the burrows of the smaller species. *Pappogeomys gymnurus* was abundant at these localities, but *Pappogeomys alcorni* was much less common (only four specimens were obtained in several days of intensive trapping on two different occasions).

In western Coahuila, on the desert plains north of Torreón, the smaller *Pappogeomys castanops perexiguus* and the larger subspecies *Pappogeomys castanops excelsus* seem to overlap in range although both have not been taken from the same site. In this instance their ranges probably simply come into contact, or interdigitate, and local allopatry is maintained.

In the two known cases of local sympatry, involving in one case *Thomomys umbrinus* and *Pappogeomys gymnurus* and in the other *Pappogeomys gymnurus* and *Pappogeomys alcorni*, the local habitat is shared by a small and a large species.

The unsociable and often pugnacious nature of pocket gophers manifests itself in vigorous defense of their territories (individual burrow systems). Intense territorial defense and the allopatric patterns of distribution common to geomyids seem to me to be correlated with a small ecological valence (see Hesse, Allee, and Schmidt, 1934:20). Hence, the completely fossorial niche for an herbivorous rodent is conceived as an ecological situation with little latitude of adaptability. Pocket gophers depend mostly upon roots of various sorts as food, supplemented in small degree by above-ground parts of the plants. Where the food material is practically homogeneous, only slight diversity in food habits is possible; consequently the requirements for survival of different kinds of pocket gophers are nearly identical. Selection has resulted in intolerance of other occupants of this restricted niche, as a necessity for survival. On a larger scale, allopatric distributions are the result with intensive competition for local habitat where ranges are contiguous.

Once a group of species is well adapted to a restricted fossorial niche it would be difficult for other kinds of rodents to invade that niche since they probably would be less well adapted at first than the occupants. Full adaptation should evolve only with actual occupancy of the niche for some time. Intense competition for such a specialized habitat as that occupied by a modern geomyid, would surely end in failure for the invader. For this reason, it is not surprising that there are few kinds of completely fossorial rodents in any one geographic region. In North America only the Geomyidae, among many kinds of semifossorial rodents, have succeeded in fully establishing claim to the completely fossorial adaptive zone.

Intraspecific Relationships

Each individual of *Pappogeomys*, after leaving its mother, excavates its own burrow. Individuals remain solitary most of the year; visits between males and females probably take place only in the rutting season, and males may linger with females that are in breeding condition. Connecting tunnels have been noted, usually plugged with earth, between adjacent burrows. These tunnels could easily be opened to allow entrance of another gopher.

The unsociable disposition of pocket gophers is well known (see Scheffer, 1931:8). Hermann (1950:379-380) wrote of vicious fighting that occurred when adult male and female *Pappogeomys castanops* were placed in the same cage. Incompatibility is indicated also by the infrequency of plural captures of reproductively mature (adult and subadult) individuals, and those that do occur are usually in the breeding season. Blair and Miller (1949:13) took an adult female and a "young adult" (?subadult) male from one burrow on the Valentine Plain in the Trans-Pecos of Texas, and Russell (1954:122) took an adult male, nursing female, and a young (immature) female from a single burrow entrance in one night in the same trap-set near Muralla, Coahuila. No other plural captures are known to me. If social contact was usual, multiple catches would be expected to have been made with greater frequency.

Judging from my observations in the field, *Pappogeomys* occurs in breeding demes (local colonies). Each deme is composed mostly of reproductively mature females (both adult and subadult) and usually one adult male. Less commonly two or three adult males live in a deme. Museum collections of these gophers reflect the population structure of the demes in that the collections contain more than five females for each male. Traps set in a colony yield mostly females, whereas traps set in the isolated and scattered burrows between colonies, or near the peripheries of large colonies nearly always yield subadult males. Of course, young gophers of both sexes are found within the colonies when the females are nursing, and occasionally subadult males, probably those not yet sexually mature, are taken there.

I suppose that a harem of females is served by an aggressive adult male and that during the breeding season he does not tolerate other reproductively mature males in the colony, or, within that part of it that he is able to defend in the case of large aggregations. How large an area or how many females one male can control is not known.

Colonies usually are in areas of deep, well-developed soils that provide suitable environment to gophers. Isolated burrows of males (sometimes females are taken in isolated burrows, but not so commonly as males) are often in marginal habitat as judged by type of soil and kind of vegetation. A certain amount of travel overland, above-ground, is required to reach these bachelor quarters. Most of the remains of pocket gophers recovered from the digestive tracts of carnivorous vertebrates could have been caught only when the gophers were above-ground—for instance those eaten by owls. A gopher above-ground is more likely to be caught and eaten than is a gopher below-ground. Therefore, the mortality rate among subadult and young adult males, many of which seem to live in marginal sites until they can compete for a harem, probably is greater than in females of the same age-classes, most of which remain within the colonies.

A large population that is split into many semi-isolated demes is the most advantageous population-structure for rapid and sustained evolution, according to Wright (see summary in Simpson, 1954:123). The population structure of *Pappogeomys* seems to fit this model. Therefore, the high degree of geographical variation demonstrable in the genus *Pappogeomys* (and also other genera of geomyids) is not surprising; rather it is to be expected. Gene flow would certainly be reduced, and in many cases nonexistent, between the numerous local populations. The result would be a high degree of adaptation to local environments through selection. In such a situation, subspeciation reaches its maximum, and even then only a few subspecies are homogeneous throughout their range but rather reflect many divergences in local populations.

CLIMATE, TOPOGRAPHY, AND VEGETATION

Pappogeomys occurs in arid environments. Even in mountainous regions, where annual precipitation is usually greater than on the plateaus and desert plains, *Pappogeomys* shows a preference for the drier sites. Most species of *Pappogeomys* do not commonly occur in forest; they are found at the edge of woodlands and in open areas. The humid and well forested slopes of mountains such as the eastern slopes of the Sierra Madre Oriental and the south-facing slopes of the transverse Neovolcanic Range are not inhabited by *Pappogeomys.* The one species *P. merriami* seems to tolerate more mesic conditions than the others, and at several places in the mountains around the Valley of México it occurs in decidedly moist situations, some of them in the forest, inhabited also by *Sorex, Microtus,* and *Romerolagus.*

Also, *Pappogeomys fumosus* and some subspecies of *P. bulleri* occur on the Pacific coastal plains of Colima and Jalisco in semitropical situations, but the climate there is not markedly humid.

Although the climate on the Anahuac Plateau of central México is everywhere suitable for *Pappogeomys,* it does not occur everywhere because some soils are unsuitable and because some soils that are suitable are not occupied owing to failure of the gophers to reach those soils.

Northward, the less elevated Mesa del Norte, mantled by deep sandy soils, and having an arid environment, provides excellent habitat for these gophers and they are abundant there. Nevertheless, the high degree of aridity in some places there seems beyond the ecological tolerance of the genus. *Pappogeomys* is uncommon, or absent from, regions where the annual precipitation is eight inches or less. In such regions, plants are widely spaced and the lesser amount of plant material may be the factor that prevents *Pappogeomys* from living there.

In mountainous areas gophers of the genus *Pappogeomys* occur in the intermontane valleys, and are unusually abundant in cultivated fields especially where corn or agave is grown. Deforestation by man has probably opened new habit for these gophers.

Pocket gophers of all kinds depend predominantly on the subterranean parts of plants for food. Species of *Pappogeomys,* especially those of the subgenus *Cratogeomys,* prefer the deep-growing, succulent and woody roots of xerophitic shrubs. Even so, these gophers will turn to roots of grasses and forbs if they are common locally. Sometimes the upper parts of the plants are eaten, but not so much as are roots and tubers. Roots of many kinds of plants are used by *Pappogeomys*, and it seems unlikely that gophers are excluded from any areas by reason of unacceptable food.

Life under-ground buffers pocket gophers from the direct effects of climate. When the surface soil is extremely dry they will burrow deeper, pushing newly excavated earth into old tunnels. Immediately after rains the amount of newly excavated earth expelled onto the surface increases. Extremes in temperature, within limits of course, have little effect on gophers. The effect of climate is indirect by determining the kind of vegetation and influencing the rate of soil formation. Also, the life form (that is, widely spaced desert shrubs, forest, grassland, etc.) of the vegetation probably is more important than the presence or absence of individual species of plants. Decidedly tropical environments with their dense vegetation restrict the distribution of pocket gophers of the genus *Pappogeomys*.

These gophers occur from sea level to altitudes as high as 15,000 feet. So long as suitable vegetation and soils are present, elevation itself seems to have little effect on these fossorial mammals. Desert mountains are effective barriers to dispersal of the populations because of the shallowness of soils and their rocky nature. Rivers are partial barriers because pocket gophers cannot swim (Kennerly, 1963:86-87), but they commonly live in the floodplains of streams and, through ultimate changes in the channel, eventually are moved from one side of the stream to the other.

Climate, topography, or vegetation (within broad limits) is less effective in determining the pattern of distribution in *Pappogeomys* than are edaphic conditions and interspecific competition.

Detailed accounts of the topography, climate, and vegetation of particular regions may be found in the species accounts and in the section on centers of differentiation.

MAJOR AREAS OF DIFFERENTIATION

The Transverse Volcanic Mountain Range, including some of the highest peaks in North America, marks the southern boundary of the Central Plateau of México and dramatically separates the temperate Nearctic region of the north from the Tropical region to the south. This mountain range forms a barrier of tremendous proportions and great effect in a small region where tropical, Sonoran, and boreal faunas converge. Some of the effects have been analyzed by Moore (1945), Goldman and Moore (1945), Hall and Villa (1949), Davis and Russell (1954), Villa (1953), Sibley (1954), Hooper (1952), and Packard (1960).

Although this region is scarcely 400 miles long and 100 miles wide, it includes arctic-alpine areas, boreal cloud forest of pine and fir, tropical rain forests, transitional zones of pine-oak-madrone woodland, savannah grasslands, arid tropical scrub, and arid Sonoran deserts (see Leopold, 1950). The irregular mosaic of a large variety of soil types (see Tamayo, 1949) is especially important in determining the distribution of geomyids. Blackish, highly friable volcanic soils of the mountains and valleys, and the deep, pale sands that occur on the Anahuac Plateau alternate with clayey soils and thin, rocky soils. The two types last mentioned are uninhabitable for pocket gophers. Sears (1955) showed clearly that the surface soils of local areas have changed in the recent past owing both to outwash from glaciers and to volcanic activity.

The transverse volcanic region is separated indistinctly into two major areas: The Neovolcanic Range and the arid Anahuac Plateau to the north. This Plateau is the southern part of the Central Plateau of México, and is more elevated and less arid than the northern part of the Central Plateau (Mesa del Norte). The Anahuac Plateau is an undulating plain set with widely scattered mountains. Grasses and desert shrubs are the dominant types of vegetation. The Neovolcanic Range rises several thousand feet above the plateau, but in most places the Anahuac Plateau gradually slopes into the mountains. The north-facing slopes are more arid than the higher elevations and the south-facing slopes, which receive more rainfall. Forest associations are dominant in the mountains, but numerous open intermountain valleys support grasses and shrubs of the same species that occur on the Anahuac Plateau.

The transverse volcanic region seems to have been the principal area of evolution for the genus *Pappogeomys* throughout the Pleistocene. As pointed out in the previous section, the advanced subgenus *Cratogeomys* had its origin and subsequent evolution in this region in the Pleistocene. Indeed, the *gymnurus* species-group of *Cratogeomys* is, with the exception of one species that occurs in an adjacent area, endemic to the region. In the late Pleistocene (Wisconsin) and continuing to the present time, speciation in the *gymnurus*-group has led to the formation of five distinct species and two incipient species (*Pappogeomys tylorhinus zodius* and *Pappogeomys gymnurus imparilis*), both of which are treated here as highly divergent subspecies. With more time, these two incipient species probably will evolve into species (discussed fully in the next section). Moreover, subspeciation is taking place today in most of the widely distributed species of the region; the *gymnurus*-group is an example.

At the present both the subgenera *Pappogeomys* and *Cratogeomys* occur in the Neovolcanic region. The subgenus *Pappogeomys* and the *gymnurus*-group of the subgenus *Cratogeomys* are, respectively, the most primitive and the most specialized, and are almost restricted to the region; only one subspecies of *P. bulleri* of the subgenus *Pappogeomys* and two species of the *gymnurus* group occur beyond the region. Of the nine species, seven (78%) occur in the Transverse Volcanic region.

The subgenus *Cratogeomys* now is undergoing secondary differentiation in northern México and the southwestern part of the United States—a differentiation which probably began in the early stages of the Sangamon interglacial. One species of *Cratogeomys* (*P. castanops*) is well adapted to the xeric conditions found on the Mesa del Norte, and this species has been highly successful and has expanded its range widely over the northern desert region whereas the ranges of species of *Cratogeomys* in the Transverse Volcanic region have become smaller. The Mesa del Norte-Sierra Madre Occidental region, therefore, forms a secondary area of differentiation. The *castanops* species-complex seems to have evolved in the late Pleistocene, and as yet has not come in contact with other species of the genus to the south. Because the evolution of *P. castanops* has involved movement into a new adaptive zone (see Simpson, 1953:349-359), the group could reasonably be regarded as an incipient subgenus that in the future could become one of the dominant geomyids of the desert and grassland environment. In such event, the Mesa del Norte would be viewed in retrospect as a major area of differentiation.

In summary, there are two major areas of differentiation in which speciation, subspeciation, and the evolution of subgenera have taken place. Of the two, the Transverse Volcanic region is of first importance, and most of the phyletic development of *Pappogeomys* has taken place there. The Transverse Volcanic region is still an area of active differentiation of the genus. The Mesa del Norte-Sierra Madre Occidental region of northern México is of secondary importance as an area of differentiation. Furthermore, the desert plains of this region, and adjacent arid regions of southwestern Texas, eastern New Mexico, and southeastern Colorado, comprise a region of active subspeciation in the *castanops* species-group.

EVOLUTION OF THE GENUS

The fossil record of the genus *Pappogeomys* is meager, the genus being represented in the late Pliocene (early Blancan) of Arizona by the extinct species *Pappogeomys bensoni* (Gidley, 1922) and in the late Pleistocene by several finds of the living species *Pappogeomys castanops* (Russell, 1960) and *Pappogeomys tylorhinus* (Hibbard, 1955). The rostral fragment from San Josecito Cave reported only as *Cratogeomys* (=*Pappogeomys*) sp. by Russell (*op. cit.*:543) cannot be identified with any known species, and probably belongs to some unnamed species that was related to *P. castanops* and that became extinct in the Wisconsin period (for details on this and other fossils of *Pappogeomys*, see Russell 1957 and 1968).

The fragments of *Pappogeomys bensoni* do show that the genus had become differentiated from the ancestral stock of the tribe Geomyini by Pliocene time. But, the cranium and upper dentition are unknown and therefore the relationship of *P. bensoni* to the modern species remains unknown (see account of *bensoni* for further discussion). The late Pleistocene records, mentioned above, of living species serve chiefly to extend the known vertical range of those species back into the Pleistocene, as expected, but those specimens provide no evidence as to the phyletic history of the genus except, perhaps, to suggest that most of the living species had differentiated by Wisconsin time.

The time and sequence of origin of the subgenera *Pappogeomys* and *Cratogeomys*, the species-groups of *Cratogeomys*, and the living species and their immediate ancestors are not documented by fossil evidence. Probably most of the speciation within the genus took place in the Pleistocene. Owing to the lack of fossils, construction of a diagram to show the probable phyletic development of the genus has been based on an interpretation of the morphology, geographic distribution, and taxonomic relationships of the modern species and is necessarily tentative. See Fig. 10. The points of dichotomy are relative and not intended to be correlated with any specific stratigraphic division of the Pleistocene.

Most morphological features of the earliest species of the genus *Pappogeomys* (perhaps *P. bensoni*) are unknown. The ancestor of the genus is thought to have been a small gopher having a smoothly rounded skull without marked angularity or rugosity, occiput convex posteriorly, slender zygomata lacking platelike expansions at lateral angles, temporal ridges on braincase but lacking a sagittal crest, squamosal not extended either laterally or medially, small paroccipital processes without platelike expansion, short angular processes, single median sulcus on upper incisor, posterior wall of P4 without enamel plate, enamel plate extending completely across posterior wall of M1 and M2, occlusal surface of M3 subtriangular or suborbicular, with posterior loph indistinctly separated from anterior loph. The skull of the ancestral species was probably also generalized and without the advanced platycephalic specializations that developed subsequently in the subgenus *Cratogeomys.* Fossorial specializations of the postcranial anatomy were probably already well developed as in other Geomyini.

All known taxa of the genus could have been derived from the hypothetical morphotype described above. Of the living species, *P. bulleri* of the subgenus *Pappogeomys* most closely resembles the ancestral morphotype, differing only in minor details. The restricted range of *P. bulleri* suggests that it is a relict species, possibly a late survivor of the ancestral stock of the genus. Therefore, *P. bulleri* is regarded as the most primitive living member of the genus and the most closely related to the ancestral taxa.

P. alcorni, also a living member of the subgenus *Pappogeomys,* closely resembles *P. bulleri* and probably differentiated from *bulleri*-stock in the late Pleistocene. Probably *alcorni*-stock became isolated from the main population of *bulleri* during Wisconsin glaciation of the Neovolcanic Range. According to evidence presented by Maldonado-Koerdell (1964:26-29), White (1960), Hutchinson, Patrick, and Deevey (1956), DeTerra, Romero, and Steward (1949), and Sears (1955), ice caps formed at higher elevations on the mountains bordering the plateau in central México. Glaciers advanced down the slopes of the mountains, and vegetation and climatic zones were displaced to lower elevations. Glacial maxima have been correlated with Iowan glaciation in the mid-Pleistocene, when ice descended to 2450 meters (White, *loc. cit.*), and with the Wisconsin, when ice sheets formed at 3135-3400 meters (Maldonado-Koerdell, *op. cit.*:29). Moreover, the post-Wisconsin trend toward aridity has resulted in the desiccation of the playa basins in southern Jalisco. The adverse environment of these lowlands prevents contact between *P. alcorni* and *P. bulleri* at this time (Russell, 1957).

P. alcorni differs from *P. bulleri* in the slightly more specialized first upper molar. This partial loss of enamel of M1 occurs also occasionally in *P. bulleri,* and rarely also on M2, suggesting selection pressure for loss of these enamel plates in the subgenus *Pappogeomys.* A specialization of the subgenus *Cratogeomys* is the loss of enamel plates on the posterior wall of M1 and M2. Probably *Cratogeomys* evolved from *Pappogeomys,* and the ancestral stock of *Cratogeomys* evidently was characterized by a trend toward loss of these enamel plates. The reduction evidently began on the labial side of the tooth (as it obviously did in *P. alcorni*) with loss occurring progressively toward the lingual side. Loss probably occurred in M1 before it did in M2, although reduction may have commenced in M2 before it was completed in M1. In any event, loss of both enamel plates had taken place before the ancestral stock of *Cratogeomys* split into the two lineages that gave rise to the *castanops* species-group and the *gymnurus* species-group. Other features that developed in the ancestral stock of the subgenus and that, therefore, are common to all kinds of *Cratogeomys* are the following: Increased angularity and rugosity of the skull; flattening of the occiput; formation of sagittal crest with increasing age; development of a platelike expansion of the lateral angles of the zygomata. The initial stages in the trend toward a platycephalic skull may have been present before the two species-groups arose. The early stages in evolution in *Cratogeomys* probably occurred in the early Pleistocene; consequently much time remained in which additional differentiation of the subgenus could occur.

Both the *castanops* species-group and *gymnurus* species-group are specialized in comparison with the species of the subgenus *Pappageomys.* In the *castanops*-group, one of the major specializations has occurred in M3. The quadriform M3 of *P. castanops* and especially the obcordate M3 of *P. merriami* are clearly specializations of the primitive subtriangular M3. One trend in the *castanops*-group was toward an increase in size, reaching its maximum in *P. merriami. P. castanops* is smaller and otherwise less specialized than *P. merriami,* and, of the living species of *Cratogeomys,* it is probably most nearly like the ancestral stock of the subgenus. In addition to specializations of M3, *P. merriami* has evolved cranial specializations including medial expansion of the squamosal and increase in size of the rostrum (especially in vertical depth) and the upper incisors.

In the *gymnurus*-group, M3 has remained unspecialized and the surface of the tooth is subtriangular as in the subgenus *Pappogeomys.* The major specializations in the *gymnurus*-group have been in the broadening and flattening of the skull, including lateral expansion of the squamosals and angular processes. Also, the paroccipital processes are enlarged, the lambdoidal crest is deeply concave posteriorly, and the crest is sinuous in dorsal outline. As in the *castanops*-group, the most recently developed features in the *gymnurus*-group include an increase in size, reaching its maximum in the species *P. gymnurus*. *P. neglectus* is clearly the most primitive species of the group, and, except for its broad, shallow skull, it is probably little specialized from the ancestral stock of the subgenus. *P. fumosus* represents a later offshoot and its specializations mostly are ecological.

Among the living species, *P. castanops* includes the most subspecies—25. They are divided into the *subnubilus*-group and *excelsus*-group. The two groups differ primarily in size of skull, especially its length, mostly are allopatric, and in most places are separated by mountain ranges such as the Sierra Guadalupe-Sierra Parras chain in southern Coahuila and the Sierra Pina-Sierra de la Madera chain in northwestern Coahuila. But, contact does occur in some areas as depicted by diagonal lines in Figure 3. In these areas subspecies of the large gophers, *excelsus*-group, and small gophers, *subnubilus*-group, occur without intergrading and behave toward each other as do species. Difference in size between geographically adjacent members of pairs of subspecies of the two groups is depicted in Figure 9.

Gene flow between the *excelsus*-group and *subnubilus*-group occurs, insofar as I can determine, only between *goldmani* of the *excelsus*-group and *rubellus* of the *subnubilus*-group. The exchange of genes between these two subspecies, and their introgression, has resulted in a larger skull in *rubellus* (see Fig. 9) and a smaller skull in *goldmani*. Even so, *goldmani* occurs sympatrically with *surculus* of the *subnubilus* group over an area of considerable size, although the two probably do not occupy the same local sites.

