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CHARACTER GRADIENTS IN THE SPINY POCKET
MOUSE, *LIOMYS IRRORATUS*

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INTRODUCTION

THE Museum of Zoology has long had especial interest in zoogeographic problems in Mexico. In 1908, Ruthven demonstrated the great importance of Mexico as a differentiation and dispersal center for terrestrial vertebrates (Ruthven, 1908). Since then, many studies have been conducted in that country by members of the staff and their students. Each study is part of a long-term project designed to yield detailed knowledge of the Mexican fauna. That information is essential to an understanding of the evolutionary development and systematic relationships of the North American fauna. Current emphasis is placed on the south-central part of the Mexican highlands, and several expeditions recently have been sent to that section. Also, large collections, principally of mammals, have been obtained from the area by Dr. Helmuth O. Wagner. As a result there is now at hand sufficient data on a few mammal kinds to permit critical analysis of some zoogeographic problems.

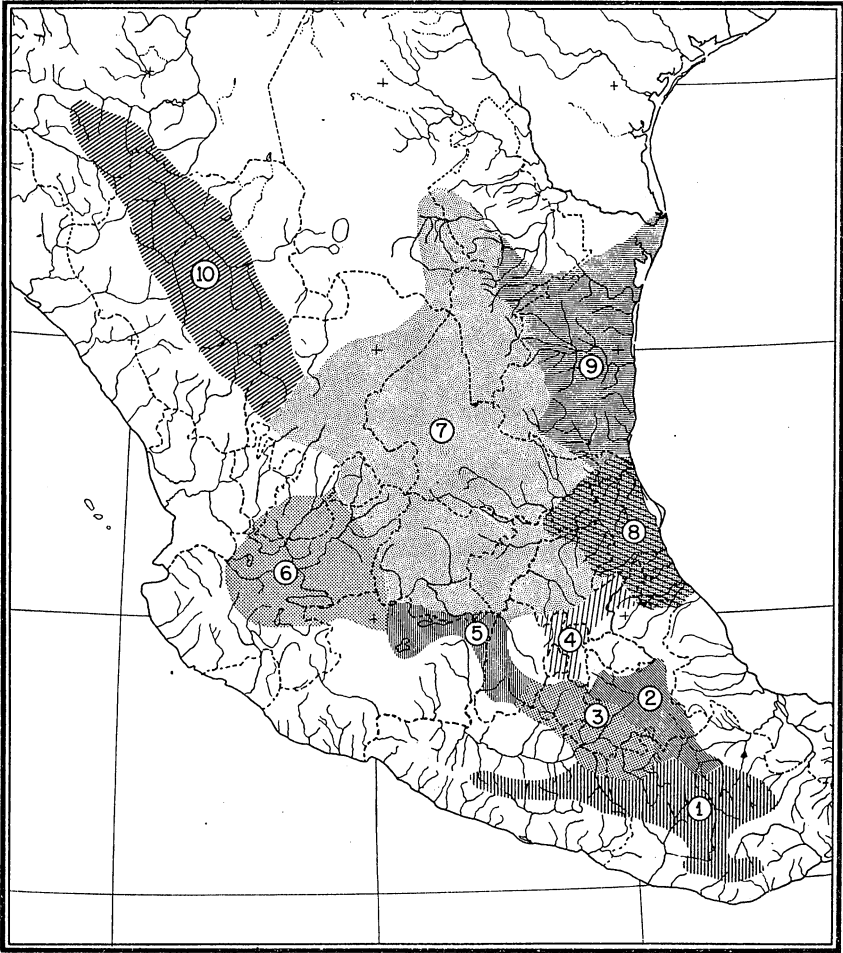
In the present study we have been interested primarily in the distribution of the external and cranial characteristics of

Liomys irroratus in the region about the Balsas basin. There the interior highlands and adjoining lofty mountains that extend from northern Mexico to the Isthmus of Tehuantepec are interrupted by a series of low-lying valleys and ridges, which are drained by the Río Balsas to the west and the Río Santo Domingo to the east. These areas are hot and dry and contrast strongly with the cooler, more humid mountains and plains, several thousand feet higher, of the *tierra templada* and *tierra fría* to the north and south. Altitudinal gradients vary greatly in the region, but in general, with respect to horizontal distance, they are steep on the west and more gradual on the east.

Our best samples are from the northern and eastern segment of the region and represent localities in a transect across the southern part of the Mexican Plateau, from the oak-pine zone, 7000–8500 feet, near Patzcuaro (Michoacán) and Mexico City, down the southeastern slope of the Plateau to the xeric shrub of the dry valley at Teotitlán and Cuicatlan, elevation 2000–3000 feet, thence upslope into the *tierra templada* in the vicinity of Oaxaca City. Insofar as known the species does not occur below 2000 feet in the Balsas Valley. (It is replaced there by *Liomys pictus*.) It ranges approximately from sea level in northern Veracruz, Tamaulipas, and southern Texas to 8500 feet near Mexico City.

To appraise fully the systematic value of some of the character gradients observed in the specimens from the Balsas basin region, we found it necessary to study specimens of the other subspecies. In so doing we accumulated facts which permit a cursory review of geographic variation in the species. Some of those data are presented in the accounts which follow.

Most of the specimens used in the study are deposited in the Museum of Zoology, University of Michigan. Those identified with the symbol (U.S.) or (M.V.Z.) are contained, respectively, in the collections of the U. S. Fish and Wildlife Service and of the Museum of Vertebrate Zoology of the University of California. For the use of specimens from those collections we thank Stanley P. Young and Seth B. Benson.



MAP 1.—A part of Mexico showing the distribution of the ten subspecies of *Liomys irroratus* here recognized, as determined from specimens examined and from published records. The subspecies are as follows: 1, *irroratus*; 2, *torridus*; 3, *minor*; 4, *pullus*; 5, *acutus*; 6, *jaliscensis*; 7, *alleni*; 8, *pretiosus*; 9, *texensis*; 10, *canus*.

William B. McIntosh assisted with the statistical calculations.

Capitalized color terms are from Ridgway (1912). All measurements are in millimeters. Those of the skin were taken by the collector. The authors measured the skulls, using dial calipers reading to tenths of millimeters and aided by a low-power microscope. Some of the measurements are standard in mammalogy. Others require description:

Cranial breadth.—The greatest transverse breadth of the brain case on a plane dorsal to the zygomatic process of the squamosal. The error in determining this dimension is greater than that for the other cranial measurements except length of interparietal.

Cranial depth.—The dorsoventral diameter of the skull, from the dorsal limit of the brain case to a plane that passes through the tips of the incisors and the ventral border of the auditory bullae.

Nasal length.—The total distance between the anterior and posterior limits of the nasal bone, including attenuate processes. In most skulls, because the posterior limit of the nasal bone is situated laterally, whereas the anterior limit is medial, this dimension is determined on the oblique, not parallel to the internasal suture.

Breadth of rostrum.—The greatest breadth of the dorsal face of the rostrum, anterior to the zygomatic arch. Measured on the dorsal surface of the skull, from the anterodorsal junction of the premaxilla (ascending branch) and maxilla (anterior base of zygomatic arch) to the corresponding point on the opposite side of the rostrum.

Breadth of interparietals.—The greatest transverse diameter of both interparietals, including attenuate processes. Measured at a right angle to the long axis of the skull.

Length of interparietals.—The anteroposterior diameter of the interparietals, as measured on the mid-dorsal, longitudinal axis. Narrow processes of the interparietals or of the supra-occipital or parietals are not included. The amount of error in determining this dimension is greater than that for the others.

The rectangles in Figure 1 require explanation. Each represents the upper and lower limits of two standard errors (of the mean) added to and subtracted from the mean. A difference between two means greater than two standard errors of each of those means is considered to be statistically significant; in that instance the two rectangles do not overlap.

GENERAL ACCOUNTS

Liomys irroratus irroratus Gray

Heteromys irroratus Gray (1868: 205). Oaxaca, near Oaxaca City (fide Goldman, 1911: 53).

Heteromys albolimbatus Gray (1868: 205). Oaxaca, 15 miles northeast of Oaxaca City, La Parada (fide Goldman, *ibid.*).

Liomys irroratus Gray, Goldman (*ibid.*).

Liomys irroratus irroratus Gray, Miller (1912: 257).

RANGE.—High plains and mountain slopes of central Oaxaca and Guerrero. Known range from Cerro Zempoaltepec and the Sierra Juarez, Oaxaca, west to the vicinity of Chilpancingo, Guerrero. Altitudinal range, approximately 4500–8000 feet.

CHARACTERS AND COMPARISONS.—A moderate-sized spiny pocket mouse, with pale grizzled upper parts, a narrow but distinct lateral line, white underparts, relatively small zygomatic spread, long, posteriorly attenuate nasals, narrow rostrum and narrow frontals (interorbitally).

Skull: Dorsal profile convex, sloping gradually anteriorly and posteriorly from dorsal limit of the skull near the junction of the frontals and parietals. Supraorbital and parietal ridges lyre-shaped and continuous with the lambdoidal ridge. Nasals broad and slightly, notched terminally, narrowing gradually to acuminate bases anterior to the posterior limits of the premaxillae. Zygomata moderately spread, their lateral limits about those of the auditory bullae. Premaxillae extending almost to a level of the orbits, their dorsal faces usually broader than the nasals posteriorly, and gradually narrowed and depressed toward the base of the incisors. The combined interparietals vary from rectangular to obovoid, and are about

TABLE I

Average and extreme measurements of females of ten subspecies of *Liomys irroratus*. All specimens are of medium age; premolar and molar teeth worn. Measurements in millimeters; superscripts indicate number of specimens, if fewer than given in column at left.