It is my view that the *subnubilus*-group and the *excelsus*-group differentiated in a period of isolation in the Wisconsin pluvial cycle. Recent studies by Martin and Mehringer (1965), Hafsten (1961), and Martin (1958, 1961, and 1963) have demonstrated that cooler and more moist climates prevailed over northern Mexico and the southwestern United States during the Wisconsin from about 35,000 years BP to 14,000 years BP. During the times of pluvial maxima, boreal forests of pine and spruce covered most of the lowlands of this region, and the xerophytic vegetation, previously dominant in the lowlands, was restricted to small areas, probably in the rain shadow of the mountains. Conditions unfavorable for gophers in the pluvial cycles isolated small populations of *P. castanops*. The *subnubilus*-group probably evolved from populations so isolated south of the Sierra Guadalupe and Sierra Parras, and the *excelsus*-

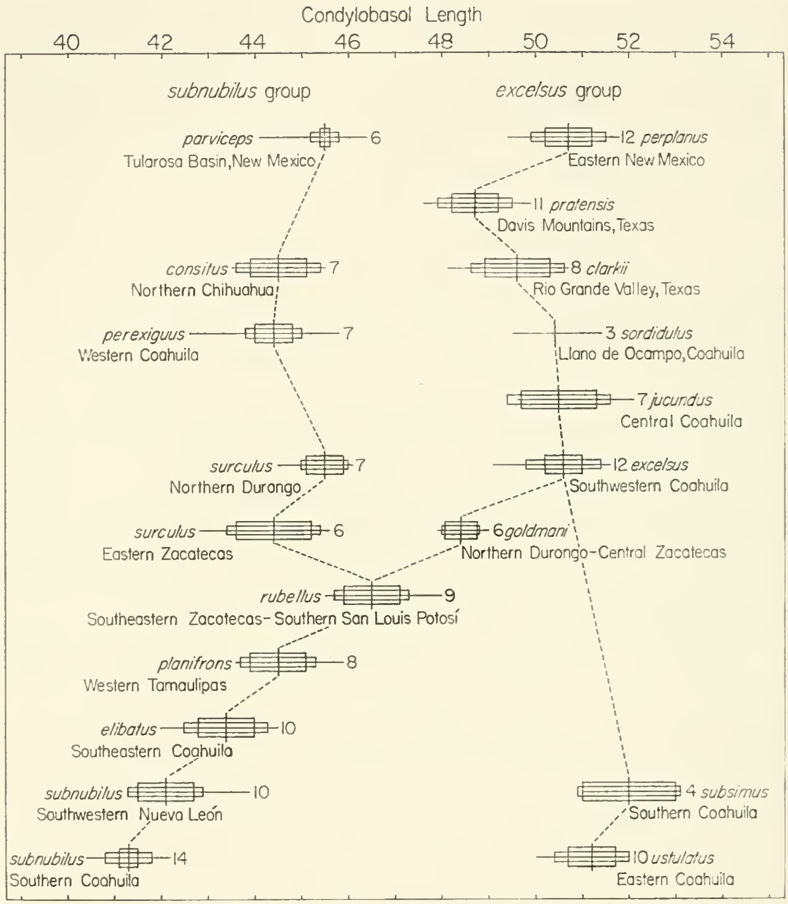

FIG. 9. Subspecies of *Pappogeomys castanops* in the areas where the *subnubilus* group and *excelsus* group intergrade (see *goldmani* and *rubellus*), or overlap geographically (for example *subsimus* and *subnubilus*), or approach each other geographically (*pratensis* and *parviceps*). Extremes, one standard deviation from the mean, two standard errors from the mean, and the mean are shown for each sample. A numeral shows the number of individuals (adult females) in each sample. The dashed line indicates intergradation.

group from populations north of these mountains. With the trend toward aridity in the post-Wisconsin, the two groups of subspecies expanded their ranges from their Wisconsin refugia, and in most places where they made contact the two groups have maintained reproductive isolation. Subsequently, both groups of subspecies expanded their ranges northward into the southwestern United States.

Probably Wisconsin glaciation resulted also in the fractionation of previously continuous populations of the ancestral species that differentiated into *P. tylorhinus*, *P. zinseri*, and *P. gymnurus* of the *gymnurus* species-group. The three living species mentioned above were probably differentiated from isolated populations of a common ancestor; anyhow the three closely resemble one another morphologically. Subsequent readjustment of their ranges in the post-Wisconsin has resulted in interdigitation of ranges in the Neovolcanic mountains and the currently disjunct populations.

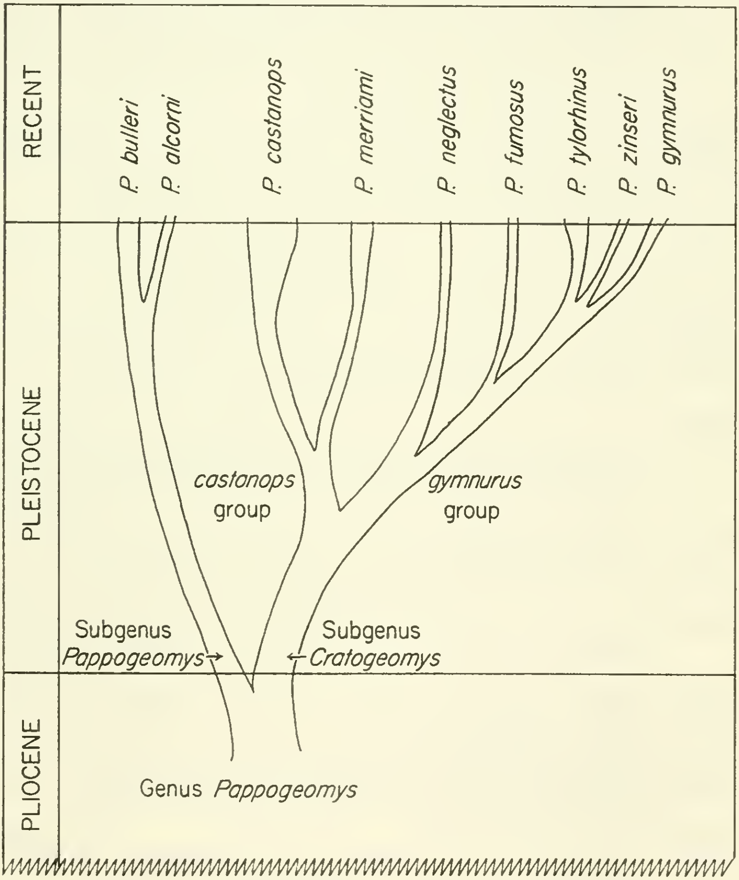

FIG. 10. Phylogeny of the genus *Pappogeomys*.

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Systematics of Megachiropteran Bats in the Solomon Islands

BY

CARLETON J. PHILLIPS

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CONTENTS

INTRODUCTION

The Solomon Islands constitute an archipelago east of the large island of New Guinea and more than a thousand miles off the northeastern coast of Australia. This archipelago, which is principally of volcanic origin although sedimentary layers of calcareous rocks occur on many islands (Lever, 1934; Belkin, 1962), consists of a double chain of islands having a northwest-southeast axis of more than 600 miles. The archipelago is more or less an extension of New Guinea and in fact is connected to it in stepping-stone fashion by New Britain, New Ireland, and numerous smaller islands (see Fig. 1).

Australia and New Guinea have many kinds of mammals but the only terrestrial mammals in the Solomon Islands are a species of the genus *Phalanger* (order Marsupialia), and several species of four genera of rodents, one genus of which probably was introduced by man. Additionally, several kinds of bats have reached and colonized the Solomon Islands.

In the past 100 years at least 43 species and subspecies of Chiroptera of 16 genera have been recorded from the Solomon Islands; of these 27 species and subspecies of seven genera are in the suborder

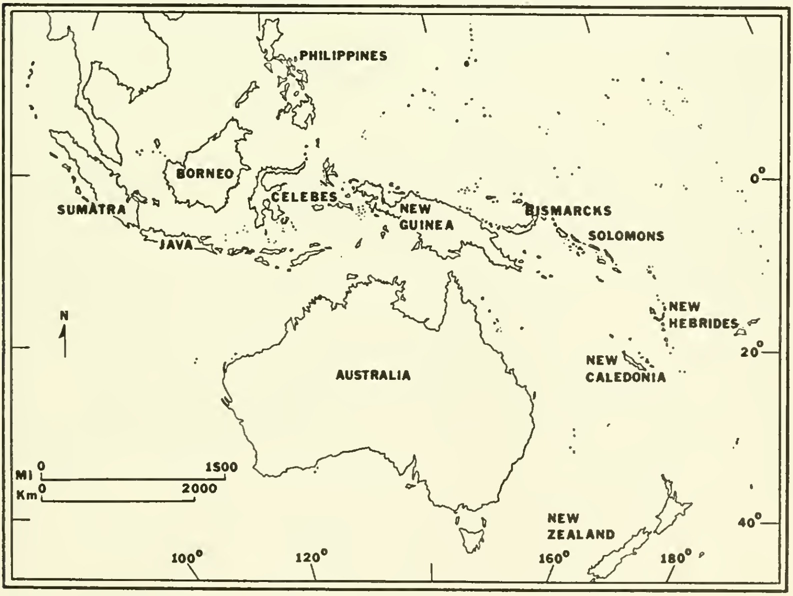

FIG. 1. Showing the Solomon Islands in relation to major adjacent land masses.

Megachiroptera. At least one genus of Megachiroptera is endemic as are numerous species of other genera, and subspecies of still other species.

In 1963 and 1964, the Bernice P. Bishop Museum sent several collecting parties to the British Solomon Islands Protectorate and the Australian Trust Territory of New Guinea. In the Solomons, J. Linsley Gressitt, Philip Temple, Peter Shanahan, and Ray Straatmann visited many of the larger and more accessible islands and collected a wealth of zoological materials. I have had the opportunity to study and report on specimens of mammals, especially bats, collected by the persons named and deposited in the Bishop Museum. This report is the third in a series on bats from the Solomons (Phillips, 1966; 1967). Other specimens, mostly obtained in 1944 by personnel of United States military units, are stored in the United States National Museum and have been available for study. Aims of the following report are to (1) identify the megachiropteran bats to species and subspecies and (2) discuss distribution of these bats in the Solomon Islands.

In all, 27 kinds (subspecies and monotypic species) of the order Megachiroptera are known from the Solomon Islands. These pertain to three subfamilies of the one family Pteropodidae.

The 43 Solomon Islands, having a total land area of more than 15,300 square miles (see Belkin, 1962:42-43), are listed in the gazetteer (see also Figure 2). Politically, all of the Solomon Islands except Buka and Bougainville, which are included in New Guinea Trust Territory under mandate to Australia, are in the British Solomon Islands Protectorate.

The Solomons are within 300 to 700 miles of the equator and have a fairly constant tropical climate, except at high elevations. The temperature varies little; monthly mean temperature is between 81° and 83° F. and at sea level ranges from about 70° to 93° F. yearly (Belkin, 1962:42).

Southeast tradewinds are relatively constant from May to October and this period, in general, is a dry season except at higher elevations on windward coasts. From December to March prevailing winds are from the north and precipitation throughout the island group is especially heavy. Rainfall on the island of Tulagi averages about 120 inches per year (Bryan, Edwin H., 1941; MS, p. 2, at Pacific Sci. Information Center, Bishop Museum) and up to 300 inches have been recorded on the north coast of Guadalcanal (Belkin, 1962: 42-43). Occasional dry periods occur even in the period of December to March.

Most islands of the Solomon Group support dense tropical rain forest. Much of it has been modified by man. Some clearings and scattered coconut plantations are found along coasts. On some of the larger islands (for example, Guadalcanal) coastal scrub (especially on leeward coasts) and extensive grassy areas are to be found. Additional notes on vegetation are in the gazetteer.

The 165,000 persons living on the Solomon Islands are mostly Melanesians but some are mixed Papuan, Malay, and Polynesian. These native peoples are notorious for their cannibalistic tendencies; the eating of human flesh usually was related to warfare, although malefactors and human sacrifices accounted for some of the cannibalism (Cranstone, 1961:29). Prior to the Second World War few Europeans visited the Solomons and several islands still remain beyond reach of modern-day technology. For example, Rennell and Bellona islands, south of the main part of the archipelago, are visited only rarely, and then only by a medical officer or the Resident Commissioner. According to Troughton (1936:341), the islanders in the interior of Bougainville as late as 1935, were prone to kill and feast upon strangers. In 1932, Lewis (1951:37) felt that the natives of Malaita Island were especially resistant to outside interference by Caucasians and reported that no "white man or foreigner" was safe on Malaita.

Troughton (1936), who listed Melanesian names for mammals, indicated that the native peoples distinguished between kinds of bats that closely resembled one another. Of these, the only bats that seem to be used as food belong to the genus *Pteropus*.

GAZETTEER

In the following list, currently-used names of islands are given; when available, older names and variant spellings are indicated in parentheses. For certain islands, especially those visited by field parties from the Bishop Museum or those frequently mentioned in previous literature on bats, some descriptive and ecological information also is provided.

Latitude and longitude of islands are from publication no. 881 of the Hydrographic Office of the United States Navy Department (Anonymous, 1944); names of islands were checked against a list by Brigham (1900); descriptive information mostly is from reports by Temple and Straatmann (1964, field notes, at the Department of Entomology, Bishop Museum).

ALU.—7°07′ S, 155° 54′ E.

BANIKA.—9° 05′ S, 155° 13′ E.

BARA (Gera).—9° 31′ S, 160° 31′ E.

BELLONA (Bello).—11° 18′ S, 159° 48′ E.

BOUGAINVILLE (Mamamolimo).—6° 12′ S, 155° 15′ E. This is the largest island in the Solomon Group, being 127 miles long (northwest to southeast) and about 59 miles across at the widest place. The highest elevations are 9850 and 10171 feet, at the tops of active volcanoes. Ecologically, Bougainville is mostly dense rain forest, which is less dense on the summits of higher mountains.

BUKA.—5° 15′ S, 154° 38′ E.

CHOISEUL.—7° 04′ S, 157° 01′ E. This island, formed along a northwest-southeast line of low mountains (maximum elevation of 3500 feet), is about 90 miles long and 20 miles wide. Most collecting was at Malangona (Sasamunga on some maps) on the southwestern coast.

FAURO.—6° 55′ S, 156° 07′ E. This small island, about 14 miles long (north-south) and six miles wide (east-west), lies about 10 miles south and east of Bougainville. Fauro is formed around a volcanic cone having a maximum elevation of 1925 feet; it has considerable dense mangrove swamp along the west coast, and mature rain forest with little understory growth. Most collecting was at Toumoa, on one of two southern peninsulas.

FLORIDA (Nggela).—9° 05′ S, 160° 16′ E. Florida, the main island in the Nggela Island Subgroup, is mountainous and except for some small grassy areas, supports dense rain forest. It is nearly 25 miles long (east-west) and nine miles wide (north-south), with a maximum elevation, at Mount Barnett, of about 1366 feet. Most collecting was at Haleta, on the southwestern coast. At this locality there were scattered mangrove swamps, rain forest, and gardens inland.

GANONGGA (Ronogo, Ronongo).—8° 03′ S, 156° 35′ E.

GATUKAI.—8° 47′ S, 158° 12′ E.

GHIZO (Gizo, Keso).—8° 05′ S, 156° 59′ E.

GOWER (N'dai).—7° 54′ S, 160° 34′ E.

GUADALCANAL (Guadalcanar).—9° 15′ S, 159° 35′ E. Guadalcanal is mostly of volcanic origin and has an irregular chain of mountains along the southern coast. The highest elevation is 8005 feet at Mount Popomanasiu. This large island is nearly 80 miles long (east-west) and 25 miles wide (north-south). Most of the northwestern part of Guadalcanal supports *alang-alang* grass. The remainder of the island is heavily wooded.

KILINAILAU (Cartaret).—4° 44′ S, 155° 28′ E.

KOLOMBANGARA (Duki, Kulambangara).—8° 00′ S, 157° 05′ E. Kolombangara, formed from an extinct volcano, is about 18 miles in diameter and nearly circular. The highest peaks, rising as precipitous cliffs in some places, reach a maximum elevation of about 5000 feet. The vegetation is mostly virgin rain forest. Mangrove swamp and small coconut groves occur along the coast. Field parties from the Bishop Museum were able to reach the highest elevations, and concentrated their work along the southwestern side of the island.

MALAITA (Mala, Malanta, Malayta).—9° 00′ S, 161° 00′ E. This long (104 miles northwest to southeast), narrow (about 23 miles at its widest spot) island, between Santa Ysabel and San Cristobal islands, is basically of volcanic origin with some limestone (coral) deposits along the coast. Mount Kolovrat,

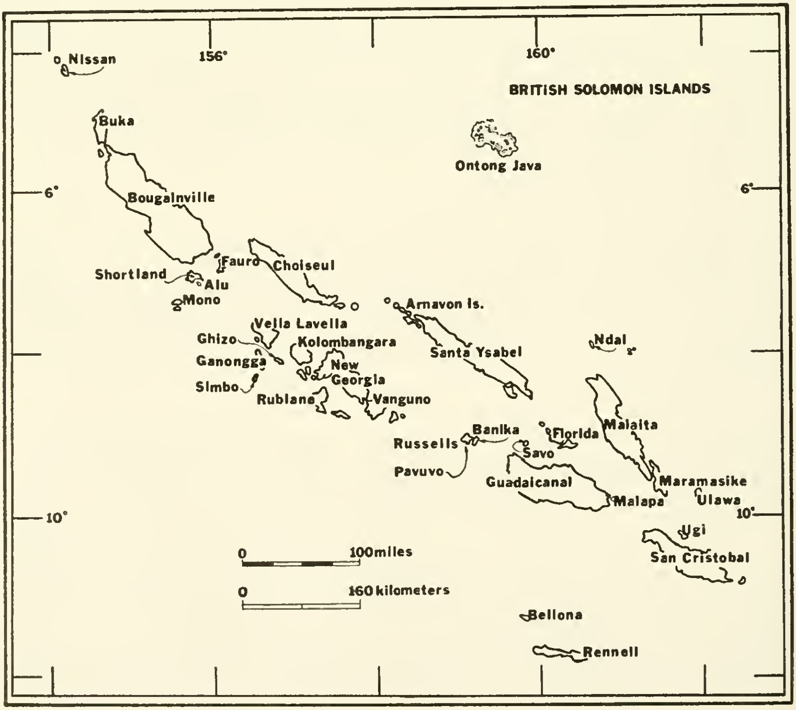

FIG. 2. Solomon Islands. Principal islands are named.

having an elevation of 4275 feet, is the highest point. The Bishop Museum field party lived at Dala, in dense rain forest about 12 miles north of Auki on the northwestern coast of Malaita.

MALAPA.—9° 49′ S, 160° 53′ E.

MONO (Treasury).—7° 22′ S, 155° 35′ E. This is a small island (maximum elevation 1150 feet) in the Treasury Island Subgroup just south of Bougainville. Mono is about nine miles long (east-west) and five and one half miles wide (north-south). The basic volcanic core is described in field notes as topped with coral limestone.

NEW GEORGIA (Kausagi).—8° 20′ S, 157° 30′ E. The New Georgia Subgroup is composed of 11 moderate-sized islands and islets. New Georgia Island, the main member of the subgroup, is 50 miles long (northwest to southeast) and from five to 30 miles wide. On the northern side several volcanic peaks attain an elevation of about 3000 feet. The entire island is forested.

NGGELA (Florida Islands).—4° 31′ S, 154° 11′ E. This subgroup consists of several small to medium-sized islands between Guadalcanal and Malaita. Florida is the main island.

NISSAN (Green, Sir Charles Hardy's).—4° 31′ S, 154° 11′ E.

NUKUMANU (Le Maira, Tasman).—4° 32′ S, 159° 25′ E.

ONTONG JAVA (Lord Howe Atoll, Liuinuwu).—5° 25′ S, 159° 30′ E.

PAVUVO.—9° 04′ S, 159° 08′ E.

RAMOS.—8° 16′ S, 160° 11′ E.

RENNELL.—11° 38′ S, 160° 14′ E. This island, of limestone (coral) origin, along with Bellona, is nearly 100 miles southwest of any other member of the Solomons and has been regarded, because of this distance, as an oceanic island instead of a continental island. It is about 50 miles long (east-west) and nine miles wide (north-south); its highest elevation is 500 feet.

ROVIANA (Rendova, Rovianna, Rubiana).—8° 21′ S, 157° 20′ E.

RUSSELL.—9° 04′ S, 159° 12′ E.

SAN CRISTOBAL (San Christoval, Bauro, Makira, Arussi).—11° 33′ S, 161° 43′ E. This island is composed mostly of ancient volcanic rock, has a maximum elevation of 4100 feet, is nearly 70 miles long (northwest to southeast) and 24 miles wide, and supports a dense rain forest.

SANTA YSABEL (George, Ysabel, San Isabel, Isbel, Mahaga).—8° 00′ S, 159° 07′ E. Santa Ysabel is a long (90 miles from northwest to southeast), narrow (19 miles at the widest spot), forested island, consisting of a single chain of volcanic mountains. The numerous bays and mouths of rivers provide excellent anchorages. Collecting was at Tatamba approximately two miles south of Tanambuli where the considerable area of forest was dense and bamboo thickets were abundant.

SAVO (Savu).—9° 08′ S, 159° 49′ E.

SHORTLAND.—7° 03′ S, 155° 47′ E.

SIKAIANA (Stewart).—8° 22′ S, 162° 44′ E.

SIMBO (Narovo, Naorovo, Naravo, Navoro, Sembo).—8° 16′ S, 156° 31′ E.

STIRLING.—7° 25′ S, 155° 35′ E.

TANABULI (Tanambuli, Tunnibili, Tunnibilis, Tunnibul, Tunnivula).—8° 24′ S, 159° 35′ E.

TAUU (Marqueen, Mortlock).—4° 48′ S, 157° 32′ E.

TELIPARI.—8° 15′ S, 157° 32′ E.

UGI.—10° 14′ S, 161° 44′ E.

VANGUNO (Vangunu).—8° 39′ S, 158° 00′ E.

VELLA LAVELLA.—7° 43′ S, 156° 40′ E. The coastline is rugged and indented by numerous small bays. Some peaks are 3000 feet high. The southeastern half of Vella Lavella is said to consist of uplifted coral, and to be thickly planted to coconut palms. The native population is concentrated here.

The northwestern half of the island is rain forest and is nearly uninhabited. Most of the collecting was at Pusisama, on the southern beach and on Ulo Crater, an extinct volcano at the middle of the island.

YANNTA.—10° 20′ S, 161° 20′ E.

METHODS AND MATERIALS

The phylogenetic arrangement and nomenclature in the text beyond are mainly that of Laurie and Hill (1954). The synonymies for accounts of genera are as follows: (1) first use of the generic name employed along with the original description, and (2) original proposals, in chronological order, of other generic names subsequently applied to the bat in the Solomons. The synonymies in accounts of species and subspecies are as follows: (1) first use of the accepted name, followed by its type locality, followed, in chronological order, by other references to the first name-combination, (2) first use of the name-combination employed herein (if different from the original combination), followed, in chronological order, by other references to the present name-combination, and (3) other name-combinations, in chronological order, employed for the bat in the Solomons. The word "part" is used in parentheses after a name if some specimens listed under that name are from the Solomon Islands and are referable to the species or subspecies being written about.