Subspecies and Specimens	Locality	Total Length	Tail Vertebrae	Hind Foot	Ear from Notch	Greatest Length of Skull	Zygomatic Breadth	Cranial Breadth
<i>irroratus</i> , 5	Oaxaca City	265 252-275	143 132-157	32 31-32	32.8 31.8-33.4	15.4 15.1-15.7	13.1 12.6-13.4
<i>torridus</i> , 11	Teotitlán	236 ¹⁰ 221-262	130 ¹⁰ 118-153	27 26-29	14 12-16	30.3 ⁹ 29.2-31.4	14.4 ¹⁰ 13.4-15.1	12.2 ¹⁰ 11.6-12.7
<i>minor</i> , 4	Morelos	224 202-238	119 108-133	27 26-28	29.9 ² 29.5-30.2	14.83 14.0-15.4	12.03 11.9-12.1
<i>pallus</i> , 5	Distrito Federal	238 ⁴ 229-250	128 ⁴ 124-132	31 29-32	15 14-15	34.0 ⁴ 33.3-34.6	16.4 ⁴ 15.4-17.4	13.1 ⁴ 12.9-13.3
<i>acutus</i> , 4	Patzcuaro	244 230-251	118 105-129	31 30-33	14 ³ 13-15	33.4 ³ 32.5-34.2	16.4 16.1-17.0	13.3 13.1-13.5
<i>jalscensis</i> , 6	Chapala	222 ⁵ 212-235	114 ⁵ 108-123	28 27-29	15 14-16	30.8 30.3-31.4	15.1 14.9-15.4	12.9 12.7-13.1
<i>alleni</i> , 3	Parral	248 236-255	132 123-141	33 32-34	33.5 ² 32.0-34.9	15.8 ² 15.5-16.0	12.9 12.7-13.1
<i>pretiosus</i> , 3	Río Verde	224 216-233	114 107-123	29 28-31	15 15-15	32.1 31.2-33.3	15.2 15.1-15.3	12.5 12.4-12.7
<i>teacensis</i> , 2	Nautla	220 219-221	113 111-115	28 27-29	14 14-14	31.0 30.9-31.0	15.5 ¹ 15.5 ¹	12.6 12.4-12.7
<i>canus</i> , 3	Antiguo Morelos	255 ² 247-263	130 ² 128-132	33 33-34	34.6 ² 34.4-34.7	16.9 ¹ 16.9 ¹	12.8 ² 12.7-12.9

TABLE I (Cont.)

Subspecies and Specimens	Locality	Cranial Depth	Interorbital Breadth	Length of Nasals	Breadth of Rostrum	Breadth of Interparietals	Length of Interparietals
<i>irroratus</i> , 5	Oaxaca City	11.1 10.8-11.5	7.8 7.5-8.0	13.5 12.5-14.1	6.0 5.7-6.3	8.6 8.5-8.8	3.9 3.7-4.1
<i>torridus</i> , 11	Teotitlán	10.310 10.1-10.6	7.6 7.0-8.1	12.2 11.5-13.0	5.6 5.1-6.1	8.210 6.7-9.1	3.4 3.0-3.9
<i>minor</i> , 4	Morelos	10.63 10.4-10.7	7.2 7.0-7.3	12.12 12.0-12.2	5.4 4.9-5.9	7.83 7.6-8.1	3.63 3.4-3.9
<i>pallus</i> , 5	Distrito Federal	11.53 11.3-11.7	8.4 8.1-8.7	13.4 12.9-14.1	6.2 6.0-6.6	8.5 8.0-8.7	4.1* 3.8-4.3
<i>acutus</i> , 4	Patzcuaro	11.8 11.5-11.9	7.8 7.5-8.0	13.9 13.2-14.5	6.5 6.5-6.6	7.9 7.2-8.5	4.1 3.4-4.5
<i>jalsicensis</i> , 6	Chapala	10.9 10.6-11.1	7.9 7.7-8.2	12.2 11.7-12.6	5.7 5.4-5.9	8.4 8.2-8.7	3.4 3.3-3.7
<i>alleni</i> , 3	Río Verde	11.22 11.0-11.4	8.1 7.6-8.8	13.6 13.0-13.9	6.4 6.0-7.0	9.1 8.5-9.8	4.3 4.0-4.9
<i>pretiosus</i> , 3	Nautla	10.9 10.6-11.1	7.7 7.4-8.0	13.1 12.6-13.9	6.7 6.4-7.0	8.8 8.6-8.9	4.1 3.9-4.4
<i>texensis</i> , 2	Antiguo Morelos	11.1 10.6-11.6	7.6 7.5-7.7	12.1 11.9-12.2	5.9 5.8-6.0	7.7 7.5-7.8	3.7 3.6-3.8
<i>canus</i> , 3	Parral	11.72 11.5-11.8	8.6 8.5-8.8	13.6 13.3-14.0	6.6 6.5-6.7	8.6 8.2-9.0	4.22 4.1-4.2

TABLE II

Average and extreme measurements of males of ten subspecies of *Liomys irroratus*. All specimens are of medium age; premolar and molar teeth worn. Measurements in millimeters; superscripts indicate number of specimens, if fewer than given in column at left.

Subspecies and Specimens	Locality	Total Length	Tail Vertebrae	Hind Foot	Ear from Notch	Greatest Length of Skull	Zygomatic Breadth	Cranial Breadth
<i>irroratus</i> , 4	Oaxaca City	271 ³ 259-295	149 ³ 139-163	33 ³ 32-35	33.8 32.8-35.4	15.9 15.2-17.2	13.0 ³ 12.8-13.4
<i>torridus</i> , 16	Teotitlán	246 ¹⁴ 230-275	136 ¹⁴ 121-150	28 ¹⁵ 26-29	15 13-16	31.4 29.9-32.6	14.6 ¹⁴ 14.1-15.4	12.1 11.7-12.5
<i>minor</i> , 3	Morelos	240 215-263	129 112-142	27 26-27	30.7 ¹	14.7 ² 14.3-15.1	12.4 ² 12.2-12.6
<i>pullus</i> , 7	Distrito Federal	261 251-275	137 130-147	30 ⁶ 28-32	16 14-17	34.5 ³ 34.1-34.9	16.5 ⁵ 16.3-17.0	13.0 ⁵ 12.6-13.3
<i>acutus</i> , 4	Patzcuaro	252 235-267	124 114-130	31 29-32	16 15-16	34.3 32.6-35.1	17.0 ³ 15.8-17.7	13.5 13.1-13.9
<i>jaliscensis</i> , 2	Chapala	238 226-250	122 112-132	30 29-30	16 15-17	32.2 31.7-32.6	15.7 15.4-15.9	12.8 12.5-13.0
<i>alleni</i> , 1	Río Verde	260	133	32	34.2	16.1	12.9
<i>pretiosus</i> , 3	Puebla, Veracruz	249 240-263	135 125-145	30 28-34	14 ² 14-14	32.5 ² 32.4-32.5	12.9 12.7-13.1
<i>texensis</i> , 2	Antiguo Morelos	231 230-232	118 115-121	28 27-28	14 14-14	32.4 31.9-32.9	15.6 15.4-15.7	12.2 12.0-12.3
<i>canus</i> , 1	Parral	276	138	34	37.0	18.0	13.5

TABLE II (Cont.)

Subspecies and Specimens	Locality	Cranial Depth	Interorbital Breadth	Length of Nasals	Breadth of Rostrum	Breadth of Interparietals	Length of Interparietals
<i>irroratus</i> , 4	Oaxaca City	11.4 11.0-11.9	8.2 7.8-8.4	14.2 13.5-14.8	6.1 5.2-6.8	8.7 ³ 8.5-9.0	4.0 3.8-4.2
<i>torridus</i> , 16	Teotitlán	10.5 10.0-11.1	7.6 7.2-7.9	12.9 11.8-13.6	5.7 5.1-6.4	8.3 7.2-9.0	3.6 3.2-4.0
<i>minor</i> , 3	Morelos	10.8 10.6-11.0	7.2 7.0-7.3	11.8 ¹	5.4 5.1-5.7	8.1 7.6-8.7	3.6 3.5-3.8
<i>pullus</i> , 7	Distrito Federal	11.5 ⁶ 11.2-11.6	8.6 8.3-8.9	14.1 13.8-14.5	6.3 5.9-6.6	8.6 ⁵ 8.0-9.1	3.9 ³ 3.6-4.1
<i>acutus</i> , 4	Patzcuaro	11.9 11.7-12.0	8.1 7.8-8.5	14.6 13.9-15.2	6.4 5.8-7.1	7.4 7.1-7.8	3.5 3.0-4.0
<i>jaliscensis</i> , 2	Chapala	11.0 10.8-11.2	8.1 8.0-8.2	12.6 12.2-13.0	5.9 5.6-6.2	8.7 8.6-8.7	3.7 3.7-3.7
<i>alleni</i> , 1	Río Verde	11.6	8.5	14.2	6.2	8.5	4.2
<i>pretiosus</i> , 3	Puebla, Veracruz	11.1 ² 11.0-11.2	7.6 7.3-8.2	13.0 12.6-13.5	6.4 6.0-6.8	9.0 ² 9.0-9.0	4.1 ² 4.0-4.1
<i>texensis</i> , 2	Antiguo Morelos	11.0 10.9-11.0	8.0 7.9-8.0	13.0 12.5-13.4	6.4 6.1-6.7	7.7 7.5-7.8	3.5 3.4-3.6
<i>canus</i> , 1	Parral	12.2	9.3	14.7	7.3	9.5	4.2

twice as wide as long. Audital and mastoidal bullae small, the former discoidal in shape.