Unless noted otherwise, specimens listed as examined were prepared originally as museum skins with skulls. Approximately 70 per cent of bats collected in the Solomons were preserved in formalin and now are stored in alcohol. Because it was necessary to obtain dimensions and examine various morphological characteristics of skulls, many crania were extracted from bats preserved in alcohol.

Although all specimens in the Bishop Museum from the Solomon Islands have been catalogued with the prefix BBM-BSIP, catalogue numbers without prefixes in the lists of specimens examined refer to this museum. Catalogue numbers with the prefix USNM refer to specimens in the U. S. National Museum and those with the prefix AM-M refer to specimens in the Australian Museum.

Unless indicated otherwise, all measurements in this paper are in millimeters and are of adults. Cranial measurements, and external measurements of specimens stored in alcohol, were taken by me. The cranial measurements were taken with dial calipers using techniques described by Hall (1946:672-685). External measurements (except length of forearm) of specimens originally prepared as dried study skins, were transcribed from specimen labels.

Capitalized color nomenclature is from Ridgway (1912). Noncapitalized color terms are from published reports that did not use Ridgway's terminology.

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Key to Genera

1. Uropatagium lacking, or, if present, deeply indented in center; tail vertebrae absent, or if present, free 2
1′. Uropatagium present, not indented; tail vertebrae present, free or in uropatagium .... MICROCHIROPTERA 1
2(1). External tail-vertebrae lacking, or, if present, less than 3 mm long ... 3
2′. External tail-vertebrae more than 3 mm long 6
3(2). Small or medium-sized (forearm less than 50); tongue long, extensile 4
3′. Large (forearm more than 80); tongue not long and extensile 5
4(3). Uropatagium present; small claw present on second phalanx of second digit; tail short (about 3 mm) .... **Macroglossus,** p. 812
4′. Uropatagium absent; no claw on second phalanx of second digit; no tail .... **Melonycteris,** p. 814
5(3′). Entire back set with hair; wing membranes not meeting at middle of back .... **Pteropus,** p. 793
5′. Back naked; wing membranes meeting at middle of back, **Pteralopex,** p. 790
6(2′). Nostrils having definite tubelike extensions .... **Nyctimene,** p. 817
6′. Nostrils lacking tubelike extensions 7
7(6′). Forearm less than 80; large, sharp claw on second phalanx of second digit; four upper incisors .... **Rousettus,** p. 787
7′. Forearm more than 90; small, blunt claw on second phalanx of second digit; two upper incisors .... **Dobsonia,** p. 807

Family PTEROPODIDAE

Subfamily Pteropodinae

Rousettus Gray

1821. *Rousettus* Gray, London Medical Repository, 15:299, April 1.
1843. *Xantharpyia* Gray, List of species . . . British Museum, p. 37.
1852. *Cynonycteris* Peters, Reise nach Mossambique, p. 25.

The genus *Rousettus* occurs throughout the tropical regions of the Old World, and in the Solomons is readily distinguished from all other megachiropteran genera by having both a small claw on the second digit and free caudal vertebrae. The oriental species have been divided into two groups on the basis of size (Tate, 1942:344). The subspecies *Rousettus amplexicaudatus hedigeri* appears to be the sole representative of this genus in the Solomon

Islands. Prior to 1953, several workers (Thomas, 1887b:323, 1888b:475; Matschie, 1899:68; Sanborn, 1931:11) used the name *Rousettus amplexicaudatus brachyotis* for it, but Pohle (1953) suggested that the specimens from the Solomons recorded by earlier workers were *R. a. hedigeri* named by him on the basis of the specimen that he saw from Bougainville.

Rousettus amplexicaudatus

Rousettus amplexicaudatus has at least three subspecies, one of which is endemic to the Solomon Islands. The species is wide-ranging, being known from as far west as Thailand (Ellerman and Morrison-Scott, 1966:93) and as far east as the Solomons.

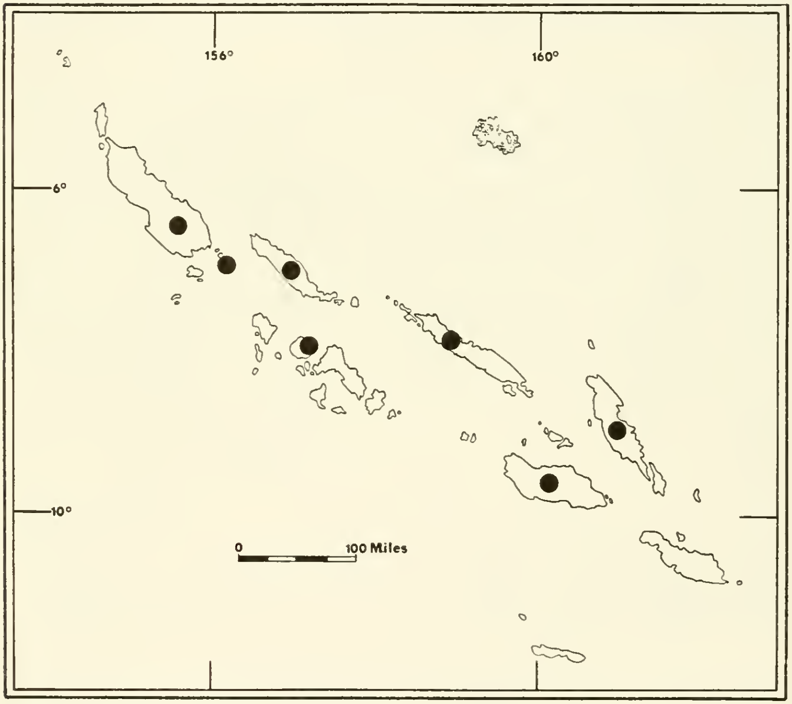

FIG. 3. Distribution of *Rousettus amplexicaudatus hedigeri.* For names of islands see Fig. 2.

Rousettus amplexicaudatus hedigeri Pohle

1953. *Rousettus amplexicaudatus hedigeri* Pohle, Z. Säugetierk., 17:127, October 27, type from Bougainville.

1887. *Cynonycteris brachyotis,* Thomas, Proc. Zool. Soc. London, p. 323, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 475, December 4, from Fauro.

1889. *Xantharpyia brachyotis,* Matschie, Die Megachiroptera . . . naturkunde, p. 68, from Guadalcanal.

1912. *Rousettus brachyotis*, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:809; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:11, February 12, from Santa Ysabel.

Specimens examined (20 males and 21 females; all in alcohol; ten crania extracted and cleaned).—Guadalcanal in May, 23863, 23915; Fauro in April, 23804-5; Malaita in June, 24079; Choiseul in March, 23563-4, 23616, 23627, 23630, 23632-3, 23642, 23658, 23663-4, 23680, 23692-3, 23713, 23722; Kolombangara in January and February, 23343, 23366, 23382-4, 23389-90, 23408-9, 23424, 23455, 23471-4, 23501.

Measurements.—Average and extreme external measurements of 13 males and 18 females are, respectively, as follows: Length of head and body, 104.4 (99-118), 108.6 (104-117); tail vertebrae, 16.8 (13-19), 17.6 (15-24); hind foot, 18.0 (16-19), 16.2 (12-18); ear, 15.9 (15-17), 15.0 (14-16); length of forearm, 70.1 (66.0-74.1), 68.1 (65.0-69.1). Average and extreme measurements of skulls of five males and five females are, respectively, as follows: Greatest length of skull, 33.2 (33.0-33.7), 31.5 (30.9-32.1); condylobasal length, 31.3 (30.9-31.9), 30.1 (29.3-30.8); palatal length, 14.0 (13.3-14.8), 13.3 (13.0-13.7); zygomatic breadth, 20.8 (19.8-21.8), 19.4 (18.7-20.8); length of maxillary tooth-row, 11.0 (10.9-11.3), 10.3 (10.1-10.6); length of mandibular tooth-row, 12.6 (12.4-12.9), 11.8 (11.7-12.2).

Remarks.—The specimens from Choiseul, Kolombangara, and Malaita islands provide new records of distribution for *Rousettus amplexicaudatus hedigeri* (Fig. 3). It was described as smaller than *R. a. brachyotis* Dobson, which is known from New Guinea, Amboina, and the Bismarck Archipelago (Pohle, 1953:127-128). Andersen (1912:809) gave the range of length of forearm in *R. a. brachyotis* as 73-81, whereas Pohle (1953:127) gave the length of forearm of the type specimen of *R. a. hedigeri* (adult male) as 67. Measurements of specimens examined by me indicate that *hedigeri* occurs throughout the Solomon Islands. Cranial measurements of my specimens and Pohle's type are less than those of *R. a. brachyotis* (see Andersen, 1912:48).

Sanborn (1931:11) noted that the forearms of three males examined by him were longer than that of a female. Mean and range for length of forearm of males and females listed herein, respectively, are 70.1 (66.0-74.1) and 68.1 (65.0-69.1). Also, each of seven cranial measurements taken by me averaged more in males than in females. Sagittal and lambdoidal crests are more prominent in males than in females.

As shown in Table 1, adult females obtained in December and January were lactating when captured whereas those obtained in March, April, and

TABLE 1. A Summary of Breeding Data for Females of *Rousettus amplexicaudatus hedigeri* Collected December to June.

MONTH	Total number collected	Number adult ♀♀ collected	Number lactating	Number of immature individuals
December	3	3	3	0
January	11	11	8	0
February	6	0	..	1
March	16	1	0	9
April	2	2	0	0
June	1	1	0	0

June were not. More than half of the individuals collected in March were immature (judging from small size, unfused epiphyses, and lack of wear on teeth). The immature individuals probably had been nursing in December and January.

Pteralopex Thomas

1888. *Pteralopex* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:155, February 1.
1762. *Pteropus* Brisson, Regnum animale . . ., ed. 2, p. 153.

Pteralopex, with one species and two subspecies, is the only megachiropteran genus endemic to the Solomons. Thomas (1888b:475) considered this unusual bat a relic, isolated from the time when pteropodids had cuspidate cheek-teeth. Although two workers (Matschie, 1899:11; Simpson, 1945:54) have synonymized *Pteralopex* with *Pteropus*, I regard *Pteralopex* as a morphologically distinct genus.

Individuals of *Pteralopex* can be distinguished from all species of *Pteropus* in the Solomon Islands by the following features: wing membranes originate along dorsal midline; braincase diminutive relative to rest of skull; sagittal crest pronounced; cheek-teeth cuspidate, broad and massive; i2 about 10 times larger than i1; upper canines with well-developed secondary cusp; postorbital process fused with zygomatic arch, forming complete bony ring around orbit.

Andersen (1909a:216; 1912:436) considered the relationships of *Pteralopex* and *Pteropus* and concluded that *Pteropus pselaphon* Lay, 1829, from the Sulphur Islands east of Taiwan, and *Pteropus samoensis* Peale, 1848, from the Samoan Islands, were the "closest" living relatives of *Pteralopex*. He stated further that *Pteralopex* "presents in fact scarcely a single character which is not either developed to a certain extent or at least distinctly foreshadowed in *Pteropus pselaphon, pilosus, tuberculatus,* or *leucopterus*." In summary, Andersen thought several species of *Pteropus* had undergone evolutionary development resembling that in *Pteralopex*, and that the latter, with its massive, cuspidate cheek-teeth, could be considered a highly modified *Pteropus*. For this hypothesis to be plausible, one must assume that the originally complex cheek-teeth of pteropodids became simple and, at least in the case of *Pteralopex*, secondarily became complex once again. According to present-day theory of evolutionary development, his hypothesis is improbable. Thomas (1888b:475) probably was correct when he considered *Pteralopex* an isolated relic.

Although *Pteralopex* usually is listed after *Pteropus* in phylogenetic arrangements (see, for example, Sanborn, 1931:21; Pohle, 1953:129; Laurie and Hill, 1954:40), I have placed *Pteralopex* before *Pteropus*.

Pteralopex atrata

Two subspecies of *Pteralopex atrata* (*P. a. atrata* and *P. a. anceps*) have been named; specimens of both are rare in museum collections. Thomas (1888*a*: 155) described adults of *atrata*. Sanborn (1931:21) examined the one additional specimen known to me and reported that it agreed with Thomas' description.

Andersen (1909*b*:266) used a subadult female ("nearly fully grown") as the holotype of *anceps*. At least five additional specimens, all adults, of *anceps* now are housed in various collections. Judging from these individuals, the holotype of *anceps* was only four-fifths grown and because he used an immature individual, Andersen's (1912:437) criteria for distinguishing the two subspecies mostly are invalid.

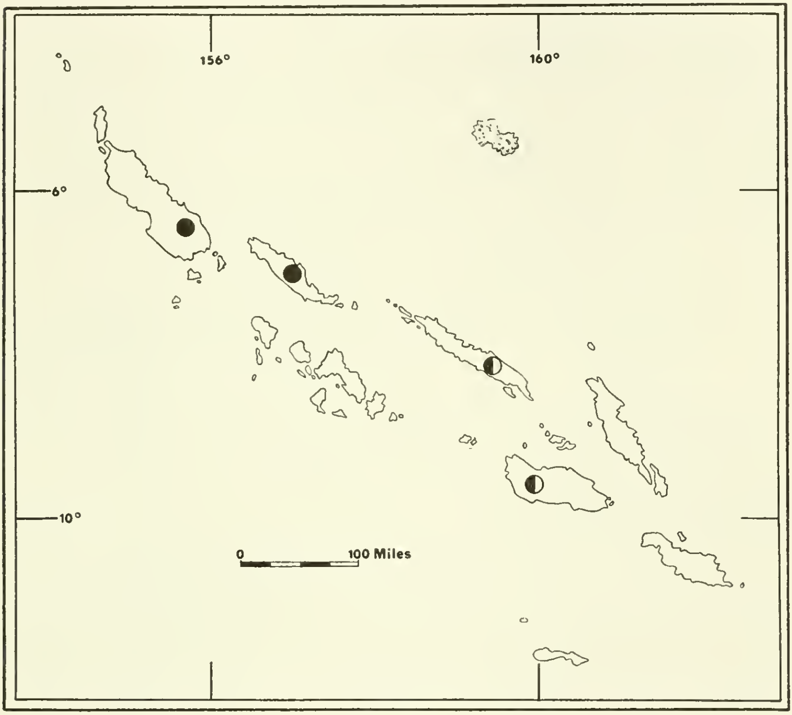

FIG. 4. Distribution of *Pteralopex atrata*; *P. atrata atrata* (◐) and *P. atrata anceps* (●). For names of islands see Fig. 2.

Key to Subspecies of *Pteralopex atrata*

1. Length of forearm 139-144 mm.; dorsal surface of distal one-fourth of tibia and entire metatarsus naked; known only from Guadalcanal and Santa Ysabel islands........................*Pteralopex atrata atrata*

1′. Length of forearm 162-166 mm.; dorsal surface of distal one-fourth of tibia and entire metatarsus furred; known only from Bougainville and Choiseul islands............................*Pteralopex atrata anceps*

Pteralopex atrata atrata Thomas

1888. *Pteralopex atrata* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:155, February, type from Guadalcanal; 1888, Thomas, Proc. Zool. Soc. London, p. 475, December 4; 1896, Heude, Mém. Hist. Nat. Emp. China, 3:179; 1897, Trouessart, Catalogus Mammalium . . ., 1:83; 1907, Miller, Bull. U. S. Nat. Mus., 57:60, June 29; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:439; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:21, February 12, from Santa Ysabel.

1954. *Pteralopex atrata atrata,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 40, June 30.

1899. *Pteropus (Pteralopex) atrata,* Matschie, Die Megachiroptera . . . naturkunde, p. 11; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 49.

Specimens examined.—None.

Remarks.—*Pteralopex atrata atrata* is known from four specimens from Guadalcanal and one from Santa Ysabel (Sanborn, 1931:21).

Sanborn (*loc. cit.*) reported that a specimen wounded at night, while feeding on young green coconuts, was the only fruit bat that attempted to attack the collectors. Troughton (1936:348) has suggested, on the basis of his experiences with *Pteropus,* that this behavior probably was a reaction from fear rather than an indication of general aggressiveness on the part of *Pteralopex.*

Pteralopex atrata anceps Andersen

1909. *Pteralopex anceps* Andersen, Ann. Mag. Nat. Hist., ser. 8, 3:266, March, type from Bougainville; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:437; 1936, Troughton, Rec. Australian Mus., 14:348, April 7; 1953, Pohle, Z. Säugetierk., 17:129, October 27.

1954. *Pteralopex atrata anceps,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 40, June 30.

Specimens examined (three males, two females; one skull-only and one in alcohol).—Choiseul in March, 23682; Bougainville in July, USNM 276973-74, USNM 276928, USNM 277112.

Measurements.—Measurements of three males and one female are, respectively, as follows: Length of head and body, 280, 271, 261, 255; hind foot, 50, 54, 52, 59; ear, 23, 23, 26, 22; length of forearm, 160, 162, 166, 171; greatest length of skull, 77.6, 77.9, 78.9, 77.0; condylobasal length, 74.3, 74.3, 75.5, 73.8; zygomatic breadth, 42.2, 45.4, 43.1, 42.6; breadth across upper canines, 18.7, 21.1, 19.0, 19.0; breadth across first upper molars, 22.2, 25.3, 22.9, 22.0; length of maxillary tooth-row, 29.3, 29.8, 28.9, 28.2; length of mandibular tooth-row, 32.8, 32.8, 32.1, 31.4.

Remarks.—Heretofore, *Pteralopex atrata anceps* was not known from Choiseul. The specimen from that island agrees well with specimens in the U. S. National Museum from Cape Torokina, Bougainville.

The type specimen of this subspecies is a subadult and is smaller than the specimens examined by me; Andersen (1912:440) gave length of forearm of the type as 137 (as opposed to 164 in adults). He (1912:438) figured the dentition of *anceps* and described the ways in which it differed from the dentition of *atrata.* Although he (1912:437) concluded that *anceps* and *atrata* represented "two stages of specialization of . . . dentition," there apparently are few, if any, dental differences between the two subspecies. Teeth of adults of *anceps* differ from teeth of the immature type of *anceps* as follows: in adults the anterior basal ledge of P4 extends onto the labial surface, whereas in the type it does not; and maxillary and mandibular teeth in adults are spaced as in the subspecies *atrata* (see Andersen, 1912:438, fig. 22) and not crowded as in the type of *anceps.* Distance between individual cheek-teeth apparently increases with growth of the cranium and mandible.

Adults of *P. a. anceps* that I examined are darker than the subadult type. The mantle in these adults is black, whereas it is seal-brown in the type (Andersen, 1912:439).

An adult female was lactating when obtained on Bougainville in July (USNM 276928).

Pteropus Brisson

1762. *Pteropus* Brisson, Regnum animale . . ., ed. 2, p. 153.

Remarks.—More species (seven) and subspecies (12) of *Pteropus* occur in the Solomon Islands than of any other chiropteran genus. Other kinds of *Pteropus*, as yet unknown, may live there.

The relationships among the species of these large fruit-eating bats, com-

Key to *Pteropus* in the Solomon Islands

1\. Premolars having distinct basal ledges; molars 2.5-4.0 wide.......2
1'. Premolars lacking definite basal ledges; molars 1.0-2.4 wide......14
2(1). Rostrum unshortened (orbit to anterior tip of nasals about one-third greatest length of skull); dorsal surface of tibiae nearly naked.....3
2'. Rostrum shortened (orbit to anterior tip of nasals less than one-third greatest length of skull); dorsal surface of tibiae usually at least partially furred........8
3(2). Forearm more than 128........4
3'. Forearm less than 128........5
4(3). Forearm about 155; venter and dorsum nearly black, mantle pale yellow........**P. tonganus geddiei,** p. 798
4'. Forearm 128-136; venter and dorsum near Mars Brown, mantle Ochraceous or Cream-Buff............**P. hypomelanus luteus,** p. 796
5(3'). Mantle dark, russet or cinnamon, not strongly contrasting with color of back....................**P. admiralitatum solomonis,** p. 796
5'. Mantle pale, Ochraceous-Buff or Cream-Buff, strongly contrasting with color of back........6
6(5'). Mantle Ochraceous-Orange to Ochraceous-Buff, hairs pale basally; forearm 108-111....................**P. admiralitatum goweri,** p. 797
6'. Mantle Ochraceous to Cream-Buff, but hairs dark brown basally; forearm 110-122........7
7(6'). Length of forearm 110-112...........**P. admiralitatum colonus,** p. 796
7'. Length of forearm about 122....................**P. howensis,** p. 797
8(2'). Forearm more than 145........9
8'. Forearm less than 144........12
9(8). Forearm more than 162........10
9'. Forearm less than 162........11
10(9). Forearm 167-173........................**P. rayneri grandis,** p. 801
10'. Forearm about 164......................**P. rayneri rubianus,** p. 802
11(9'). Flanks and lower belly brightly colored, Burnt Sienna to Sanford's Brown; forearm less than 150............**P. rayneri monoensis,** p. 803
11'. Flanks and lower belly darker, near tawny; forearm more than 150, **P. rayneri lavellanus,** p. 802
12(8'). Pelage of dorsum tricolored; rump brightly colored; forearm 139-141, **P. rayneri rayneri,** p. 800
12'. Pelage of dorsum bicolored; rump dark; forearm less than 135.....13
13(12'). Mantle tawny with some Ochraceous-Buff; forearm about 130, **P. rayneri rennelli,** p. 804
13'. Mantle russet, lacking Ochraceous-Buff; forearm about 121, **P. rayneri cognatus,** p. 803
14(1'). Forearm more than 131; dorsum Tawny Olive. . . **P. mahaganus,** p. 806
14'. Forearm less than 100; dorsum dark brown........**P. woodfordi,** p. 804

monly termed "flying foxes," are obscure and the genus is in need of revision. The basic, definitive work is still that of Andersen (1912). Tate (1942) and Felten (1964*a*, 1964*b*) have offered some additional remarks but groupings and suggested relationships of species of *Pteropus* almost entirely are the products of Kund Andersen. According to present-day concepts of variation and speciation, Andersen's criteria are artificial.

Basically, there are three "species-groups" of *Pteropus* in the Solomon Islands. The first is composed of species in which the rostrum is "unshortened" (its length about one third of greatest length of skull), and the cheek-teeth are of moderate size (M1 is 2.8—3.2 wide). The species are *P. hypomelanus*, *P. admiralitatum*, *P. tonganus*, and *P. howensis*. The first and second species were placed in the *Pteropus hypomelanus* group by Andersen (1912:98).