Color: (May pelage from Oaxaca and Ejutla) Mass effect of upper parts grizzled orange buff and black, the buff purest on the sides, the black concentrated dorsally in a faint, broad, longitudinal band. Spines translucent and apparently without pigment except terminally; the tips are black. Soft body hairs four-banded: a basal band (comprising about one-half of the hair) colorless or pale gray, a medial band of black, a subterminal band of Orange-Cinnamon, and a terminal colorless or white band. Lower sides paler than back, the spines and soft body hairs gray, and sharply demarked from the entirely white underparts by a lateral line of Light Pinkish Cinnamon which extends from the nose almost to the ankles. Ears fuscous, rimmed with white. Nose grizzled, without cinnamon hues. Forelegs white ventrally, and white, pale gray, or Light Pinkish Cinnamon dorsally; upper surface of forefeet white. Hind legs white ventrally, pale gray dorsally, and Light Pinkish Cinnamon or white laterally; upper surface of hind feet white; ankles dusky, edged with Light Pinkish Cinnamon. Tail sharply bicolor, fuscous above and white below, except at the tip where it is dark all around.

REMARKS.—*Liomys irroratus irroratus* is the largest of the three known pale races that inhabit the mountains and valleys south of the Río Balsas. Its coloration is similar to that of *minor*; both are darker than *torridus*. Its relatively narrow rostrum and long nasals are essentially matched in both *torridus* and *minor*.

The specimens from Chilpancingo are morphologically between *irroratus*, *minor*, and *torridus*, as we see the characters in topotypes of those races. In average size they are between *irroratus* and *minor* and *torridus*. In characters of the rostrum they resemble *minor*. They are darker and more pinkish than in either of those races, as judged from the specimens at hand. Specimens from Tehuacan and Tepanco, here referred to *torridus*, resemble them in color. All features considered,

the Chilpancingo specimens perhaps can best be included with *irroratus*.

We have followed Goldman in treating *albolimbatus* as a synonym of *L. i. irroratus*.

A specimen from Ixtlan, in the Sierra Juarez, and another from Miahuatlan, Oaxaca, have blackish, rather than gray, upper parts, including back, sides, head, ears, legs, and upper surface of the tail. They resemble some examples of *acutus* from Michoacán and *pullus* from Mexico City. No other specimens of *Liomys irroratus* from the plains and mountains of Oaxaca are so deeply pigmented. They are so much darker than any other example from Oaxaca that one suspects a second species. Except in coloration we find no other characters to distinguish them from topotypes of *irroratus*. We do not now understand the reasons for the occurrence of a few black examples among many much paler specimens.

SPECIMENS EXAMINED.—A total of sixty-nine from localities as follows: Guerrero, Chilpancingo, 4500 feet, forty-six. Oaxaca, Cerro San Felipe, two (U.S.); Cerro Zempoaltepec, five (U.S.); Ejutla, 4700 feet, two; Sierra Juarez, Ixtlan, 8000 feet, one; Miahuatlan, 5000 feet, one; Oaxaca City, 5000 feet, ten (9 U.S.); Sola de la Vega, one; Yalalag, one (U.S.).

Liomys irroratus torridus Merriam

Liomys torridus Merriam (1902: 45). Oaxaca, Cuicatlan.

Liomys irroratus torridus Merriam, Goldman (1911: 55).

RANGE.—Arid interior slopes and valleys east of the Río Balsas drainage in northern Oaxaca and southeastern Puebla. Known geographic and altitudinal range from Cuicatlan, 2500 feet, Oaxaca, north to Tepanco, 5700 feet, Puebla.

COMPARISONS.—One of the smallest and palest of the races of *Liomys irroratus*. Similar to *minor* (see measurements), but slightly paler and possibly slightly larger; and on the average with longer nasals, longer and less tapered rostrum, shallower, longer brain case, and parallel-sided zygomata (markedly narrowed posteriorly in *minor*). Smaller than

irroratus; colors of upper parts more dilute, the cinnamon hues (prominent in *irroratus*) essentially lacking, the mass effect thus buffy gray rather than pinkish gray; lateral line paler; skull less massive; and interparietals relatively broader. Compared with *pullus*, *torridus* is much smaller, has a relatively longer tail (averages 120–30 per cent of head and body length in *torridus* and 110–16 per cent in *pullus*), and is everywhere less intensely pigmented; the upper parts are pale buffy gray, rather than deeply grizzled, on the back, ears, legs, and tail; the underparts are white, without a buffy wash; the mid-dorsal stripe is indistinct or absent, and the lateral line is much more prominent. Relative to the length of the skull the nasals average shorter and the interparietals narrower.

REMARKS.—The combination of paleness, smallness, relatively long tail and long nasals, and broad interparietals is best developed in the samples from Teotitlán and Cuicatlan. Specimens from other localities—all of higher elevation and outside the valley in which those towns are situated—grade toward other races. As is usual when one is dealing with character gradients, the assignment of specimens that are geographically and morphologically between two or more namable extremes is to a certain extent arbitrary. Total resemblance usually decides the placement. The specimens from Tehuacan and Tepanco present a combination of characters that is different from the set observed in other areas of southern Puebla and in Oaxaca. However, each of those characters attains its maximum or minimum development in populations to the north, south, east, or west of Tehuacan and Tepanco. In every sense, then, those specimens are intermediate. To recognize them by name as representing a geographic race would acknowledge unduly intermediate populations. The Tehuacan and Tepanco specimens are about as pale as those from Teotitlán, but they are pinkish cinnamon rather than creamy buff in hue, and they are larger. In size and hue, but not tone, they resemble the specimens from Chilpancingo—here referred to the race *irroratus*—and fur-

ther like those, are intergrades between pale and dark, and large and small forms that occupy adjoining areas.

Two immature specimens from Acultzingo are tentatively referred to *torridus*, although the only skull present has a relatively much larger brain case than have other examples of that race.

SPECIMENS EXAMINED.—A total of ninety-eight from the following localities: Oaxaca, Cuicatlan, 2500 feet, twelve (U.S.); Teotitlán, 3100 feet, thirty-six. Puebla, Tehuacan, 5400 feet, thirty; Tepanco, 5700 feet, eighteen. Veracruz, Acultzingo, 7000 feet, two.

Liomys irroratus minor Merriam

Liomys torridus minor Merriam (1902: 45). Oaxaca, Huajuapam.

Liomys irroratus minor Merriam, Goldman (1911: 56).

RANGE.—Upper slopes and plains of the Río Balsas drainage basin in northwestern Oaxaca, eastern Guerrero, southwestern Puebla, and Morelos. Known range from Huajuapam and Tlapacingo, Oaxaca, north to Cuernavaca and Yautepec, Morelos. Altitudinal range from 3000 feet at Puente de Ixtle, to 5000 feet at Huajuapam.

COMPARISONS.—Size as in *torridus*; color much as in *irroratus*; distinguishable from both, and from other races to the north, by its relatively short and strongly tapered rostrum, deep brain case, and posteriorly narrowed zygomata—the anterior diameter of which is greater than is the posterior diameter, a character which is also shared by *pullus*.

For comparisons with *pretiosus*, *acutus*, and *pullus*, see the accounts of those forms.

REMARKS.—More complete material than is now available may show that *minor* is unrecognizable as a geographic race. Of the thirty specimens to which the name is here applied, only nine are old enough for close comparison with our examples of other races; they differ considerably from each other. The skull of the type specimen is unlike the other examples of *minor*, and, for that matter, it is dissimilar to most examples

of *L. irroratus* from southern Mexico. In shape of brain case and rostrum it resembles some specimens of *Liomys pictus*. The specimens from Ixtle approach the type in some characters; those from Cuernavaca and, especially, those from Yautepec are less like the type. In coloration, all are indistinguishable from specimens of *irroratus* from Chilpancingo; the Chilpancingo specimens, however, are larger and slightly different cranially. In size, our specimens of *minor* are matched by examples of *torridus* from Teotitlán. However, the short, strongly tapered rostrum, deep brain case, and posteriorly narrowed zygomata that are seen in the scanty samples from the area here ascribed to *minor* are not well shown elsewhere. These features tentatively are interpreted as population characteristics.

SPECIMENS EXAMINED.—A total of thirty from the following localities (all specimens U.S.): Morelos, Cuernavaca, 5000 feet, two; Puente de Ixtle, 3000 feet, four; Yautepec, 5000 feet, twenty-two. Oaxaca, Huajuapam, 5000 feet, one; Tlapancingo, one.

Liomys irroratus pullus Hooper

Liomys irroratus pullus Hooper (1947: 47). Mexico, Distrito Federal, Tlalpam, elevation 7500 feet.

RANGE.—Known only from localities near Mexico City, 7500–8500 feet.

COMPARISONS.—*L. i. pullus* is one of the larger and darker races of the species. Its size apparently is exceeded only by the pale form, *canus*, of northern Mexico. It is closely matched in size and color by *acutus*, but the two forms are distinct in cranial characters (see the account of *acutus*). Compared with *alleni*, *pullus* averages larger and more blackish dorsally; its lateral line is less distinct; its skull is larger, with anteriorly broad zygomata (broadest posteriorly or parallel in *alleni*), smaller auditory bullae, and smaller interparietals (seen in both length and breadth). It is much larger and darker than *minor* is. For comparisons with *pretiosus* and *torridus*, see the accounts of those races.

REMARKS.—To the north of the Valley of Mexico the characters of *pullus* grade into those of the paler and slightly smaller *alleni*. Examples at hand from Zimapan, Hidalgo, are referable to *alleni*. We have not examined the specimens listed by Davis (1944: 389) from a locality 23 kilometers east of Mexico City and can make no original statement regarding their racial identity.

SPECIMENS EXAMINED.—A total of forty-two from the following localities: Distrito Federal, Contreras, 8500 feet, three; San Gerónimo, 7800 feet, twenty-seven; Tlalpam, 7500 feet, eleven. Mexico, Hacienda Cordoba, 8500 feet, one.

Liomys irroratus acutus Hall and Villa

Liomys irroratus acutus Hall and Villa (1948: 253-55). Michoacán, two miles west of Patzcuaro, 7700 feet elevation.

RANGE.—Mountainous southern part of the Mexican Plateau in northeastern Michoacán and western Mexico. Known geographic and altitudinal range from the vicinity of Patzcuaro, 7800 feet, and Cuitzeo, Michoacán, east to Temescaltepec, Mexico, 5000 feet.