In the second group the rostrum is "shortened" (its length less than one third of greatest length of skull) and the cheek-teeth are of moderate to large size (M1 3.3-4.1 wide). *Pteropus rayneri*, endemic to the Solomons and represented there by at least seven subspecies, fits into this category.

The third group is represented by *P. mahaganus* and *P. woodfordi*. Both species are endemic to the Solomon Islands. In these species the rostrum is unshortened but the cheek-teeth are greatly reduced, especially in width (M1 is 1.0—2.2 wide). Both *P. mahaganus* and *P. woodfordi* can be included in the *Pteropus scapulatus* group of Andersen (1912:402).

Pteropus hypomelanus

Pteropus hypomelanus is a wide-ranging species of flying fox having at least seven subspecies; three occur in southeastern Asia, two on and near Celebes, and two in New Guinea and islands adjacent to the southeastern coast of New Guinea, including one island in the Solomons (Ellerman and Morrison-Scott, 1966:95; Laurie and Hill, 1954:32-33).

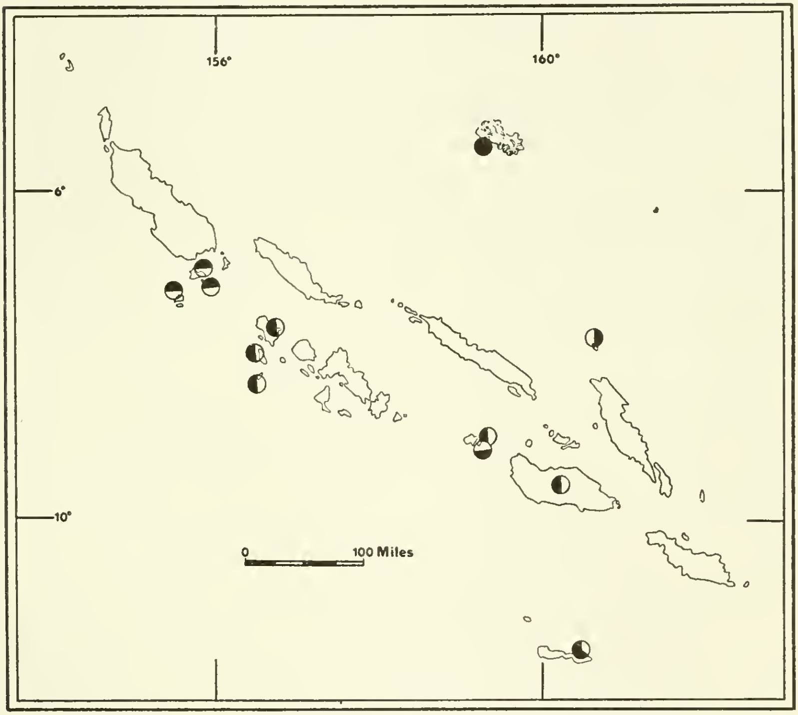

FIG. 5. Distribution of *Pteropus hypomelanus luteus* (◒), *Pteropus admiralitatum solomonis* (◐), *Pteropus a. colonus* (◓), *Pteropus a. goweri* (◑), *Pteropus tonganus geddiei* (◕), and *Pteropus howensis* (●). For names of islands see Fig. 2.

Pteropus hypomelanus luteus Andersen

1908. *Pteropus hypomelanus luteus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:362, October, type from Kiriwini Island, Trobriand Islands; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:128; 1947, Sanborn and Beecher, Jour. Mamm., 28:388, November 19, from Banika Island, Russell Islands.

Specimens examined.—None.

Remarks.—Andersen (1908:362) identified specimens of *Pteropus hypomelanus* from eastern New Guinea and three nearby islands (Conflict Islands, Trobriand Islands, and Woodlark Island) as *P. hypomelanus luteus.* Sanborn and Beecher (1947:388) identified a female from Banika Island in the Solomons as of this subspecies although this specimen was darker and had a slightly smaller skull than typical *P. hypomelanus luteus.* They noted that the pelage of the venter of the female was uniformly dark rather than the typical Ochraceous-Buff to Cream-Buff; the specimen was regarded as a dark phase of the subspecies. Although not recorded previously for *luteus,* other subspecies of *P. hypomelanus* were known in dark phase as well as pale and intermediate phases of coloration (Andersen, 1912:122). The reported occurrence of *P. h. luteus* on Banika Island extended the known geographic range about 450 miles eastward from Woodlark Island.

Pteropus admiralitatum

Three subspecies, all about the same size but differing in coloration, have been described from the Solomon Islands. *P. a. goweri* is known only from Gower (Ndai) Island, notably removed from the western chain of islands inhabited by *P. a. colonus* and *P. a. solomonis.* Only one other subspecies, from the Admiralty Islands, is known.

Pteropus admiralitatum solomonis Thomas

1904. *Pteropus solomonis* Thomas, Novit. Zool., 11:597, type from Ghizo Island; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:149; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:12, February 12, from Ronongo (Ganongga), Vella Lavella, and Narovo (Simbo) islands; 1947, Sanborn and Beecher, Jour. Mamm., 28:389, November 19, from Banika and Guadalcanal islands.

1954. *Pteropus admiralitatum solomonis,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.

Specimens examined.—None.

Remarks.—Andersen (1912:149) considered *Pteropus admiralitatum,* and especially the subspecies *P. a. solomonis,* to be the easternmost "representative" of *Pteropus hypomelanus.* In comparison with *P. hypomelanus luteus, P. a. solomonis* differs mostly in size, being much smaller (length of forearm about 110 rather than 134). It is now known that both species occur on Banika Island in the Solomons.

The subspecies *P. a. solomonis* has been recorded from a "chain" of islands that included Vella Lavella, Simbo, Ghizo, Ganongga, Banika, and Guadalcanal (see Fig. 5).

Pteropus admiralitatum colonus Andersen

1908. *Pteropus colonus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:363, October, type from Shortland Island; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:150; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:12, February 12, from Mono Island.

1954. *Pteropus admiralitatum colonus,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.

1887. *Pteropus hypomelanus* (part), Thomas, Proc. Zool. Soc. London, p. 471, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:82, from "I. Salomonis."

1899. *Pteropus* (*Spectrum*) *hypomelanus* (part), Matschie, Die Megachiroptera . . . naturkunde, p. 24.

Specimens examined.—None.

Remarks.—*Pteropus admiralitatum colonus* is the largest of the three subspecies that occur in the Solomon Islands. It closely resembles *P. hypomelanus luteus,* except in being smaller throughout (see Andersen, 1912:151-152, for measurements) and darker on the underparts.

This bat has been found in a group of small islands (Alu, Mono, and Shortland) about 30 miles south of Bougainville. Because of this proximity and because yet another subspecies of this species occurs northward of Bougainville, it is interesting that neither Troughton (1936) nor Pohle (1953) included the species in their faunal lists for Bougainville.

Andersen (1912:152) indicated that the M1 in *P. admiralitatum colonus* is smaller than in *P. a. solomonis,* the subspecies found in islands to the southeast (4.4-4.5 and 5.2, respectively), but Sanborn (1931:13) studied specimens of these two subspecies that overlapped in size of M1.

Pteropus admiralitatum goweri Tate

1934. *Pteropus goweri* Tate, Amer. Mus. Novit., 718:1, May 4, type from Gower (Ndai) Island.

1954. *Pteropus admiralitatum goweri,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 33, June 30.

Specimens examined.—None.

Remarks.—*Pteropus admiralitatum goweri* was described from six specimens collected in 1930 by the Whitney South Sea Expedition (Tate, 1934:1). This subspecies closely resembles the other two subspecies of *P. admiralitatum* (*colonus* and *solomonis*) found in the Solomon Islands. Color and length of forearm (see key on p. 793) seem to be the only reliable criteria for distinguishing between these subspecies. The longitude of Gower Island, 160° 34′ E, was incorrectly listed in Laurie and Hill (1954:152) as 159° 34′ E.

Pteropus howensis Troughton

1931. *Pteropus howensis* Troughton, Proc. Linn. Soc. New South Wales, 56:204, June 24, type from Lord Howe Islands (Ontong Java); 1950, Sanborn and Nicholson, Fieldiana:Zool., 31:329, August 31.

Specimens examined (one male, three females, and two sex unknown; two embryos in alcohol).—Liuniuwu, Lord Howe Islands (Ontong Java) in August, USNM 278703-6, USNM 279715-6.

Measurements.—Average and extreme measurements of one male and three females are as follows: Length of head and body, 185.2 (176-196); hind foot, 34.5 (33-36); ear, 21.5 (21-23); forearm not measured [broken in all specimens examined]. Cranial measurements of a male and a female are, respectively, as follows: Greatest length of skull, 55.3, 53.8; condylobasal length, 54.2, 52.8; palatal length, 26.7, 26.0; zygomatic breadth, 30.6, 29.9; breadth of braincase, 19.9, 19.2; breadth across first upper molars, 14.3, 14.3; length of maxillary tooth-row, 20.7, 19.6; length of mandibular tooth-row, 23.1, ----.

Remarks.—Apparently *Pteropus howensis* is confined to Ontong Java (Lord Howe Islands) located northeastward of the main body of islands that constitute the Solomon Archipelago (see Fig. 5). According to A. J. Nicholson, who collected the specimens listed above, *P. howensis* is not abundant in Ontong Java. He related this circumstance to the fact that these small islands are nothing more than parts of a coral atoll used almost entirely for the production of coconuts (see Sanborn and Nicholson, 1950:329).

Specimens of *Pteropus howensis* deposited in the U. S. National Museum agree well in most ways with the original description of the species by Troughton (1931:204-205). Slight variation in color is evident; in two specimens, the mantle, just posterior to the ears, is Ochraceous-Buff.

The relationship of this species to other kinds of *Pteropus* known from Melanesia is not clear. Troughton (1931:204, 206) compared *P. howensis* with *P. hypomelanus* and *P. admiralitatum* and found that it resembled each of them. Tate (1934:2) noted that the skull of *P. admiralitatum goweri* was similar to that of *P. howensis* in structure. The latter species is, however, larger (length of forearm 122 according to Troughton, 1931:205) than any subspecies of *P. admiralitatum* (length of forearm 108-112). Also, the cheek-teeth of *P. howensis* that I have studied are relatively larger than those of either *P. hypomelanus* or *P. admiralitatum*. Furthermore, in *P. howensis* there is a small but distinct cusp located medio-posteriorly on P4 (most noticeable in young individuals) that is more reduced or undeveloped in specimens of the other two species. Cheek-teeth of *P. howensis* resemble those in a dull-colored specimen of *P. tonganus* from Fiji Island with which I compared the specimens listed above.

Weights and crown-rump lengths of the two embryos (in an advanced stage of development) examined were 20 and 29 grams and 43 and 51 mm. (apparently these are the specimens listed by Sanborn and Nicholson, 1950:329).

Pteropus tonganus

Pteropus tonganus has at least three subspecies, one of which has been recorded from the Solomons. The species ranges from a small island off the eastern coast of New Guinea, where there is an endemic subspecies, eastward to Tonga and the New Hebrides (Laurie and Hill, 1954:33-34). Felten (1964*a*) recently has reported on the species in the New Hebrides.

Pteropus tonganus geddiei MacGillivary

1860. *Pteropus geddiei* MacGillivary, Zoologist, 18:7134, September, type from Aneitum Island, New Hebrides; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:189; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:13, February 12, from Rennell Island in the Solomons.

1914. *Pteropus tonganus geddiei*, Revilliod, *in* Sarasin and Roux, Nova Caledonia (A), 1:341; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 34, June 30.

Specimens examined.—None.

Remarks.—*Pteropus tonganus geddiei*, as far as is known, is the widest ranging subspecies of this genus. It is the only megachiropteran in the Solomon Islands having affinities with bats to the southeast (the New Hebrides, Santa

Cruz Islands, Samoan Islands and Fiji Islands) rather than with those to the west (New Guinea). The subspecies *P. tonganus geddiei,* which ranges from the Solomons to the New Hebrides (about 500 miles straight-line distance), is said to be remarkably uniform throughout its range. Sanborn (1931:14) compared color and size in specimens from the Solomon Islands and the New Hebrides and found little variation. Another subspecies, *P. t. bascilicus* Thomas 1915, apparently closely related to *geddiei,* is known from Dampier [= Kar-kar] Island off the northeastern coast of New Guinea and therefore farther westward from the New Hebrides than are the Solomon Islands. Additional remarks on the distribution of this species are in the section on Zoogeography and Speciation.

Pteropus rayneri

Pteropus rayneri is endemic to the Solomon Islands. It is divisible into seven subspecies (see Fig. 6), which, excepting *P. r. rennelli* and *P. r. cognatus,* are strikingly colored—the mantle, back, and rump being of different colors. Differences in color and size provide characters differentiating the subspecies (see key, p. 793). Recorded lengths of forearms do not overlap between any two subspecies. *P. r. grandis,* northernmost in distribution, has the longest (about 170) forearm and *P. r. cognatus,* known from two of the southernmost islands, has the shortest (about 121).

Adult males of *Pteropus rayneri* have well-developed tufts of hair on each

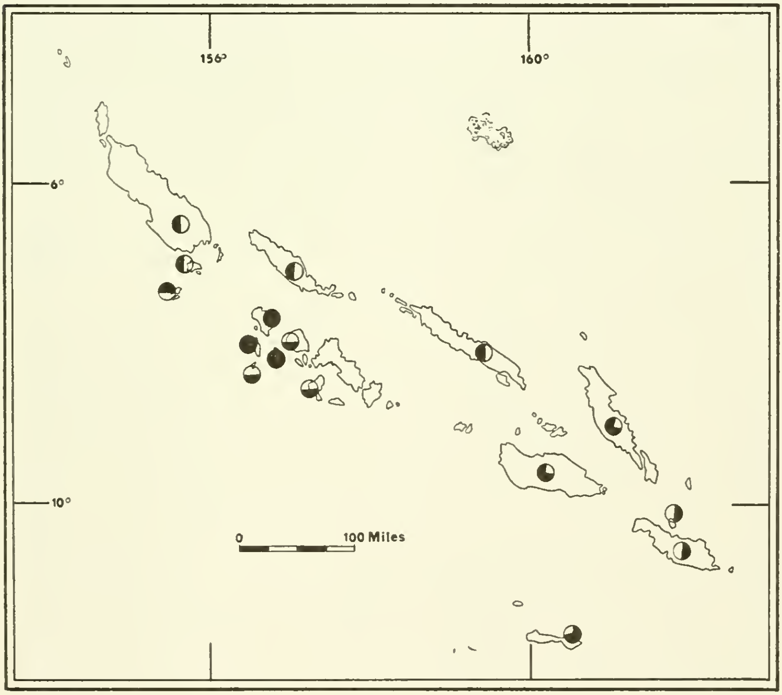

FIG. 6. Distribution of *Pteropus rayneri: P. r. rayneri* (◕); *P. r. grandis* (◐); *P. r. lavellanus* (●); *P. r. monoensis* (◓); *P. r. rubianus* (◒); *P. r. cognatus* (◑); *P. r. rennelli* (◕). For names of islands see Fig. 2.

side of the neck where a gland is located (see Andersen, 1912:259). Apparently these glands are not present in females as none were found in specimens studied by me or those reported by Sanborn (1931:16). Evidently, these glands are associated with sexual maturity in males because neither Sanborn nor I found them in subadult males.

Pteropus rayneri rayneri Gray

1870. *Pteropus rayneri* (part) Gray, Catalogue of monkeys, lemurs and fruit-eating bats . . . British Museum, p. 108, cotypes from Guadalcanal; 1878, Dobson, Catalogue of the Chiroptera . . . British Museum, p. 33; 1879, Trouessart, Rev. Mag. Zool., 6:204; 1879, Trouessart, Ann. Sci. Nat. Zool., 8:16; 1887, Thomas, Proc. Zool. Soc. London, p. 322, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 472, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:78; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, p. 254; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from Guadalcanal and Malaita.

1954. *Pteropus rayneri rayneri,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

1899. *Pteropus* (*Spectrum*) *rayneri* (part), Matschie, Die Megachiroptera . . . naturkunde, p. 22; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 51.

Specimens examined (four males and one female; one embryo in alcohol).—Guadalcanal in July and November, USNM 278700-02, USNM 278142, USNM 278714.

Measurements.—Measurements of three males and one female are, respectively, as follows: Length of head and body, —, 210, 214, 215; hind foot —, 33, 39, 42; ear, —, 23, 23, 23; length of forearm, —, 138, 136, 134; greatest length of skull, 61.5, 59.2, 61.6, 61.2; condylobasal length, 61.4, 58.2, 60.3, 60.0; zygomatic breadth, 36.6, 35.3, 35.4, 36.5; breadth of braincase, 23.7, 22.5, 22.6, 24.1; breadth across first upper molars, —, 16.9, 16.7, 16.8; width of M1, 3.4, 3.5, 3.5, 3.5; length of maxillary tooth-row, 22.4, 22.1, 23.6, 23.2; length of mandibular tooth-row, 26.4, 25.5, 25.9, 25.6.

Remarks.—*Pteropus rayneri* was named on the basis of two specimens (cotypes) obtained on Guadalcanal and listed as "male" and "female"; according to Andersen (1912:254), however, both are females.

P. r. rayneri is known from Guadalcanal and Malaita (see Fig. 6), and is of almost the same size as *P. r. cognatus,* which is known from San Cristobal and Ugi, only about 40 miles to the southeast. In the latter subspecies the back and rump are the same color (Prouts Brown), whereas in *P. r. rayneri* the rump is brightly colored and therefore contrasts strongly with the dark brown back. A specimen of *rayneri* from Malaita was reported by Sanborn (1931:15) as unusually small and having a dark-colored rump patch. In the specimens examined from Guadalcanal, there is noticeable variation in color of the mantle that does not seem related to age or sex. In two specimens (adult male and female) the mantle is Cinnamon-Rufous tinged with Russet, strongly contrasting with the crown, which is Ochraceous-Tawny and has scattered silvery hairs. Another specimen has a darker mantle (near Chestnut-Brown) and a crown of about the same color, but with a few scattered Ochraceous-Tawny hairs.

The skull of one adult male bears an extra peglike tooth posterior to M3 on the right side.

An embryo, in an advanced stage of development, in the collection of the U. S. National Museum, measures: Length of head and body, 98; hind foot, 30; ear, 8.5; length of forearm, 48 (this may be the same specimen listed by Sanborn and Nicholson, 1950:329).

Pteropus rayneri grandis Thomas

1887. *Pteropus grandis* Thomas, Ann. Mag. Nat. Hist., ser. 5, 19:147, March, type from Shortland; 1887, Thomas, Proc. Zool. Soc. London, p. 320, March 15, from Alu and Shortland; 1897, Trouessart, Catalogus Mammalium . . ., 1:80, from "I. Salomonis"; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 15; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 49; 1907, Miller, Bull. U. S. Nat. Mus., 57:58, June 29; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:259, from Bougainville; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:16, February 12, from Choiseul, and Santa Ysabel; 1936, Troughton, Rec. Australian Mus., 19:348, April 7; 1953, Pohle, Z. Säugetierk., 17:128, October 27.

1954. *Pteropus rayneri grandis,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

Specimens examined (six males and 10 females; five in alcohol).—Choiseul in March, 23580, 23644, 23593; Bougainville in July, August, September, and October, USNM 276926-7, USNM 276968, USNM 277091-9.

Measurements.—Average and extreme measurements of four males and seven females are as follows: Length of head and body, 281 (260-302); hind foot, 52.3 (50-58); ear, 33.1 (31-37); length of forearm, 173 (168-180). Average and extreme measurements of skulls of three males and six females are as follows: Greatest length of skull, 73.7 (71.3-77.7); condylobasal length, 73.1 (70.5-77.4); zygomatic breadth, 40 (36.4-41.5); breadth across first-upper molars, 20.9 (18.3-22.1); length of maxillary tooth-row, 28.1 (26.9-29.9); length of mandibular tooth-row, 31.8 (29.7-32.7).

Remarks.—*Pteropus rayneri grandis* is the largest subspecies of the species. It is also the widest ranging subspecies, being found on six islands (see Fig. 6).

Although the specimens listed above agree well with descriptions of color given by Thomas (1887*a*:147) and Andersen (1912:259, 263-264), some individual variation is noticeable. In bats not yet fully grown (judging from small size, unfused epiphyses, and lack of wear on teeth), numerous scattered hairs on the sides of the face and crown are buffy. In adults the face and crown are blackish. With regard to individual variation in color of mantle and rump patch, specimens with the following combinations were noted (1) mantle Brick Red, rump patch bright, basal three-quarters of hairs white, tips Warm Buff (2) mantle darker, near Hessian Brown, rump patch dark, Chestnut along edges, center Ochraceous-Tawny (3) mantle Brick Red, rump patch intermediate between the two other types. Size of rump patch also is variable. In some specimens it extends onto the upper parts of the thighs whereas in other specimens it does not.

Sanborn (1931:16) reported an extra tooth, behind the last lower molar, in a specimen from Choiseul. In one of three specimens in the Bishop Museum, m3 is lacking. Judging from Troughton's (1936:346) remarks, size of individuals varies considerably. Specimens that he examined from Bougainville had longer forearms (up to 177) and larger hind feet (54-57) than those examined by me from Choiseul. On the other hand, specimens listed above from Bougainville agree well with those from Choiseul. In many specimens in the U. S. National Museum, length of the right- and left-forearm differ. For example, in No. 276926 the right forearm measures 180 whereas the left is 174; in No. 277098 the right is 172 and the left is 167. Troughton (1936:346) gave standard ear measurement in *P. r. grandis* as ranging from 29.5 to 31.5. Ears of specimens that I examined varied from 31.0 to 37.0.

Pteropus rayneri rubianus Andersen

1908. *Pteropus rubianus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:366, October, type from Rubiana; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:255; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from Narovo (Simbo).

1954. *Pteropus rayneri rubianus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

1888. *Pteropus grandis* (part), Thomas, Proc. Zool. Soc. London, p. 470, December 4, from Rubiana; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 15; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 49.

Specimens examined (two males and one female).—Kolombangara, in February, 23458-60.

Measurements.—Measurements of two males and one female are, respectively, as follows: Length of head and body, 253, 265, 251; hind foot, 53, 50, 50; ear, 30, 31, 32; length of forearm, 158, 161, 160; greatest length of skull, 70.2, 67.4, —; condylobasal length, 67.0, —, 68.4; zygomatic breadth, 40.0, 39.4, 40.7; breadth across first upper molars, 19.4, 20.4, 19.9; length of mandible, 53.9, 49.4, 51.3.

Remarks.—Kolombangara Island is a new locality for *Pteropus rayneri rubianus;* heretofore this subspecies was known only from Rubiana and Narovo islands (Andersen, 1908:366; Sanborn, 1931:15). The coloration of a specimen from Narovo Island was described as between that of *P. r. rubianus* and *P. r. lavellanus.* Sanborn (1931:16) allocated it to the subspecies *rubianus* on the basis of length of forearm.