COMPARISONS.—All characters considered, *acutus* resembles *pullus* more than it does any other race of *Liomys irroratus*. In size and coloration of the upper parts the two subspecies differ very little. As judged by our series of specimens, *acutus* is less blackish and has a more distinct and continuous lateral line and pinkish cinnamon rather than buffy underparts. Because the pelages of the two series are not strictly comparable, these color differences may be seasonal variations. The tail of *acutus* is shorter (about equal to head and body; 110-16 per cent of head and body length in *pullus*). Crani-ally, *acutus* differs from *pullus* in the following characters: brain case broader and deeper; frontals narrower (see measurements of interorbital diameter); interparietals narrower; and nasals longer and posteriorly acuminate (short and truncate in *pullus*).

Compared with *alleni* and *irroratus*, *acutus* is slightly larger,

more intensely pigmented dorsally and ventrally, and shorter-tailed. It differs further from *irroratus* as follows: cranium larger (well seen in zygomatic breadth and depth of cranium); rostrum broader and heavier and interparietals narrower. Its cranium is also broader and deeper than is that of *alleni*; the frontals are narrower interorbitally; the nasals are usually longer and posteriorly acuminate in shape; and the interparietals are much smaller in length and breadth.

Compared with *minor* and *jaliscensis*, *acutus* is considerably larger (see measurements), is more blackish dorsally, and has a greater suffusion of pinkish cinnamon ventrally. On the average, its cranium is actually and relatively deeper than is that of *jaliscensis*, the interorbital diameter is proportionally smaller, the nasals are longer and more pointed posteriorly, and the interparietals narrower and oval, rather than rectangular. In general proportions, the skulls of *acutus* and *minor* are similar, except that in *acutus* the zygomata are less constricted posteriorly, the brain case is broader, the rostrum stouter and broader anteriorly, and the interparietals are shorter and narrower.

REMARKS.—That *acutus* intergrades with *jaliscensis* is indicated by specimens from Cuitzeo. These are like *jaliscensis* in size, and between the two races in color, but nearer *acutus*. They further resemble *acutus* in their short tail, relatively large brain case, narrow frontals, long, acuminate nasals, and narrow interparietals. A specimen from fifteen miles east of Morelia has shorter nasals and larger interparietals than those from Patzcuaro or Cuitzeo. Although tentatively referable to *acutus* on the basis of their coloration, length of tail, and size of brain case and interparietals, four subadult specimens from Temescaltepec grade toward the smaller, southern races, *minor* for example, in size and narrowness of the rostrum.

SPECIMENS EXAMINED.—A total of forty from the following localities: Mexico, Temescaltepec, 5000 feet, four. Michoacán, four miles south of Cuitzeo, 5900 feet, nineteen; fifteen miles

east of Morelia, 7000 feet, one; vicinity of Patzcuaro, 6700–7800 feet, sixteen (fourteen M.V.Z.).

Liomys irroratus jaliscensis Allen

Heteromys jaliscensis Allen (1906: 251–52). Jalisco, twenty miles west of Zapotlan, Las Canoas, 7000 feet elevation.

Liomys irroratus jaliscensis Allen, Goldman (1911: 60–61).

RANGE.—Southwestern part of the Mexican Plateau, in Jalisco and the adjoining states to the east and north. Known range from Ameca and Etzatlan, Jalisco, east and south to Zamora, Michoacán. Altitudinal range approximately 4500–6000 feet.

COMPARISONS.—*L. i. jaliscensis* is a moderately small, pale race that closely resembles *L. i. alleni* in most features except size (see measurements), as judged from specimens respectively from Chapala and Río Verdi. Only in the size of the interparietals and bullae do we find additional characters other than size that will distinguish the two forms. On the average, the interparietals of *jaliscensis* are relatively shorter and the auditory bullae are relatively smaller. To judge from Goldman's (1911: 60–61) data and from the small number of specimens that we have examined, *L. i. jaliscensis* averages smaller and slightly darker than *L. i. canus*.

Compared with *irroratus*, *jaliscensis* averages slightly smaller and darker; the tail is relatively much shorter, the underparts are faintly washed with pinkish cinnamon (not pure white); the dark dorsal stripe, faint or absent in *irroratus*, is prominent; the frontals are broader interorbitally; the posterior border of the nasals is usually truncate, rather than acuminate; and the rostrum is slightly heavier.

For evidence of intergradation of *jaliscensis*, see the accounts of *acutus*.

SPECIMENS EXAMINED.—A total of fifteen from the following localities in Jalisco: Ameca, 4500 feet, one (U.S.); Atemajac, three (U.S.); three miles northwest of Chapala, 5100 feet, eight; Etzatlan, 4500 feet, one (U.S.); eight miles south of Guadalajara, two.

Liomys irroratus alleni Coues

Heteromys alleni Coues (1881: 187-189). San Luis Potosí, Río Verde.
Liomys irroratus alleni Coues, Goldman (1911: 56-57).