Andersen's descriptions (1908:366; 1912:256) of *rubianus* were of a specimen stored in alcohol. Coloration of the museum skins examined by me is as follows: Dorsum from shoulders to rump near Vandyke Brown; crown and mantle Brick Red; face close to Mummy Brown; rump patch and thighs close to Warm Buff, strongly contrasting with back and mantle; base of hairs dark, Seal Brown; venter dark; chest about same as back but paler laterally (to Ochraceous Tawny); throat Brick Red.

Pteropus rayneri lavellanus Andersen

1908. *Pteropus lavellanus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:366, October, type from Vella Lavella; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:259; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:16, February 12, from Ghizo and Ronongo.

1954. *Pteropus rayneri lavellanus*, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 36, June 30.

Specimens examined (one male and one female).—Vella Lavella in November, 23192, 23142.

Measurements.—Measurements of a male and a female are, respectively, as follows: Length of head and body, 286, 282; hind foot, 55, 56; ear, 30, 30;

length of forearm, 156, 155; greatest length of skull, 72.9, 67.6; condylobasal length, 71.8, 64.2; zygomatic breadth, 38.4, 37.9; breadth across first upper molars, 19.9, 19.8; length of mandible, 54.6, 50.8.

Remarks.—Pteropus rayneri lavellanus inhabits islands geographically near those from which *P. r. rubianus* is known (see Fig. 6) and in most respects the two subspecies closely resemble each other. *P. r. lavellanus* is slightly the smaller (average length of forearm about 156 instead of 160) and darker. A bat from Narovo [Simbo] Island, only a few miles from Vella Lavella, identified by Sanborn (1931:16) on basis of its size as *P. r. rubianus*, resembled the subspecies *lavellanus* in color and probably represents an intergrade between the two populations.

The color of *P. r. lavellanus* is close to that of *P. r. rubianus* except that the crown, mantle, and foreneck are near Chestnut-Brown, the basal portions of hair black, and the fur of the venter, from sternum to pectoral region, is dark, almost black (compare with description of *P. r. rubianus* under account of that subspecies).

Measurements of the male examined are greater than those of the female studied. Andersen (1912:259) noted that the canine teeth are heavier in males than in females.

Pteropus rayneri monoensis Lawrence

1945. *Pteropus rayneri monoensis* Lawrence, Proc. New England Zool. Club, 23:63, March 26, type from Mono (Treasury); 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 36, June 30.

Specimens examined.—None.

Remarks.—Pteropus rayneri monoensis is the most recently described subspecies of *P. rayneri.* Lawrence (1945:63) judged that in most ways this bat is intermediate between *P. r. grandis* and *P. r. lavellanus.* Coloration of *monoensis* indicates affinity with the former, whereas length of forearm (145-148) approaches that in the latter. The small skull, narrow palate, and whitish rump patch of *monoensis* are differences that distinguish it from *grandis* and *lavellanus.* The relatively isolated position of Mono Island may have been important in establishment of the distinctive features of this bat.

Lawrence (1945:65) quoted a collector as stating: "They [individuals of *P. r. monoensis*] rest quietly during the day in the tops of heavy-leaved, tall jungle trees, and start flying about dusk, looking for feeding spots. There is usually quite a flight for fifteen to twenty minutes at twilight. . . ."

No additional specimens of this subspecies have been collected on small adjacent islands and *monoensis* may therefore be confined to Mono Island.

Pteropus rayneri cognatus Andersen

1908. *Pteropus cognatus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 2:365, October 1, type from San Cristobal; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:251; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:15, February 12, from San Cristobal and Ugi; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

1962. *Pteropus rayneri cognatus*, Hill, The natural history of Rennell Island, British Solomon Islands, 4:9, February.

1870. *Pteropus rayneri* (part), Gray, Catalogue of monkeys, lemurs and fruit-eating bats . . . British Museum, p. 108, from San Cristobal; 1878, Dobson, Catalogue of the Chiroptera . . . British Museum, p. 33.

1904. *Pteropus* (*Spectrum*) *rayneri* (part), Trouessart, Catalogus Mammalium . . ., Suppl., p. 51.

Specimens examined.—None.

Remarks.—Specimens of *Pteropus rayneri cognatus* first were reported under the name *Pteropus rayneri* based on three specimens (one from San Cristobal and two from Guadalcanal). Because the description was based mostly on the two specimens from Guadalcanal, the name *rayneri* is applicable to the bats from that island. Andersen (1908:365) thought that specimens that he studied, from San Cristobal, were specifically distinct from *P. rayneri* and he proposed the name *Pteropus cognatus* for them. Later, Hill (1962:9) reduced *cognatus* to subspecific status under *P. rayneri.*

Presently *P. r. cognatus* is known only from San Cristobal and the small adjacent island of Ugi (see Fig. 6).

Pteropus rayneri rennelli Troughton

1929. *Pteropus rennelli* Troughton, Rec. Australian Mus., 17:193, September 4, type from Rennell Island; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 35, June 30.

1962. *Pteropus rayneri rennelli,* Hill, The natural history of Rennell Island, British Solomon Islands, 4:7, February.

Specimens examined.—None.

Remarks.—Until recently, *Pteropus rayneri rennelli* was known from but a single specimen. Hill (1962:7) reported two additional specimens and pointed out that *P. r. cognatus* and *P. r. rennelli* probably represent the extremes of an east-west cline in size. *P. r. rennelli* and *P. r. cognatus* differ from other subspecies of the species in lacking tricolored pelage on the dorsum, but their short rostrum clearly indicates affinity with other members of this complex group in the Solomon Islands (Hill, 1962:8).

The relationship of the subspecies *rennelli* and *cognatus* is close, both geographically and genetically. Longer forearm, longer metacarpals, and longer mandibular tooth-row serve to differentiate *rennelli* from *cognatus.*

Pteropus woodfordi Thomas

1888. *Pteropus woodfordi* Thomas, Ann. Mag. Nat. Hist., ser. 6, 1:156, February, type from Guadalcanal; 1888, Thomas, Proc. Zool. Soc. London, p. 472, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:78; 1907, Elliot, Field Columbian Mus., Zool. Ser., 8:491; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:410, from New Georgia and Guadalcanal; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:19, February 12, from Kolombangara; 1947, Sanborn and Beecher, Jour. Mamm., 28: 389, November 19, from Banika and Guadalcanal; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 39, June 30.

1899. *Pteropus* (*Sericonycteris*) *woodfordi,* Matschie, Die Megachiroptera . . . naturkunde, p. 83; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 54.

1945. *Pteropus austini* Lawrence, Proc. New England Zool. Club, 23:59, March 26, from Florida.

Specimens examined (four males and three females; five in alcohol and two skin-onlys).—Fauro, in April, 23727, 23790; Guadalcanal in May and June, 23823, 23931; Pavuvo (Russell Islands) in August and October, USNM 277887, USNM 283872-3.

Measurements.—External measurements of two males and two females are, respectively, as follows: Length of head and body, 152, 128, 132, 155; hind foot, 29, 26, 31, 28; ear, 16, 14, 14, 17; length of forearm, 79, 76, 86, 90.

Remarks.—Heretofore, *Pteropus woodfordi* was known from New Georgia, Guadalcanal, Kolombangara, and Banika (see Fig. 7); specimens from Fauro and Pavuvo islands, listed above, provide new northern localities of record for this species.

Judging by small size and unfused epiphyses, a bat obtained in April and another obtained in June are subadults. Specimens of adults, examined by me, agree well with the descriptions of *P. woodfordi* by Thomas (1888*a*:156) and Andersen (1912:407-409), but are slightly smaller than specimens listed by Sanborn and Beecher (1947:389). Color of pelage in this species seems to vary. Adults seen have a pale head and mantle, contrasting strongly with the dark back. Andersen (1912:409) and Lawrence (1945:61) discussed individuals that had scattered silvery hairs mixed with dark fur dorsally and darker mantles that did not contrast noticeably with the rest of the dorsum.

Lawrence (1945:389) named *Pteropus austini* as a new species closely related to *P. woodfordi* and other species of the *P. scapulatus* group of Andersen (1912:402) and Tate (1942:336). Sanborn and Beecher (1947:389), studied a series of *P. woodfordi* from Banika and Guadalcanal and found that skulls of two subadults agreed well with cranial characteristics ascribed to *P. austini,* which was based on two subadults. Lawrence (1945:61) stated also that "the interfemoral membrane is entirely absent medially in *austini,* while in *woodfordi* it is present as a barely discernible ridge 8 mm. wide." Andersen (1912: 408) had earlier reported that in the type of *woodfordi* the interfemoral membrane was "undeveloped in [the] centre." In 13 adults (in alcohol) studied by Sanborn and Beecher (1947:389), as well as in adults examined by me, the uropatagium is not present. In size, however, these specimens agree with dimensions given for *woodfordi* by Thomas (1888*a*:156) and Andersen (1912:410); for example, length of forearm is 93-99. According to Lawrence (1945:59) *austini,* in which the interfemoral membrane is lacking, is smaller than *woodfordi* and has a forearm of about 84. In two juveniles of *P. woodfordi* in the U. S. National Museum, the medially-developed interfemoral membrane is about 7 wide. One specimen has small but distinct calcars whereas the other (slightly larger) apparently lacks calcars. This suggests individual variation in the presence or absence, as well as in the size, of the uropatagium in *Pteropus woodfordi.*

Sanborn and Beecher (1947:389) decided that "until fully adult specimens showing the characters of *austini* are available, it best be considered a synonym of *woodfordi.*" For the following reasons I agree with these authors: (1) *austini* is known from only two specimens, both of which are apparently subadults; (2) *austini* is reported to have a forearm 84 long and no interfemoral membrane, whereas *woodfordi* has a forearm about 96 long and an interfemoral membrane that is only slightly developed; (3) specimens that agree in size and cranial characters with the type of *woodfordi* but that lack an interfemoral membrane have been obtained; and (4) skulls of subadults of *woodfordi* agree with the description of skulls of *austini.*

Sanborn (1931:19) reported that specimens of *Pteropus woodfordi* were obtained at night, while feeding on young green coconuts. Lawrence (1945: 62) reported that in the late afternoon a collector found individuals of *austini* [= *woodfordi*] in the fronds of a coconut tree, apparently feeding on pollen shoots. Sanborn and Beecher (1947:388) have reported malaria (*Plasmodium*) in *P. woodfordi* obtained on Guadalcanal. They suggested that malaria might have rendered one individual helpless because when it was found, on the ground, no wounds were evident and parasites were present in the blood.

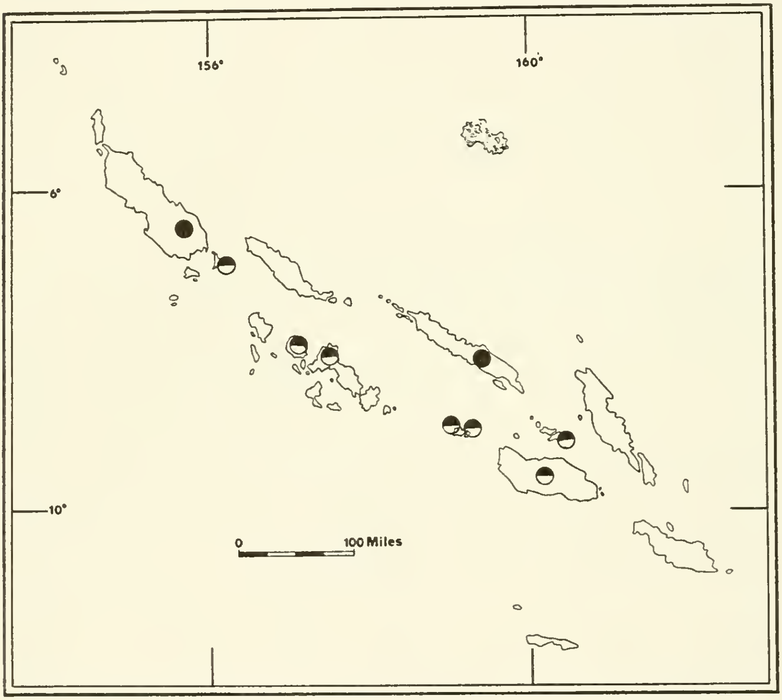

FIG. 7. Distribution of *Pteropus woodfordi* (◓) and *P. mahaganus* (●). For names of islands see Fig. 2.

Pteropus mahaganus Sanborn

1931. *Pteropus mahaganus* Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:19, February 12, type from Santa Ysabel, also reported from Bougainville; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 39, June 30.

Specimens examined (one male and two females; one in alcohol).—Bougainville, in August and October, USNM 276972, USNM 277104-5.

Measurements.—Measurements of one male and two females are, respectively, as follows: Length of head and body, 180, 204, 198; hind foot, 42, 38, 44; ear, 25, 23, 22; length of forearm, 134, 138, 140. Measurements of the skull of the male and one female are, respectively, as follows: Greatest length of skull, 52.5, 55.8; condylobasal length, 50.9, 54.3; palatal length, 24.1, 26.0;

zygomatic breadth, 28.9, 32.5; breadth across first upper molars, 14.4, 15.0; width of M1, 2.2, 2.2; length of maxillary tooth-row, 17.4, 18.4; length of mandibular tooth-row, 20.1, 21.4.

Remarks.—Sanborn (1931:19-21) described *Pteropus mahaganus* on basis of six specimens, five from Santa Ysabel and one from Bougainville. The latter was in poor condition and only provisionally allocated to this species. The specimens examined by me (listed above) confirm the occurrence of *P. mahaganus* on Bougainville.

Sanborn (1931:20) described *mahaganus* as "similar to and about the size of [*Pteropus scapulatus*] from Australia, but lighter in color," and considered it, along with *P. woodfordi*, a member of the *Pteropus scapulatus* group of Andersen (1912:402) and Tate (1942:336). I would judge, however, that *P. mahaganus* and *P. woodfordi* are much more closely related to one another than to *P. scapulatus* of Australia. The only significant characteristic that the latter has in common with the two species from the Solomons is small cheek-teeth. In fact, teeth of *scapulatus* are relatively smaller than teeth of either *mahaganus* or *woodfordi*. Also, in *scapulatus* the upper canines are widely separated due to lateral expansion of the palate at that point, whereas in *mahaganus* and *woodfordi* the width across the upper canines is relatively much less.

Dobsonia Palmer

1898. *Dobsonia* Palmer, Proc. Biol. Soc. Washington, 12:114, April 30.
1810. *Cephalotes* (part) É. Geoffroy, Ann. du Mus. d' Hist. Nat., 15:104.

Dobsonia, a genus of large to medium-sized fruit bats, occurring from Celebes to the Solomon Islands, contains at least nine species. One species and its two subspecies are endemic to the Solomons.

Dobsonia differs from all other genera of megachiropteran bats in the Solomons by combining absence of a small claw on the second digit and presence of external tail vertebrae.

The cranium of *Dobsonia* resembles, in some ways, the cranium of *Rousettus* as well as that of *Pteropus*. Even so, in *Dobsonia* the rostrum is shorter and the cheek-teeth, especially in the upper jaw, are more crowded. The anterior part of the mandible is narrow and the lower incisors are diminutive and often concealed by the flesh of the gum.

Dobsonia inermis

In a review of the genus *Dobsonia*, Andersen (1909*c*:532) named and described *D. inermis* and *D. nesea* from the Solomons. Specimens of *Dobsonia inermis* from San Cristobal and Ugi were said to differ from specimens of *D. nesea* from Alu, Shortland, and Rubiana in having perpendicular as opposed to anteriorly slanted upper canines. Andersen (1909*c*:532) reported that the two species were of ". . . the same general size." Troughton (1936:348-349) studied specimens of *Dobsonia* from Bougainville and Santa Ysabel and, because of individual variation in proclivity of the upper canines, concluded that *D. nesea* was conspecific with *D. inermis*. He (p. 349) noted that the ears were shorter in *inermis* than in *nesea*, but the size of teeth showed insular variation and a ". . . confusing amount of intergradation . . . [that obscures] . . . diagnostic importance."

Specimens of *Dobsonia* from Choiseul are smaller (externally and cranially) than those from Alu, Shortland, Rubiana, Bougainville, Fauro, Vella Lavella, Guadalcanal, Florida, Ugi, San Cristobal, and Rennell. Specimens from Santa Ysabel (see Fig. 8) are intermediate in size between those from Choiseul and the other islands listed. Judging from available specimens, two subspecies of *Dobsonia inermis* occur in the Solomons. Specimens from Choiseul (see A, Fig. 8), which are smaller than those from other islands, represent one subspecies (heretofore unrecognized), whereas specimens from other islands (except Santa Ysabel) represent a second subspecies. Specimens from Santa Ysabel are slightly larger than those on Choiseul and are regarded as intergrades between the two subspecies. Specimens from Rennell, Ugi, San Cristobal, Florida, Fauro, and Guadalcanal are slightly smaller than those from Bougainville, Vella Lavella, Shortland, and Rubiana, but the differences are not great enough to warrant recognition of two subspecies. Therefore, the subspecific name *nesea* is arranged as a synonym of *inermis,* which has priority, and the latter name is used for specimens of *Dobsonia inermis* from the Solomon islands other than Choiseul and Santa Ysabel. Additional remarks on the distribution of this species are in the section on Zoogeography and Speciation.

Pohle (1953:130) suggested that *Dobsonia inermis* (as well as *D. crenulata* and *D. praedatrix*) is conspecific with *D. viridis,* but Laurie and Hill (1954:41) did not adopt his suggestion. I have not seen adequate series of *crenulata, praedatrix,* and *viridis* (none of which occurs in the Solomons) to judge systematic relationships of these kinds; therefore I follow Laurie and Hill.

Dobsonia inermis inermis Andersen

1909. *Dobsonia inermis* Andersen, Ann. Mag. Nat. Hist., ser. 8, 4:532, December, type from San Cristobal; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:475.

1936. *Dobsonia inermis inermis,* Troughton, Rec. Australian Mus., 14:349, April 7, from Santa Ysabel; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 41, June 30; 1956, Hill, The natural history of Rennell Island, British Solomon Islands, 1:74, November 28, from Rennell Island.

1878. *Cephalotes peroni* (part), Dobson, Catalogue of the Chiroptera . . . British Museum, p. 91; 1879, Trouessart, Rev. Mag. Zool., 3:208; 1887, Thomas, Proc. Zool. Soc. London, p. 323, March 15, from Ugi and San Cristobal; 1888, Thomas, Proc. Zool. Soc. London, p. 476, December 4; 1897, Trouessart, Catalogus Mammalium . . ., 1:87.

1899. *Dobsonia peroni* (part), Trouessart, Catalogus Mammalium . . ., 2:1278.

1909. *Dobsonia nesea* Andersen, Ann. Mag. Nat. Hist., ser. 8, 4:532, December 1, type from Shortland Island; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:476, from Shortland, and Rubiana; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:22, February 12, from San Cristobal.

1936. *Dobsonia inermis nesea,* Troughton, Rec. Australian Mus., 14:348, April 7, from Bougainville; 1953, Pohle, Z. Säugetierk., 17:130, October 27; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 41, June 30, from New Georgia.

Specimens examined (13 males and three females; three in alcohol, crania extracted and cleaned).—Fauro in April, 23728, 23740, 23751; Vella Lavella in November, 23134-36, 23141, 23145, 23147, 23149, 23151, 23153; Guadalcanal in May and June, 23865, 23914, 24008; Florida in October, 24416.

Measurements.—See tables 2 and 3.

Remarks.—Heretofore, *Dobsonia inermis inermis* was unreported from Fauro, Vella Lavella, Guadalcanal, and Florida. Apparently the subspecies occurs on most islands of the archipelago (see Fig. 9).

In coloration and most cranial dimensions the specimens listed above agree with specimens of *D. i. inermis* from Alu, Shortland, and Rubiana (Andersen, 1909*c*:532; 1912:475, 476), Bougainville (Troughton, 1936:348, 349), and Rennell (Hill, 1963:74). The forearm in the adult male holotype of "*nesea,*" from Shortland, is 109.5 as opposed to 109.0 in an adult female topotype of *inermis* from Ugi (Andersen, 1912:478) in the southeastern part of the archipelago (see Fig. 9). Forearms of specimens of *D. i. inermis* from Vella Lavella are 107 to 112 (measurements from labels because forearms of these specimens were broken and therefore could not be remeasured). Forearms of specimens from Fauro, Florida, Guadalcanal, and Rennell are 103.6 to 110.0 (see Hill, 1956:74). Variation in length of forearm probably is not significant because no cline is evident (see Fig. 9 and Table 2).

In 1964, 11 specimens of *Dobsonia inermis* were collected on Choiseul. They are smaller, externally and cranially, than specimens of *D. inermis* from San Cristobal, Ugi, Rennell, Guadalcanal, Florida, Rubiana, Vella Lavella, Shortland, Alu, Bougainville, and Fauro, and may be named and described as follows:

Dobsonia intermis minimus, new subspecies

Type.—Adult male, skin and skull, in good condition (originally stored in 70 per cent alcohol for about one year), no. BBM-BSIP 23716, Bernice P. Bishop Museum; from Choiseul Island, British Solomon Islands Protectorate; obtained on 20 March 1964 by Philip Temple, original number 1524.

Distribution.—Choiseul Island (type locality); intergrades from Santa Ysabel also assigned to this subspecies.

Diagnosis.—Size small for species; wing membranes, feet, and ears black; dorsal surface of interfemoral membrane sparsely set with silvery hairs, other membranes naked; hair soft, medium length (10 on mantle, 5 on crown), black hairs and scattered white hairs on face and crown; fur of dorsal surface of mantle composed of whitish hairs having faint olive cast imparting general color of Buffy-Citrine; hair of venter short (about 5), soft, and fine; general coloration Buffy-Citrine; cranium delicate; rostrum narrow in dorsal aspect (nasals not expanded laterally); forehead (junction of nasals and frontals) pronounced in lateral aspect; teeth resembling those of other subspecies of *D. inermis* but slightly smaller.

Comparisons.—From adults of *Dobsonia inermis inermis,* which occurs on Rennell, San Cristobal, Ugi, Malaita, Florida, Guadalcanal, Rubiana, Vella Lavella, Shortland, Alu, Bougainville, and Fauro, *minimus* differs in being smaller. Average length of mandible 31.2 and 33.4. For other measurements see Table 2.

From *Dobsonia praedatrix,* which occurs on New Britain, New Ireland, and Duke of York (northward of the Solomons), *minimus* differs in being smaller in all dimensions; length of forearm averaging 100.5 as opposed to 116.0, and greatest length of skull 42.4 as opposed to 50.0.

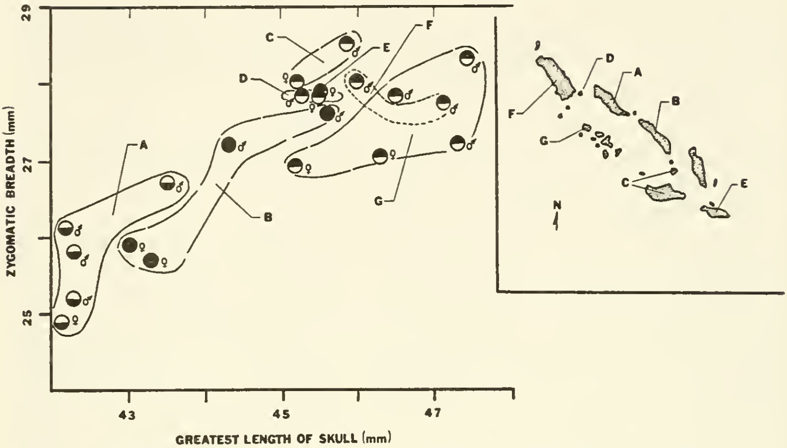

FIG. 8. Greatest length of skull plotted against zygomatic breadth for two subspecies of *Dobsonia inermis*. Symbols represent *D. i. inermis* (◓), *D. i. minimus* (◒), and intergrades assigned to *minimus* (●). Capital letters are used to relate groups of specimens to the island or islands from which they were collected; spatial distribution of specimens indicated in the scatter diagram thus is shown in the inset map. Specimens from Santa Ysabel and Bougainville are deposited in the Australian Museum. The type specimen of *D. i. inermis* is labeled "E." For names of islands see Fig. 2.

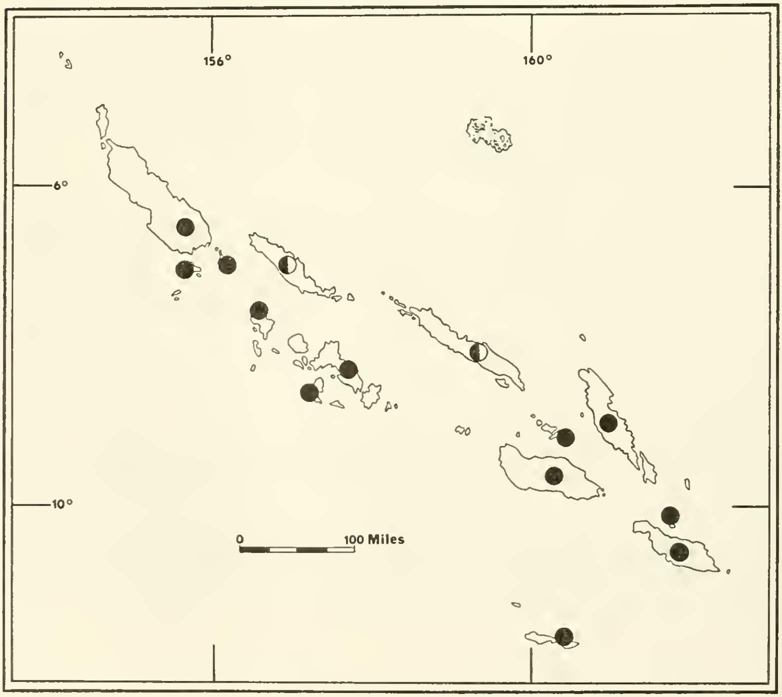

FIG. 9. Distribution of *Dobsonia inermis inermis* (●) and *D. inermis minimus* (◐). For names of islands see Fig. 2.

TABLE 2. Average and Extreme Measurements of Two Subspecies of *Dobsonia inermis.*

MEASUREMENT	*D. i. minimus*		*D. i. inermis*
	Choiseul 4 ♂, 2 ♀	Santa Ysabel 1 ♂, 2 ♀	Guadalcanal, Fauro, Vella Lavella, Florida 9 ♂, 2 ♀
Length of head and body	174.5 (170 –180)		174.5 (160 –190)
Tail vertebrae	28.5 (24 – 33)	23.0 (21.5– 24.0)	30.4 (25 – 35)
Hind foot	25.3 (25.1– 25.9)	23.5 (23.5– 24.0)	29.3 (26.0– 31.6)
Ear	21.5 (21.0– 22.9)	21.1 (21.0– 21.5)	23.1 (19 – 25)
Length of forearm	100.5 (98.1–104.0)	105.3 (104 –107)	108.4 (105 –112)
2nd metacarpal	43.6 (42.6– 45.2)		48.1 (45.9– 50.9)
3rd metacarpal	61.5 (59.8– 62.9)		67.6 (65.2– 68.5)
4th metacarpal	57.5 (56.5– 58.5)		62.5 (58.7– 65.5)
5th metacarpal	59.0 (57.0– 60.5)		64.4 (61.8– 66.0)
Greatest length of skull	42.4 (42.1– 43.5)	44.0 (43.0– 45.6)	45.9 (45.2– 47.4)
Condylobasal length	40.4 (39.5– 41.3)	41.7 (41.1– 42.6)	43.6 (43.1– 45.0)
Zygomatic breadth	25.6 (24.9– 26.8)	26.5 (25.7– 27.6)	27.9 (27.2– 28.5)
Breadth of braincase	16.8 (16.5– 17.4)	18.0 (17.1– 19.9)	17.9 (16.7– 19.0)
Breadth across upper canines	8.4 (8.1– 8.7)		9.2 (9.2– 9.5)
Breadth across first upper molars	12.1 (11.8– 12.6)		13.1 (12.6– 13.3)
Length of maxillary tooth-row	15.6 (15.5– 15.8)	16.4 (16.0– 17.2)	16.4 (15.9– 17.0)
Length of mandibular tooth-row	17.1 (16.8– 17.6)	17.8 (17.3– 18.4)	18.2 (17.8– 19.4)

Measurements.—Comparative measurements of the subspecies *inermis* and *minimus* are given in Table 2. Some measurements of the type are as follows: Length of head and body, 147; tail vertebrae, 31; hind foot, 25; ear, 21; length of forearm, 99.5; 2nd metacarpal, 42.8; 3rd metacarpal, 62.7; 4th metacarpal, 58.5; 5th metacarpal, 59.1; greatest length of skull, 42.2; condylobasal length, 40.6; zygomatic breadth, 25.8; breadth of braincase, 16.8; length of maxillary tooth-row, 15.8; length of mandible, 31.2.

Remarks.—*Dobsonia inermis minimus* is the smallest subspecies of *Dobsonia inermis.* Specimens from Santa Ysabel, southeastward of Choiseul, are slightly larger than the type and paratypes of *minimus.* As can be seen in the scatter diagram (Fig. 8), a male from Santa Ysabel is as large as one male and most females of *D. i. inermis.* The other three specimens from Santa Ysabel also are slightly larger than specimens of *minimus* from Choiseul, but are much smaller than specimens of *D. i. inermis,* and, therefore, are referred to *D. i. minimus.*

Although there is a cline in size of *Dobsonia inermis* from Choiseul to Florida (generally southward; Fig. 9), no cline in size is apparent between Choiseul and Fauro (generally westward). Specimens of *D. inermis* from Fauro are average for the subspecies *inermis;* there is no evidence, in the small series available, of intergradation between *minimus* on Choiseul and *inermis* on Fauro.

Specimens examined (eight males and three females, all originally in alcohol; seven crania, all adults, extracted and cleaned).—Choiseul in March, 23565, 23628, 23637, 23665-67, 23640, 23714, 23716 (holotype), 23717, 23720. Ellis LeG. Troughton kindly examined and measured nos. AM-M. 3693♂, AM-M. 3694♂, AM-M. 3937♀, and AM-M. 3940♀, from Santa Ysabel in the Australian Museum.

Subfamily Macroglossinae

Macroglossus F. Cuvier

1824. *Macroglossus* F. Cuvier, Des dents des mammiferes . . . zoologiques, p. 248.

1840. *Kidodotus* Blyth, *in* Cuvier's animal kingdom . . ., p. 69.

1891. *Carponycteris* Lydekker, *in* Flower and Lydekker, mammals living and extinct, p. 654.

1902. *Odontonycteris* Jentink, Notes Leyden Mus., 23:140, July 15.

Macroglossus, the widest-ranging genus of macroglossine bats, occurs from southeastern Asia to the southern islands of the Solomon Archipelago (see Ellerman and Morrison-Scott, 1966:101; Laurie and Hill, 1954:44). One species, known also from Celebes and New Guinea, occurs in the Solomons and is represented there by an endemic subspecies.

Numerous generic names have been applied, at one time or another, to bats now considered as *Macroglossus.* Trouessart (1904:65) and Miller (1907:70) listed the one bat of this genus occurring in the Solomons under *Carponycteris* and *Kiodotus,* respectively. Andersen (1911:642; 1912:767) and, later, Sanborn (1931:22) identified this bat as *Macroglossus lagochilus microtus.* Troughton (1936:350), reporting an extension of range of this species in the Solomons, used the generic name *Odontonycteris* without explanation. Andersen (1912:754) pointed out that Jentink originally established the name *Odontonycteris* on the basis of an extra premolar in each upper jaw as opposed to the usual two in *Macroglossus,* and arranged *Odontonycteris* as a synonym of *Macroglossus* because "in no genus of Megachiroptera are dental anomalies of so frequent occurrence as in *Macroglossus,* and on no point of the jaws are these anomalies . . . so often met with as on that occupied by the molar series." Sanborn (1931:22) and Phillips (1966:27) noted variation in number of incisors in *Macroglossus* as well as in *Melonycteris,* another macroglossine genus. All of the more recent workers (Ellerman and Morrison-Scott, 1966; Pohle, 1953; Laurie and Hill, 1954) use the name *Macroglossus.*

Macroglossus lagochilus

Macroglossus lagochilus has at least three subspecies, one of which is endemic to the Solomons. The species ranges from Celebes on the west to the Solomon Islands on the east, occurring not only in New Guinea but also on many of the small adjacent islands (see Laurie and Hill, 1954:44).

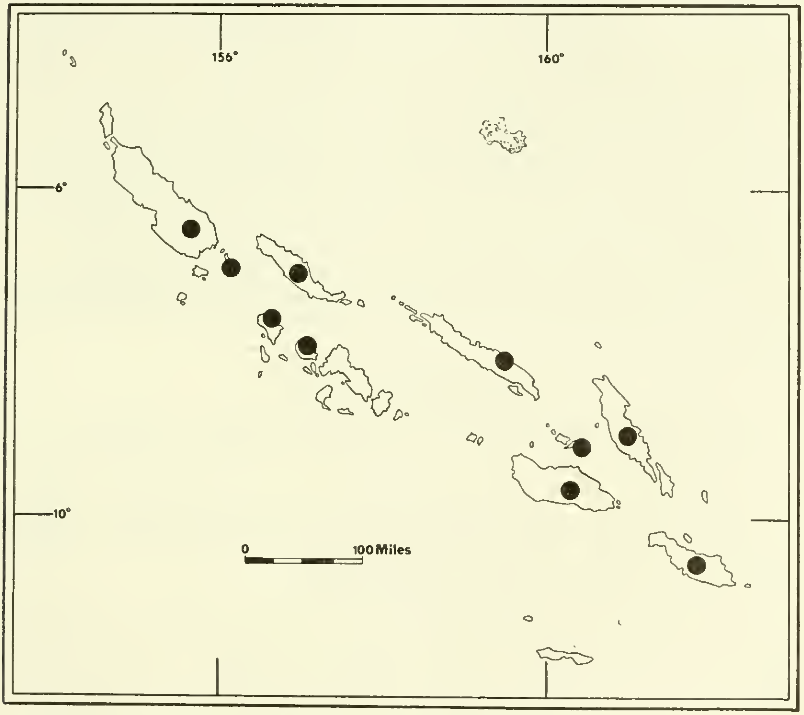

FIG. 10. Distribution of *Macroglossus lagochilus microtus.* For names of islands see Fig. 2.

Macroglossus lagochilus microtus Andersen

1911. *Macroglossus lagochilus microtus* Andersen, Ann. Mag. Nat. Hist., Ser. 8, 7:642, June, type from Guadalcanal, additional specimens from Florida; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:767; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:22, February 12, from San Cristobal; 1953, Pohle, Z. Säugetierk., 17:130, October 27, from Bougainville; 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 44, June 30.

1888. *Macroglossus australis* (part), Thomas, Proc. Zool. Soc. London, p. 476, December 4, from Guadalcanal.

1904. *Carponycteris nana* (part), Trouessart, Catalogus Mammalium . . ., Suppl., p. 65.
1907. *Kiodotus* sp., Miller, Bull. U. S. Nat. Mus., 57:70, June 29.
1936. *Odontonycteris lagochilus microtus,* Troughton, Rec. Australian Mus., 14:350, April 7, from Bougainville.

Specimens examined (14 males and 16 females; in alcohol).—Choiseul in March, 23654-57, 23614, 23629, 23643, 23645, 23647, 23677-79, 23684; Vella Lavella in December, 23277-79, 23283-84; Fauro in April, 23765; Guadalcanal in May and June, 23830, 23864, 23935; Kolombangara in January, 23385, 23399, 23397, 23407, 23420-21; Santa Ysabel in June, 24067; Malaita in June, 24067.

Measurements.—Average and extreme external measurements of 14 males and 15 females are as follows: Length of head and body, 68.3 (63-72); tail vertebrae present but scarcely perceptible and therefore not measured; hind foot, 11.4 (9.0-12.9); ear, 12.0 (10.0-12.9); length of forearm, 37.6 (36.2-39.9).

Remarks.—The distribution of *Macroglossus lagochilus microtus* has not been well known. Specimens herein reported from Choiseul, Fauro, and Vella Lavella provide new records of distribution. As shown on Figure 10, the subspecies occurs throughout the Solomon Islands.

Macroglossus lagochilus microtus differs slightly from *M. l. nanus* Matschie, the subspecies of the Bismarck Archipelago and Admiralty Islands to the north of the Solomons. *M. l. nanus* averages slightly larger than *microtus* (see Andersen, 1912:768-769, for comparative measurements) but otherwise closely resembles it.

Individual variation is evident in several measurements of the specimens at hand (in length of forearm, for example) but no clines are apparent. Four females obtained in March were lactating, as was one taken in December and one taken in January.

Melonycteris Dobson

1877. *Melonycteris* Dobson, Proc. Zool. Soc. London, p. 119, June 1.
1877. *Cheiropteruges* Ramsay, Proc. Linn. Soc. New South Wales, 2:19, July.
1887. *Nesonycteris* Thomas, Ann. Mag. Nat. Hist., ser. 5, 14:147, February.

The genus *Melonycteris* is known from three species, two apparently endemic to the Solomon Islands and the third occurring in eastern New Guinea and the Bismarck Archipelago (Laurie and Hill, 1954:45).

Heretofore, the generic name *Nesonycteris* has been applied to the species in the Solomons, whereas *Melonycteris* has been restricted to the one species in the Bismarck Archipelago and New Guinea. Andersen (1912:792) judged that *Nesonycteris* was clearly distinct from *Melonycteris* on the basis of two characters (loss of a claw on the second digit and loss of the inner, lower incisors). On the other hand, he noted striking similarities in general cranial features, dentition, palatal ridges, tongue, and external appearance of the two genera. Pohle (1953:131) synonymized the two but Laurie and Hill (1954:45) considered them distinct. I have suggested previously (Phillips, 1966:26, 27) that characteristics used to distinguish between *Melonycteris* and *Nesonycteris* are of less than generic value. Variability of number of incisors in the upper jaw of specimens of *Melonycteris* (and in other macroglossine genera, as well) indicates a lack of selective pressure for either increase or decrease in number of incisors. Furthermore, the loss of the small claw on the second digit might not be important because, as Bader and Hall (1960:15) have pointed out, limbs of bats vary more in phenotypic expression than do other parts of the skeletal structure.

The discovery of a new species (*Melonycteris aurantius*) in the Solomon Islands sheds additional light on the problem. Although *M. aurantius* possesses the distinguishing characteristics of the genus *"Nesonycteris,"* the species closely resembles *Melonycteris* in other features. Similarity in structure of hair of *Melonycteris* and *Nesonycteris,* as first reported by Benedict (1957:293), also supports the argument for synonymy (see Phillips, 1966:26).

Melonycteris aurantius lacks a small claw on the second digit and has only two lower incisors. In these ways this species is like *woodfordi,* which also is restricted to the Solomons. On the other hand, the structure of the skull of *M. aurantius* is like that of *M. melanops,* which is the species found in the Bismarck Archipelago.

Although *melanops* is not yet known from the Solomon Islands, I have included it in the following key.

Key to Known Species of *Melonycteris*

1. Ventral surface darker than dorsum, but not strongly contrasting with it; lacking a small claw on the second digit........................2
1′. Ventral surface nearly black, strongly contrasting with dorsum; small claw on second digit........................**Melonycteris melanops**
2(1′). Pelage bright, Cinnamon-Rufous; postorbital region of skull expanded (about 8.3 wide)........................**Melonycteris aurantius,** p. 816
2′. Pelage dark, near Wood-Brown or Cinnamon; postorbital region of skull constricted (about 7.5)............**Melonycteris woodfordi,** p. 816

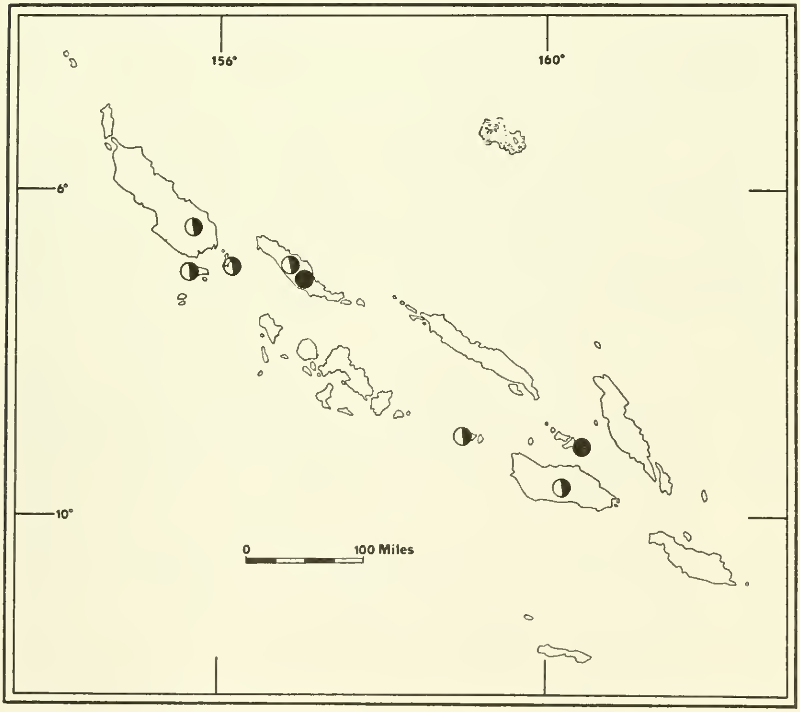

Fig. 11. Distribution of *Melonycteris aurantius* (●) and *M. woodfordi* (◑). For names of islands see Fig. 2.

Melonycteris aurantius Phillips

1966. *Melonycteris aurantius* Phillips, Jour. Mamm., 47:23-27, March 12, type from Florida Island, additional specimens from Choiseul Island.

Specimens examined (six females; three in alcohol).—Florida in October, 24440; Choiseul in March, 23615, 23617, 23558, 23694, 23681.

Measurements.—Average and extreme measurements of six females are as follows: Length of head and body, 80.8 (77-106); hind foot, 17.2 (16.0-18.7); ear, 12.7 (11.5-14.0); length of forearm, 49.3 (42.9-53.8). Average and extreme measurements of skulls of five females are as follows: Greatest length of skull, 31.8 (30.8-33.3); condylobasal length, 29.7 (28.6-32.4); zygomatic breadth, 18 (17.2-20.0); breadth of braincase, 12.6 (12.4-13.2); postorbital breadth, 8.3 (8.0-8.9); length of maxillary tooth-row, 10.1 (9.4-10.4); length of mandibular tooth-row, 11.7 (10.8-12.2).

Remarks.—On Choiseul Island *Melonycteris aurantius* was taken at the same locality as its congener, *Melonycteris woodfordi.*

Externally, *M. aurantius* resembles *M. woodfordi.* These species are the same size, but the former is brighter in color (nearly orange in adults) than the latter, which is Wood-Brown dorsally. Internally, differences between *M. aurantius* and *M. woodfordi* are more obvious. In the skull of *M. aurantius,* the postorbital region is expanded (measuring about 8.3), whereas in *M. woodfordi* the postorbital region is constricted. Furthermore, in lateral aspect the posterior portion of the skull of *M. aurantius* is down-turned and the angle of the facial axis with the basicranial axis is much more acute than in *M. woodfordi.*

The number of upper incisors is highly variable in the six specimens of *M. aurantius* that I have examined. In two specimens an extra tooth has erupted just anterior to I2 and there is a total of six upper incisors. In two other specimens an extra tooth has erupted in front of I2 on one side but not the other. I could find no trace of an extra tooth in the remaining two specimens.

Practically nothing is known about the natural history of *M. aurantius,* or, indeed, that of either of the other two species of this genus. One field collector (Temple, *in litt.*) for the Bishop Museum reported that he obtained both *M. aurantius* and *M. woodfordi* in the same mist net in one night. The holotype, an adult female, was lactating when obtained in October.

Melonycteris woodfordi (Thomas)

1887. *Nesonycteris woodfordi* Thomas, Ann. Mag. Nat. Hist., ser. 5, 14:147, February, type from Shortland Island; 1887, Thomas, Proc. Zool. Soc. London, p. 324, March 15; 1888, Thomas, Proc. Zool. Soc. London, p. 476, December 4; 1898, Trouessart, Catalogus Mammalium . . ., 1:90; 1899, Matschie, Die Megachiroptera . . . naturkunde, p. 91; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 66; 1907, Miller, Bull. U. S. Nat. Mus., 57:74, June 29; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:792, from Alu, Shortland, Fauro, and Guadalcanal; 1931, Sanborn, Publ. Field Mus. Nat. Hist., Zool. Ser., 18:23, February 12, from Russell Island (Pavuvo); 1954, Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 45, June 30.

1953. *Melonycteris woodfordi,* Pohle, Z. Säugetierk., 17:130, October 27, from Bougainville Island; 1966, Phillips, Jour. Mamm., 47:23, March 12, from Choiseul.

Specimens examined (three males and one female; in alcohol).—Choiseul, in April, 23413-14, 23434, 23275.

Measurements.—Average and extreme measurements of three males and one female are as follows: Length of head and body, 86.1 (83.1-91.0); hind foot, 19.6 (17.2-22.2); ear, 11.3 (10.8-11.7); length of forearm, 54.4 (52.1-57.7).

Remarks.—Specimens of *Melonycteris woodfordi* from Choiseul constitute a new locality of occurrence for the species. Apparently *M. woodfordi* occurs throughout the Solomons (see Fig. 11).

Thomas (1887*a*:147) named *Nesonycteris woodfordi* in a preliminary report that appeared before the publication of the more detailed description of the genus and species (1887*b*:323-324). In the second paper he stated that the anterior projections of the premaxillary bones are separated distinctly in both *Nesonycteris* and *Melonycteris.* According to Thomas (1887*b*:323), it was by some "accident" that Dobson (1878:4) reported the anterior projections of the premaxillary bones in *Melonycteris melanops* to be united. Writing at a later date, Andersen (1912:785) reported that in *Melonycteris melanops* the premaxillary bones have "simple contact with each other." Furthermore, in Andersen's (1912:791) illustration of *M. woodfordi* the premaxillary bones are in contact anteriorly. In specimens of *woodfordi* and *melanops* examined by me, the premaxillary bones are in contact. In *M. aurantius* the premaxillary bones are not in contact, and it differs from *woodfordi* in several other respects.

In *M. woodfordi,* as in other macroglossine bats, there is variability in dentition. One specimen examined has a total of three upper incisors, and another had an extra peglike tooth just anterior to I 1.

Subfamily Nyctimeninae

Nyctimene Borkhausen

1797. *Nyctimene* Borkhausen, Deutsche fauna . . ., 1:86.
1810. *Cephalotes* É. Geoffroy, Ann. du Mus. d' Hist. Nat., 15:104.
1811. *Harpyia* Illiger, Prodr. Syst. Mamm. et Avium, p. 118.
1837. *Gelasinus* Temminck, Monographe de Mammalia . . ., 2:100.

Tube-nosed bats of the genus *Nyctimene* occur from Celebes on the west to the Santa Cruz Islands on the east. Heretofore, two species (*N. albiventer* and *N. major*), each with an endemic subspecies, were known from the Solomon Islands. Both species occur also in New Guinea and on many adjacent islands. A new species of *Nyctimene,* apparently endemic to the Solomons, and a new subspecies of *N. albiventer* are named beyond.

Nyctimene is related closely to *Cynopterus* and the "Cynopterus group" of Andersen (1912:691). Because *Nyctimene* is a highly specialized bat, Miller (1907:75) placed it in a subfamily separate from that of *Cynopterus* and its allies.

Andersen (1912:696, 697) placed the species of *Nyctimene* previously known from the Solomons in two groups, the "papuanus" group and the "cephalotes" group, on the basis of difference in length of forearm and length of maxillary tooth-row. Because of its short forearm (about 58), *N. albiventer* is in the *papuanus* group; and *N. major,* because of its long forearm (about 74), is in the *cephalotes* group.

Key to Species of Nyctimene in the Solomons

1. Forearm longer than 70; males grayish-brown, females pale gray, **N. major scitulus,** p. 825
1′. Forearm shorter than 70; males dark brown, females pale brown.....2
2(1′). Forearm about 65..............................**N. malaitensis,** p. 822
2′. Forearm less than 61..............................**N. albiventer,** p. 818

Nyctimene albiventer

This species occurs throughout New Guinea and on many adjacent islands, including the Bismarck Archipelago and the Admiralty and Solomon islands. The species varies geographically and five subspecies are recognized. The two subspecies in the Solomons resemble *N. albiventer papuanus,* the subspecies that ranges from eastern New Guinea to New Britain. *N. albiventer bougainville* occurs in the western chain of islands of the Solomons, whereas another subspecies, named as new beyond, occurs in the eastern chain of islands (see Fig. 12).

Sexual dichromatism is striking. As Andersen (1912:690) previously reported, females generally are paler, more brownish than males, which are dark and have a better defined black dorsal stripe.

Nyctimene albiventer bougainville Troughton

1936. *Nyctimene bougainville* Troughton, Rec. Australian Mus., 19:349, April 7, type from Bougainville.
1954. *Nyctimene albiventer bougainville,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 46, June 30.
1953. *Nyctimene papuanus bougainville,* Pohle, Z. Säugetierk., 17:130, October 27.

Specimens examined (nine males, one female; nine in alcohol, nine crania extracted and cleaned).—Bougainville in December, AM-M. 5786 (paratype); Guadalcanal in May, 23812, 23815, 23827; Kolombangara in January and February, 23369, 23381, 23388, 23406, 23444, 23456.

Measurements.—See Table 3.

Remarks.—Heretofore, *Nyctimene albiventer bougainville* was not known from Kolombangara and Guadalcanal. The subspecies apparently ranges throughout the western chain of the Solomons.

Troughton (1936:350) considered *Nyctimene bougainville* specifically distinct from its nearest ally, *N. papuanus.* Pohle (1953:130) did not examine specimens of either kind, but on the basis of Troughton's description decided that *N. bougainville* differed only subspecifically from *N. papuanus.* Laurie and Hill (1954:46) synonymized *bougainville* and *papuanus* with *N. albiventer.* However, Troughton (1936:350) pointed out that in addition to size *bougainville* differed from *papuanus* by having narrower and longer pm 3 and pm 4. Judging from specimens examined by me, such is the case, and the difference is even more pronounced in m1.

Specimens of *N. a. bougainville* from Kolombangara and Guadalcanal agree with a paratype of this subspecies from Bougainville. Geographic variation, if present in the population in the western chain of islands (see Fig. 12), is slight and not notable in the series available. Some individual variation was found, especially in the shape of the interorbital region of the skull. An adult male from Kolombangara is unusually dark, almost black; color of the other specimens (all in alcohol) is consistent according to sex.

Nyctimene albiventer from Choiseul and Santa Ysabel is smaller, in all respects, than *N. albiventer* from Bougainville, Kolombangara, and Guadalcanal (see Table 3), and therefore may be named and described as follows:

Nyctimene albiventer minor, new subspecies

Type.—Adult male, skin and skull, in good condition (originally stored in alcohol for about one year), no. BSIP 23636, Bernice P. Bishop Museum; from Choiseul Island, British Solomon Islands Protectorate; obtained on 11 March 1964, by Philip Temple, original number 1441.

Distribution.—Known only from Choiseul and Santa Ysabel islands (see Fig. 12).

Diagnosis.—Small for *Nyctimene;* wing membranes brown with scattered yellow spots (dried specimens); uropatagium, feet, and ears brown; dorsum of tibia set with hair, ventral surface naked; dorsum of uropatagium sparsely set with pale brown hairs, ventral surface almost bare; fringe of hairs along two centimeters of dorsal and ventral surfaces of trailing edge of wing membrane; proximal third of dorsal surface of forearm sparsely set with hairs; pelage of back soft and thick, of medium length (about 7); hair on crown and nape short (about 4); well-defined black dorsal stripe, extending from uropatagium to shoulders; skull resembling that of other subspecies of *N. albiventer* but relatively smaller; zygomatic arch delicate, slender anteriorly; P2 small (see Fig. 14). Sexually dichromatic as follows: male—dorsum Hair-Brown, bases of hairs darker; hair on throat sparse, medium length (about 6), Hair-Brown; fur along sides of abdomen Drab; female—dorsum having Buffy-Brown cast, some individual hairs Hair-Brown; shoulders Sayal-Brown; hair on throat sparse, Hair-Brown on throat and mid-line of abdomen; sides of abdomen Sayal-Brown.

Comparisons.—From *Nyctimene major scitulus,* the largest member of this genus in the Solomons, *N. a. minor* differs in being smaller in all measurements taken; forearm averaging 54.8 as opposed to 73.5; greatest length of skull 28.2 as opposed to 37.0, and females pale brown instead of pale gray.

From nine adults of *Nyctimene albiventer bougainville* from Bougainville, Kolombangara, and Guadalcanal, *minor* differs as follows: averaging slightly smaller in all dimensions; forearm averaging 54.8 as opposed to 57.9; second metacarpal averaging 27.4 as opposed to 28.3; 5th metacarpal averaging 38.5 as opposed to 40.0; condylobasal length 26.7 as opposed to 28.0; length of mandibular tooth-row 10.3 as opposed to 10.9; mandible smaller (see Fig. 14); dorsal stripe fainter.

From *Nyctimene albiventer papuanus,* known from eastern New Guinea, New Britain, and the Admiralty Islands, *minor* differs as follows: slightly smaller in most dimensions; forearm averaging 54.8 as opposed to 57.0; length of maxillary tooth-row 8.9 as opposed to 9.8; length of mandibular tooth-row 10.3 as opposed to 11.0; breadth across upper third premolars notably less (7.5 as opposed to 8.4).

N. a. minor differs from *N. albiventer albiventer* Gray, which occurs about 800 miles to the west of *minor,* in ways made apparent by the description by Andersen (1912:700-701). *N. a. minor* occurs about 1500 miles eastward of the place from which *N. a. draconilla* Thomas, a subspecies essentially unknown to me, was named (see Laurie and Hill, 1954:46).

From *Nyctimene sanctacrucis,* known from the Santa Cruz Islands, *minor* differs as follows: much smaller in all dimensions; forearm averaging 54.8 as opposed to 75; greatest length of skull 28.2 as opposed to 34.5; length of maxillary tooth-row 8.9 as opposed to 12.9.

Measurements.—Measurements of the two subspecies from the Solomons are given in Table 3. Some measurements of the type are as follows: Length of head and body, 108; tail vertebrae, 20.5; hind foot, 14.7; ear, 11.3; length of

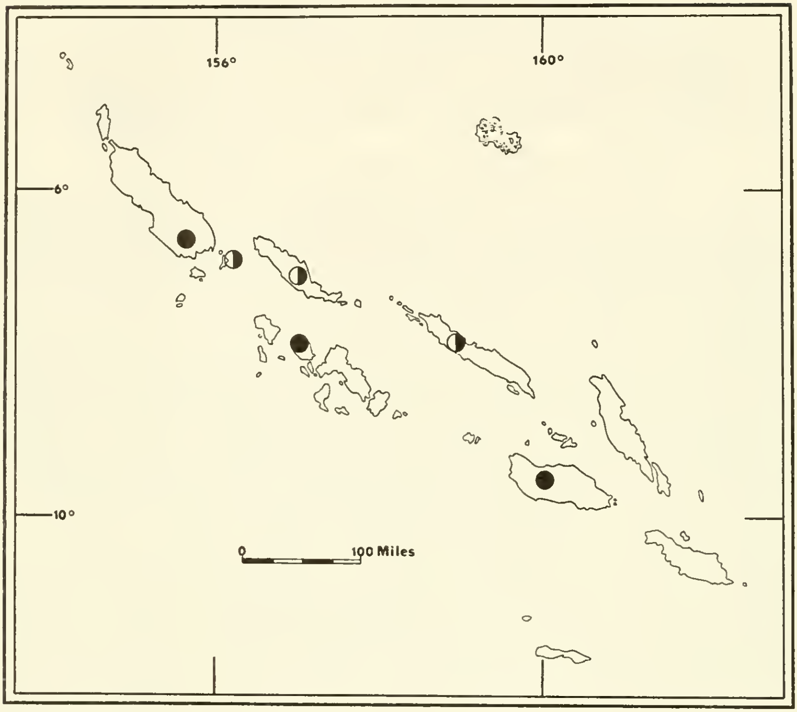

Fig. 12. Distribution of *Nyctimene albiventer bougainville* (●) and *N. albiventer minor* (◑). For names of islands see Fig. 2.

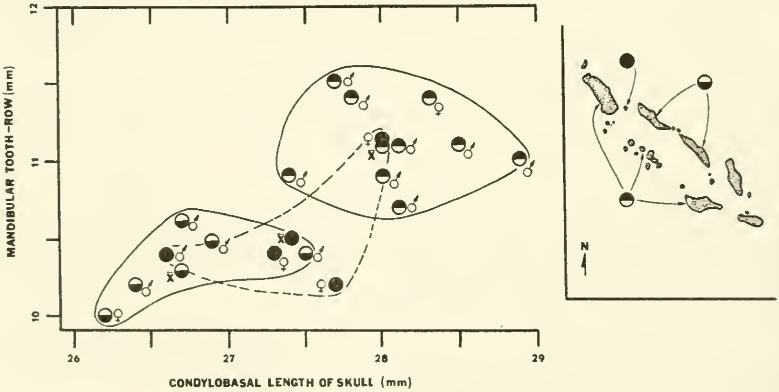

Fig. 13. Scatter diagram comparing two subspecies of *Nyctimene albiventer.* One individual of specimens thought to be intergrades is as large as specimens of *Nyctimene a. bougainville,* whereas the other three intergrades are about the same size as specimens of *N. a. minor.* Symbols represent *N. a. bougainville* (◓), *N. a. minor* (◒), and intergrades assigned to *minor* (●). For names of islands see Fig. 2.

TABLE 3. Average and Extreme Measurements of *Nyctimene albiventer bougainville* and *N. a. minor.*

MEASUREMENT	*N. a. minor* Choiseul, Santa Ysabel 4 ♂, 1 ♀	Intergrades Fauro 1 ♂, 3 ♀	*N. a. bougainville* Kolombangara, Guadalcanal 8 ♂, 1 ♀
Length of head and body	107.0 (105 –109)	109.2 (105 –112)	110.0 (106 –117)
Tail vertebrae	20.0 (19.3– 20.5)	21.0 (20 – 22)	19.2 (15.5– 23.0)
Hind foot	14.2 (13.5– 15.0)	....	14.3 (13.0– 15.9)
Ear	11.9 (11.0– 13.0)	....	12.8 (11.8– 14.5)
Length of forearm	54.8 (54.0– 55.8)	57.1 (55.9– 59.0)	57.9 (55.8– 59.8)
Greatest length of skull	28.2 (27.2– 28.9)	28.6 (28.3– 29.7)	29.7 (28.6– 30.1)
Condylobasal length	26.7 (26.2– 27.5)	27.4 (26.6– 28.0)	28.0 (27.8– 28.9)
Palatal length	11.2 (10.9– 11.9)	11.6 (11.3– 11.8)	11.7 (11.0– 12.5)
Breadth of braincase	12.0 (11.5– 12.4)	12.0 (11.7– 12.2)	12.3 (12.1– 12.8)
Zygomatic breadth	18.9 (18.4– 19.7)	18.6 (18.4– 19.2)	19.2 (18.7– 20.0)
Interorbital breadth	5.0 (4.7– 5.6)	5.3 (5.0– 5.6)	5.1 (4.7– 5.5)
Breadth across first upper molars	8.6 (8.4– 8.9)	8.9 (8.7– 9.1)	9.1 (8.8– 9.6)
Maxillary tooth-row	8.9 (8.7– 9.3)	9.3 (9.1– 9.5)	9.5 (9.2– 9.8)
Mandibular tooth-row	10.3 (10.0– 10.6)	10.5 (10.2– 11.1)	10.9 (10.7– 11.4)

forearm, 55.1; 2nd metacarpal, 27.4; 3rd metacarpal, 39.0; 4th metacarpal, 37.5; 5th metacarpal, 39.1; greatest length of skull, 28.6; condylobasal length, 27.5; zygomatic breadth, 18.4; length of maxillary tooth-row, 9.0; length of mandibular tooth-row, 10.4.

Remarks.—*Nyctimene albiventer minor* closely resembles *N. albiventer bougainville*, differing from the latter mostly in size. Although adults of *minor* average only slightly smaller than adults of *bougainville* (see Table 3), there is only slight overlap (about 0.2 at most) in most minimum dimensions of external and cranial features of *bougainville* and corresponding maximum dimensions of externals and crania of *minor*. The difference in size is clearly shown in Figs. 13 and 14.

Four specimens of *Nyctimene albiventer* from Fauro herein are considered to be intergrades between *N. a. bougainville* and *N. a. minor*. As shown in Table 3, the specimens from Fauro average slightly larger than those of *minor* from Choiseul and Santa Ysabel and slightly smaller than specimens of *bougainville* from Kolombangara and Guadalcanal. I have assigned the specimens from Fauro to *N. a. minor* because they generally are closer to *minor* in size (see Fig. 13).

Specimens examined (five males and four females; seven in alcohol; seven crania extracted and cleaned).—Choiseul in February and March, 23636 (holotype), 23631, 23540, 23646; Santa Ysabel in February, 23539; Fauro in April, 23742, 23743, 23763, 23764.

One specimen of *Nyctimene* from Malaita Island is smaller than *Nyctimene major*, which is known from Shortland, Alu, Florida, New Georgia, Guadalcanal, Choiseul, and Malapa (see Fig. 15) and is larger than either of the two subspecies of *Nyctimene albiventer* known from Bougainville, Fauro, Kolombangara, Guadalcanal, Choiseul, and Santa Ysabel. This specimen represents a previously unknown species and may be named and described as follows:

Nyctimene malaitensis, new species

Type.—Adult female, skin and skull, in good condition (originally stored in alcohol for about one year), no. BSIP 24103, Bernice P. Bishop Museum; from Malaita Island, British Solomon Islands Protectorate; obtained on 1 July 1964, by Peter Shanahan, original no. unkown.

Distribution.—Known only from Malaita (see Fig. 16).

Diagnosis.—Size average for genus but larger than closest relative, *Nyctimene albiventer;* wing membranes brown with scattered yellow spots (dried specimen); uropatagium, ears, and feet brown; dorsal surface of tibia set with hair, ventral surface bare; dorsal surface of uropatagium sparsely set with hair, ventral surface having few, scattered hairs; dorsal surface of trailing edge of wing membrane sparsely set with hairs, ventral surface bare; proximal third of upper- and under-surface of forearm set with hair; pelage of back luxuriant and soft (about 10 long); hair on crown and nape shorter than on back (4 to 8); well-defined black dorsal stripe from shoulders to rump (about 2 wide); basal half of most hairs on dorsum Deep Mouse Gray, distal half Light Buff, tips Ochraceous-Tawny; some hairs on back entirely Light Buff; hairs of crown Light Ochraceous Buff tipped with Ochraceous-Tawny; hair on throat and along sides of abdomen Light Ochraceous Buff; hairs of ventral midline Smoke Gray; braincase narrow; zygomatic breadth relatively narrow; well-developed lambdoidal crest in female; rostrum short, wide; upper canines slanted posteriorly; upper incisors large; foramen ovale large (see Fig 14).

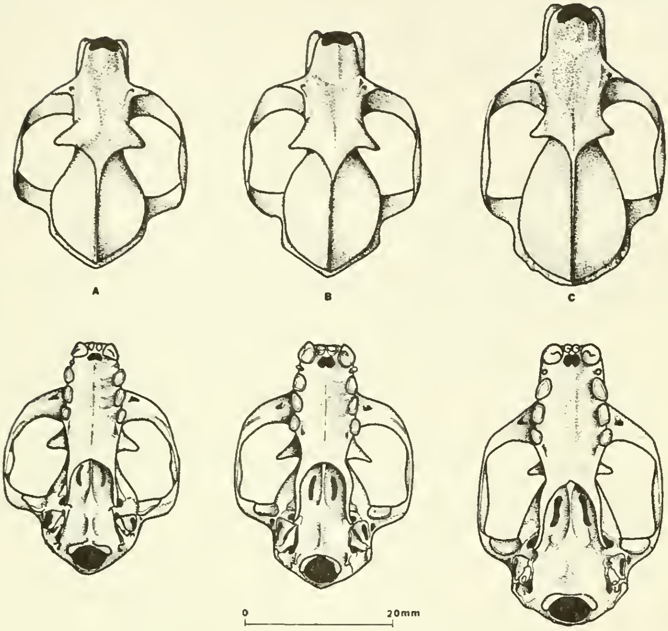

FIG. 14. Dorsal and ventral views of skulls of (A) *Nyctimene albiventer minor* [specimen 23631 ♂], (B) *N. a. bougainville* [specimen 23381 ♂], and (C) *N. malaitensis* [specimen 24103 ♀].

Comparisons.—From *Nyctimene major scitulus*, the largest kind of *Nyctimene* in the Solomons, *malaitensis* differs as follows: smaller in all dimensions (forearm 65 as opposed to 73.5); greatest length of skull 32.4 as opposed to 37.0; length of maxillary tooth-row 10.5 as opposed to 13.0; length of mandibular tooth-row 11.8 as opposed to 14.2.

From nine adults of *Nyctimene albiventer bougainville* from Bougainville, Kolombangara, and Guadalcanal, *malaitensis* differs as follows: larger in all dimensions: forearm 65 as opposed to 57.9; greatest length of skull 32.4 as opposed to 29.7; zygomatic breadth 20.4 as opposed to 19.2; and length of maxillary tooth-row 10.5 as opposed to 9.5; length of mandibular tooth-row 11.8 as opposed to 11.1.

From five adults of *Nyctimene albiventer minor*, from Choiseul and Santa Ysabel, *malaitensis* differs in the same ways it differs from *N. a. bougainville*, but the contrast is even greater when *malaitensis* and *minor* are compared.

From *Nyctimene santacrucis*, known only from the Santa Cruz Islands, *malaitensis* differs in being smaller in all dimensions: forearm 65 as opposed to 75; greatest length of skull 32.4 as opposed to 34.5; and length of maxillary tooth-row 10.5 as opposed to 12.9.

Measurements of the holotype.—Length of head and body, 118; tail vertebrae, 23.0; hind foot, 16.0; ear, 14.0; length of forearm, 65.0; 2nd metacarpal, 33.2; 3rd metacarpal, 46.4; 4th metacarpal, 44.3; 5th metacarpal, 46.0; greatest length of skull, 32.4; condylobasal length, 30.6; palatal length, 13.0; breadth of braincase, 12.5; zygomatic breadth, 20.4; interorbital breadth, 5.5; breadth across first upper molars, 9.5; length of maxillary tooth-row, 10.5; length of mandibular tooth-row, 11.8.

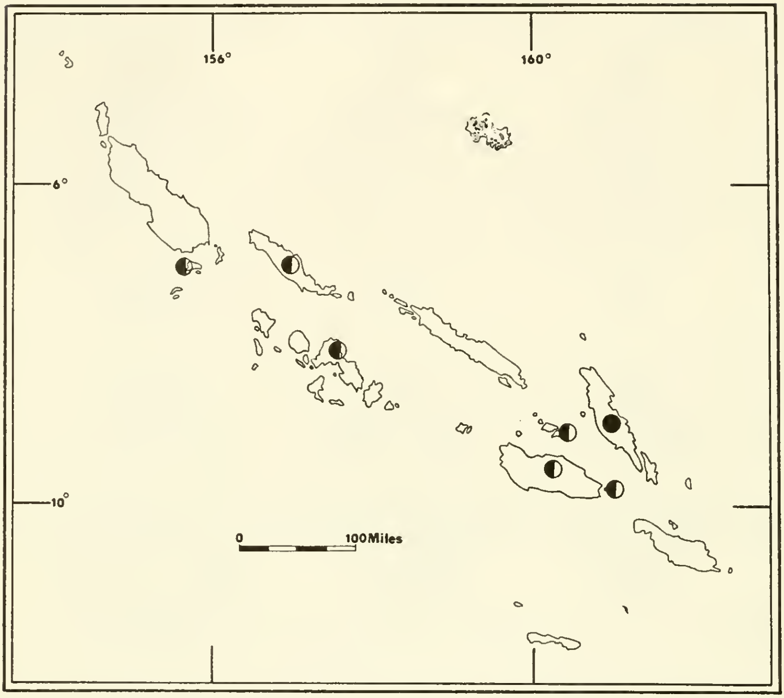

FIG. 15. Distribution of *Nyctimene malaitensis* (●) and *N. major scitulus* (◐). For names of islands see Fig. 2.

Remarks.—In size, *Nyctimene malaitensis* is intermediate between *N. adbiventer* and *N. major.* Because the type of *malaitensis* is brown and not pale gray, as are females of *major, N. malaitensis* most likely is more closely related to *N. albiventer,* in which the females are brown. The teeth of the holotype and only known specimen of *malaitensis* are too worn to be useful in determining the relationships between these species.

When more specimens are available, *N. malaitensis* may prove to be a subspecies of *N. albiventer.* At present, *malaitensis* is accorded specific rank in order not to obscure the apparent relationships of *N. albiventer bougainville* and *N. a. minor.* Additionally, *N. malaitensis* is given specific rank because (1) it is larger (especially in external dimensions) than the largest subspecies of *N. albiventer* (compare above measurements with those in Table 3), and (2) *malaitensis* does not form a cline with either of the two subspecies of *N. albiventer.*

Specimen examined (one female).—Malaita in July, 24103 (holotype).

Nyctimene major

This large species of tube-nosed bat has at least four subspecies, one of which (*N. major scitulus*) is endemic to the Solomons. The species occurs throughout eastern New Guinea and on many of the islands adjacent to the eastern coast of New Guinea, including the Trobriand Islands, the Bismarck Archipelago, and the Solomons (see Laurie and Hill, 1954:47). The geographic distribution of the species generally is the same as that of *N. albiventer.*

In *Nyctimene major,* as in *N. albiventer,* most males are grayish-brown, whereas most females are pale gray.

Nyctimene major scitulus Andersen

1910. *Nyctimene scitulus* Andersen, Ann. Mag. Nat. Hist., ser. 8, 6:623, December 1, type from Shortland; 1912, Andersen, Catalogue of the Chiroptera . . . British Museum, 1:711, from Shortland, New Georgia, Florida, Guadalcanal; 1931, Troughton, Proc. Linnean Soc. New South Wales, 56:206, July 15; 1931, Sanborn, Publ. Field Mus. Nat. Hist., 18:22, February 12, from Choiseul and Malapa; 1942, Tate, Bull. Amer. Mus. Nat. Hist., 80:342, December 31.

1954. *Nyctimene major scitulus,* Laurie and Hill, List of land mammals of New Guinea, Celebes and adjacent islands, p. 47, June 30.

1862. *Harpyia pallasi,* Gerrard, Catalogue of the bones . . . British Museum, p. 58.

1870. *Harpyia cephalotes,* Gray, Catalogue of monkeys, lemurs and fruit-eating bats in the British Muesum, p. 121.

1878. *Harpyia major,* Dobson, Catalogue of the Chiroptera . . . British Museum, p. 90; 1879, Trouessart, Rev. Mag. Zool., 3:207; 1887, Thomas, Proc. Zool. Soc. London, p. 323; 1888, Thomas, Proc. Zool. Soc. London, p. 476; 1897, Trouessart, Catalogus Mammalium . . ., 1:87.

1899. *Cephalotes major,* Trouessart, Catalogus Mammalium . . ., 2:1277.

1899. *Gelasinus major,* Matschie, Die Megachiroptera . . . naturkunde, p. 84; 1904, Trouessart, Catalogus Mammalium . . ., Suppl., p. 64.

Specimens examined (four males and one female; dried skins with skulls inside).—Florida in October, 24397, 24413, 24418, 24419.

Measurements.—External measurements of four males and one female are, respectively, as follows: Length of head and body, 134, 128, 134, 134, 136; tail vertebrae, 28, 23, 27, 26, 21; hind foot, 20, 16, 19, 16, 21; ear, 17, 17, 17, 17, 18; length of forearm, 73.8, 68.0, 74.0, 73.6, 78.0.

Remarks.—*Nyctimene major scitulus* has been recorded only from the western chain of islands in the Solomons (see Fig. 15). Specimens examined by me agree well in external dimensions and color with specimens described by Andersen (1912:712) and Troughton (1931:206-207).

ZOOGEOGRAPHY AND SPECIATION

De Beaufort (1951:113) considered bats of "less zoogeographical importance" than other mammals because the ocean is not an "absolute barrier to their dispersal." Volant animals are ecologically terrestrial and therefore are more nearly earthbound than De Beaufort's remarks would suggest (see Miller, 1966:10). Indeed, many kinds of volant animals are endemic to the Solomons. Birds, for example, are well adapted for flight but pose some of the most complex zoogeographic problems in the area of New Guinea and the Solomon Islands (Mayr, 1940:198; 1942:81-83; Koopman, 1957). Rapid speciation can take place in any situation where there is a high degree of isolation (Wright, 1931; Lack, 1947). In fact, isolation is a most important factor in speciation of insular populations (Baker, 1951:55). The one genus, nine species, and 19 subspecies of megachiropterans that are endemic to the Solomons (Table 4) obviously indicate that bats, although volant, can be restricted to one or more islands long enough for new taxa to evolve.

The megachiropteran bats of the Solomons have their affinities with the fauna of New Guinea (Table 4); the Solomons and New Guinea have six genera and six species in common. Because the two areas never have been connected (*via* the Bismarck Archipelago) by dry land, bats probably have reached the Solomons by flying from island to island (see Durham, 1963:357, 359, 361, 363). Deignan (1963:266) has dismissed voluntary or involuntary flight as possible explanations for distributions of bats and birds on islands of the Pacific.

TABLE 4. A Summary of the Kinds of Megachiropteran Bats in the Solomon Islands and Their Affinities with Faunas of Adjacent Islands.

	Totals	Endemic to Solomons	Common only to Solomons and Bismarcks	Common to Solomons, Bismarcks, and New Guinea	Common to Solomons, New Hebrides, and New Caledonia
Genera....	7	1	0	6	0
Species....	16	9	1	6	1
Subspecies	20	19	0	0	1

The taxonomic level of endemism can be used as an indicator of antiquity (Dobzhansky, 1941; Koopman, 1958:429-430). The one megachiropteran genus (*Pteralopex*) endemic to the Solomons apparently is an ancient relic. Bats of this monotypic genus occur on Bougainville, Choiseul, Santa Ysabel, and Guadalcanal (see Fig. 4). These four islands probably were contiguous during the maximum lowering of sea level in the Pleistocene (see Durham, 1963:362-363). Bats of the genus *Pteralopex* are the only kind in the Solomons having a distribution that can be correlated with former land connections between islands.

The distributions of 16 species of megachiropterans known from the Solomons are summarized in Table 5 and in Figure 16. The larger islands (in terms of surface area and elevation) in general have the highest number of species (Guadalcanal 10, Choiseul 9, and Bougainville 8). But Fauro, one of the smallest islands for which data are available, has six species of megachiropterans whereas San Cristobal and Malaita, two of the larger islands, have only three and four species, respectively. Possibly this difference signals the need for additional collecting.

Bougainville and Choiseul, about 60 miles apart, have seven species of megachiropterans in common (Table 5). Fauro, 25 miles southeast of Bougainville and 35 miles west of Choiseul, shares five species with each of these islands (Fig. 16). *Pteralopex atrata* and *Pteropus rayneri* occur on Choiseul and on Bougainville, but not on Fauro. Individuals of these species are the largest fruit bats in the Solomons, and their absence on Fauro suggests, therefore, that this small island is ecologically unsuitable, at least in some months, for the support of populations of bats that require relatively large amounts of food. The small size of the island is consistent with this hypothesis, but several other islands as small as Fauro do support populations of the large kinds of *Pteropus*, at least in some months.

Santa Ysabel has six species of megachiropterans and 10 occur on Guadalcanal (Table 5). These two islands, separated by about 100

TABLE 5. A Summary of Distribution of All Species of Megachiropteran Bats Known from the Solomons. Only Islands Well Known Faunistically Are Listed.

SPECIES	Bougainville	Choiseul	Santa Ysabel	Ndai	Malaita	Florida	Fauro	Shortland	Vella Lavella	Kolombangara	Russell	Guadalcanal	San Cristobal	Ugi	Rennell	Ontong Java
R. amplexicaudatus	X	X	X		X		X			X		X				
P. atrata	X	X	X									X				
Pt. hypomelanus											X					
Pt. admiralitatum				X				X	X		X	X				
Pt. tonganus															X	
Pt. howensis																X
Pt. rayneri	X	X	X		X				X	X		X	X	X	X	
Pt. woodfordi							X			X	X	X				
Pt. mahaganus	X		X													
D. inermis	X	X	X		X	X	X	X	X			X	X	X	X	
M. lagochilus	X	X				X	X			X		X	X			
M. woodfordi	X	X					X	X			X	X				
M. aurantius		X				X										
N. albiventer	X	X	X				X			X		X				
N. major		X				X		X				X				
N. malaitensis					X											
Totals	8	9	6	1	4	4	6	4	3	5	4	10	3	2	3	1

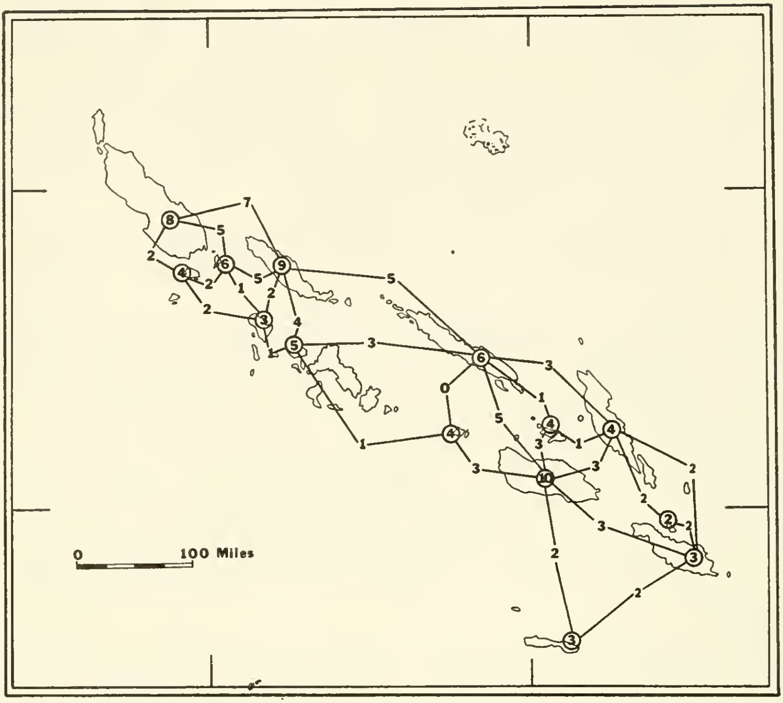

FIG. 16. The number of megachiropteran species known from individual islands (number within a circle) is compared with the number of species common to two different islands (number without a circle). For names of islands see Fig. 2.

miles of water, share five species (*Rousettus amplexicaudatus, Pteralopex atrata, Pteropus rayneri, Dobsonia inermis,* and *Nyctimene albiventer*). The Nggela Group, in which Florida is the largest island and the only one from which bats have been collected, is 50 miles southeast of Santa Ysabel and 30 miles north of Guadalcanal (Fig. 16). Four species of megachiropterans are known from Florida (*Dobsonia inermis, Macroglossus lagochilus, Melonycteris aurantius,* and *Nyctimene major*). Three of these are known from Guadalcanal and one occurs on Santa Ysabel. This situation resembles the one involving Fauro, Bougainville, and Choiseul because none of the large bats (*Pteropus* and *Pteralopex*) is known from Florida, even though two species of large bats that occur on Santa Ysabel to the northwest occur also on Guadalcanal to the south. Possibly Florida and the smaller islands that comprise the Nggela Group are ecologically unsuitable for large bats, or perhaps these small islands can support only limited numbers of individuals during part of a year.

Some of the small islands in the Solomons have populations of large fruit bats. For example, *Pteropus admiralitatum* and *P. hypomelanus* have been reported from the small islands in the Russell Group (Table 5). Possibly these species do not live concurrently in the Russells; specimens of the two were obtained in different years. Two small megachiropterans, *P. woodfordi* and *Melonycteris woodfordi,* also inhabit the Russells. Shortland, a small island about 15 miles south of Bougainville, supports one large bat, *P. admiralitatum,* as well as smaller megachiropterans.

Kolombangara and Vella Lavella are about the same size and are separated by about 15 miles of water. *Rousettus amplexicaudatus, Pteropus rayneri, P. woodfordi, Macroglossus lagochilus,* and *Nyctimene albiventer* have been collected on Kolombangara but only *P. admiralitatum, P. rayneri,* and *Dobsonia inermis* have been found on Vella Lavella. The difference in the known megachiropteran faunas is more striking when one compares each island with adjacent islands. Two species on Vella Lavella occur also on Choiseul, which is about 35 miles northeastward, and two species occur also on Shortland, which is 120 miles northwestward (Fig. 16). Four of the five megachiropterans on Kolombangara also have been found on Choiseul, about 50 miles northward (Table 5). *Pteropus rayneri* is the only megachiropteran known from both Kolombangara and Vella Lavella, even though the islands are separated by only a few miles of water. Inadequate data possibly account for the differences in the megachiropteran fauna, but I suspect that some other factors are involved. Although Vella Lavella and Kolombangara do have one species (*P. rayneri*) in common, a different subspecies occurs on each island—*rubianus* on Kolombangara and *lavellanus* on Vella Lavella (Fig. 17 and Table 6). This indicates that some factor or factors are operating to keep megachiropterans from moving frequently or easily from one island to the other.

Each of several subspecies of species in the genus *Pteropus* are known from one or two small islands separated by only a few miles from other islands on which different subspecies occur (see Fig. 6). Judging from this kind of distribution, these bats do not move frequently from island to island. Possibly this is because they cannot easily cross water barriers, or are not inclined to do so because food is abundantly available throughout the year on their home

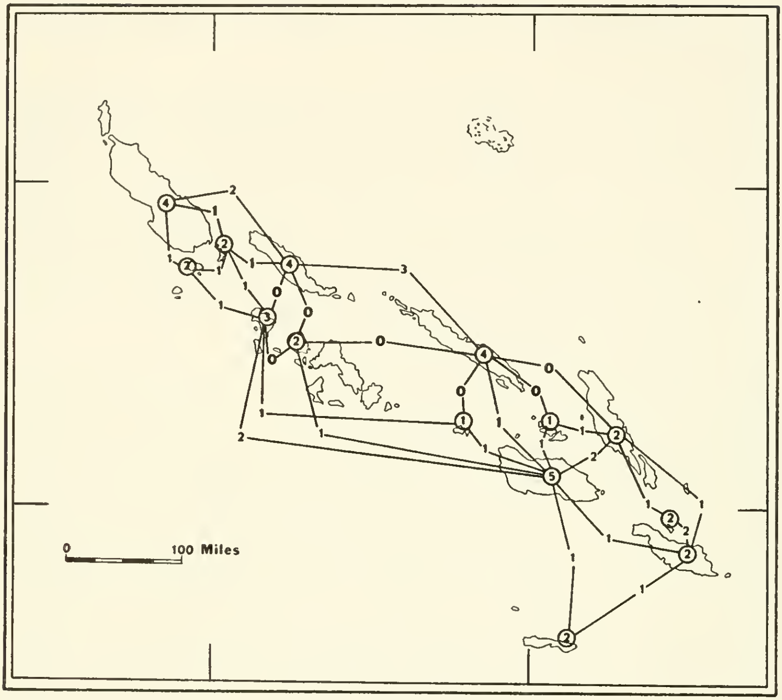

FIG. 17. The number of subspecies of megachiropterans known from individual islands (number within a circle) is compared with the number of subspecies common to different islands (number without a circle). For names of islands see Fig. 2.

island. Because "flying foxes" frequently are seen in flight over water several hundred yards from shore, the first factor probably is unimportant—at least where short distances are involved. It seems most likely that when abundant food is available these bats have no reason to move even moderate distances.

Distributions of subspecies of polytypic species are summarized in Table 6 and Figure 17. Generally, more subspecies are known from the larger islands than from the smaller islands (Guadalcanal with 5, Bougainville, Choiseul, and Santa Ysabel with 4, Fauro with 2.) The distributions of some subspecies can be used to judge the differential effectiveness of water gaps between islands. The distribution of *Pteropus rayneri lavellanus* and *P. rayneri rubianus* is an example.

Choiseul and Santa Ysabel are separated by about 50 miles of water see Fig. 17) but have three subspecies in common (*Pteropus rayneri grandis, Dobsonia inermis minimus,* and *Nyctimene albi-*

venter minor.) Choiseul is about 50 miles from Kolombangara and about 35 miles from Vella Lavella, but shares no subspecies with these smaller islands although some species are shared (Tables 5 and 6). From these data one can conclude that exchange of genes between populations on Choiseul and populations on Santa Ysabel is frequent but for some reason exchange of genes between populations on Vella Lavella and Choiseul and Kolombangara and Choiseul is infrequent. A series of small islands (Rob Roy, Wagina, and the Arnavon Islands, not named on the maps) connect Choiseul and Santa Ysabel in stepping-stone fashion (see Fig. 17). Possibly these small islands enhance movement of megachiropterans between Choiseul and Santa Ysabel.

TABLE 6. A Summary of Distribution of Polytypic Species of Megachiropteran Bats in the Solomon Islands. Only Islands Well Known Faunistically Are Listed.

SUBSPECIES	Bougainville	Choiseul	Santa Ysabel	Ndai	Malaita	Florida	Fauro	Shortland	Vella Lavella	Kolombangara	Russell	Guadalcanal	San Cristobal	Ugi	Rennell	Ontong Java
P. atrata atrata	X	X														
P. atrata anceps			X									X				
Pt. a. solomonis									X		X	X				
Pt. a. colonus								X								
Pt. a. grandis				X												
Pt. r. rayneri					X							X				
Pt. r. grandis	X	X	X													
Pt. r. rubianus										X						
Pt. r. lavellanus									X							
Pt. r. monoensis																X
Pt. r. cognatus													X	X		
Pt. r. rennelli															X	
D. i. inermis	X				X	X	X	X	X			X	X	X	X	
D. i. minimus		X	X													
N. a. bougainville	X									X		X				
N. a. minor		X	X				X									
Totals	4	4	4	1	2	1	2	2	3	2	1	5	2	2	2	1

Florida, of the Nggela Group, is approximately halfway between Santa Ysabel and Guadalcanal. *Pteralopex atrata anceps* occurs on Santa Ysabel and on Guadalcanal but is unknown from Florida. Fauro lies between Bougainville and Choiseul. *Pteralopex atrata atrata* and *Pteropus rayneri grandis* occur on Choiseul and on Bougainville but are unknown from Fauro. As suggested earlier, small islands like Fauro and Florida possibly cannot support large fruit bats, although they probably would utilize these small islands when in transit between larger islands.

Fauro apparently is important to the distribution of the two subspecies of *Dobsonia inermis* and *Nyctimene albiventer* in the Solomons (see Figs. 9 and 13). In both species, one subspecies is found in the eastern chain of islands and one subspecies is found in the western chain. Specimens of *Dobsonia inermis* from Fauro and Bougainville can be identified as the subspecies *inermis* whereas those from Choiseul are assignable to the subspecies *minimus*. *Nyctimene albiventer bougainville* occurs on Bougainville but specimens of *N. albiventer* from Fauro and Choiseul can be identified as the subspecies *minor*. Although interchange of genes occurs between populations on Bougainville and Fauro in the case of *D. inermis,* the population of *N. albiventer* on Fauro is at least partially isolated from the population on Bougainville.

Rennell and Ontong Java are relatively isolated from other islands in the Solomons (see Fig. 17). Only one kind of bat (*Pteropus howensis*) is known from Ontong Java and apparently is endemic to that atoll. *Pteropus tonganus geddiei,* one of the megachiropterans that occurs on Rennell (Table 5), also is found in the New Hebrides and on New Caledonia (Table 4). This makes *P. t. geddiei* the only megachiropteran bat in the Solomons that is more closely related to bats on islands to the southeast of the Solomons than to bats on other islands of the Solomons, the Bismarcks, or New Guinea, to the north and west. The other species of megachiropterans (*Dobsonia inermis* and *Pteropus rayneri*) on Rennell are found also on other islands in the Solomons. It is to be noted that Mayr (1931) regarded the avifauna of Rennell as most nearly like that of the New Hebrides and New Caledonia. He suggested that the prevailing winds from the southeast have been important for birds that have reached Rennell. The New Hebrides and New Caledonia are four and a half times farther from Rennell than are San Cristobal and Guadalcanal. On first consideration a person might doubt that the winds would be favorable enough to compensate for the great distance between Rennell and the New Hebrides and New Caledonia. Darlington (1938) has used the formula $X^{n/m}$ to obtain a comparison of barriers of different widths. [$X =$ the probability of an individual crossing a barrier of width m; the probability of an individual crossing a similar barrier of width n is the ratio n/m.] If this formula is applied here, one finds that winds from the southeast (that is, from the New Hebrides and New Caledonia) would have to be more than 100 times more favorable than winds from the northeast (from Gaudalcanal and San Cristobal) in order to compensate for the distance of Rennell from the New Hebrides and New Caledonia. Even so, tropical storms with unusually strong winds, frequent during some parts of the year, possibly account for the present distributional pattern of bats and birds that live on Rennell.

Whatever the means by which bats of the species *P. tonganus* reached Rennell, the fact remains that specimens from Rennell cannot be distinguished from specimens of *P. tonganus geddiei* from the New Hebrides and New Caledonia, more than 500 miles to the southeast.

NOTE: An important and interesting paper on zoogeography of bats, which was published too late to be included here, is: Krzanowski, A., 1967, The magnitude of islands and the size of bats (Chiroptera), Acta Zool. Cracoviensia, 12:281-348.

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New systematic names are in **boldface** type