RANGE.—Central and eastern parts of the Mexican Plateau. Known range from the vicinity of Monterrey, Nuevo Leon, south to Chicalote, Aguascalientes, at west (*fide* Goldman, 1911: 56-57) and at least to Zimapan, Hidalgo, at east. Altitudinal range from 2700 feet, near Jaumave, Tamaulipas, to about 6000 feet at Zimapan.

COMPARISONS.—The race *alleni* differs from *irroratus* in average paler coloration, larger size, broader rostrum, posteriorly truncate (rather than acuminate) nasals, and consistently broader and longer interparietals. For other comparisons, see the accounts of other races.

REMARKS.—To judge from Goldman's data (1911: 56-57) and our more scanty material, the populations of spiny pocket mice of the north-central part of the Mexican Plateau are morphologically between those from adjoining areas. To these populations Goldman applied the name *alleni*. None of the characters ascribed to *alleni* is unique; each attains maximum or minimum development, or remains essentially unchanged, in adjoining areas. They provide the basis for recognition of the races *canus* and *jaliscensis* on the north and west, *texensis* and *pretiosus* on the east, and *pullus* and *acutus* on the south. All characters of *alleni*, so far as we have observed, are between two extremes or are equally shared by the races around the periphery of the plateau. Thus, in size, *canus*, *pullus*, and *acutus* are larger than *alleni*; *texensis* and *jaliscensis* are smaller. The race *texensis* is slightly paler; *pullus* and *acutus* are more intensely pigmented. The frontals are relatively broad in *texensis*, narrow in *acutus*, and intermediate in *alleni*. The large interparietals, characteristic of *alleni*, but not of *texensis*, *pullus*, and *acutus*, are shared with *pretiosus* and perhaps with *canus*. The moderately large bullae of *alleni* are also seen in all forms of the plateau except *jaliscensis*. Other traits of *alleni* are variously shared by

other races. The only justification for recognizing these intermediate populations by formal name is that over a large area they exhibit characters, none unique to the area, that as an aggregate are not seen elsewhere.

SPECIMENS EXAMINED.—A total of twenty-nine from localities as follows: Hidalgo, Zimapan, 6200 feet, three. San Luis Potosí, Río Verde, 4500 feet, four (U.S.). Tamaulipas, Jau-mave, 2600–3300 feet, twenty-one; Tula, 3900 feet, one.

Liomys irroratus pretiosus Goldman

Liomys irroratus pretiosus Goldman (1911: 58). Puebla, Metlaltoyuca.

RANGE.—Coastal plain and basal slopes of the Sierra Madre Oriental in northern Veracruz and Puebla and eastern Queretaro and San Luis Potosí. Known range from Valles, San Luis Potosí, and Jalpan, Queretaro, east and south to Nautla, Veracruz. Altitudinal range from near sea level at Nautla to about 2500 feet at Jalpan.

COMPARISONS.—Relative to the length of the skull, the frontals are narrower interorbitally, the rostrum is broader and shorter, and the nasals are anteriorly broader and more spatulate in shape in *pretiosus* than in any other known race of *Liomys irroratus*. Characters further distinguishing *pretiosus* from *pullus* are as follows: smaller size; paler, less blackish upper parts; a distinct lateral line (faint or absent in *pullus*); smaller molariform teeth; and relatively broader and longer interparietals. The same characters of the frontals, rostrum, and nasals contrast *pretiosus* with *alleni*; in addition, *pretiosus* averages slightly darker, the black dorsal stripe is better defined, and the teeth and auditory bullae are actually and relatively smaller.

L. i. pretiosus is much darker dorsally than *irroratus*, *minor*, or *torridus*. Further unlike those races, it has a distinct dorsal stripe and a broad lateral line, broad short rostrum, short and wedge-shaped nasals (long and only slightly expanded anteriorly in *irroratus*, *minor*, and *torridus*), narrow frontals, and large interparietals. It is intermediate in size

between *irroratus* on the one hand and *torridus* and *minor* on the other, and its tail is shorter than that of either *irroratus* or *torridus* (averages 110 per cent of body length, compared with values over 120 per cent).

For comparison with *texensis*, see the account of that race.

SPECIMENS EXAMINED.—A total of twelve from localities as follows: Puebla, Metlaltoyuca, 1000 feet, one (U.S.); Pahuatlan, 3600 feet, two. Veracruz, Nautla, near sea level, nine.

Liomys irroratus texensis Merriam

Liomys texensis Merriam (1902: 44). Texas, Cameron County, Brownsville.

Liomys irroratus texensis Merriam, Goldman (1911: 59).

RANGE.—Low plains and mountains east of the Sierra Madre Oriental in southern Texas, Tamaulipas, and eastern Nuevo León. Known range from Brownsville, Texas, south to the Sierra de Tamaulipas and west to the vicinity of General Terán and Montemorelos. Altitudinal range from near sea level, at Brownsville, to 2600 feet at Acuña in the Sierra de Tamaulipas.

COMPARISONS.—Similar to *alleni*, but averaging paler and smaller (see measurements) and having a relatively narrower skull (well seen in cranial breadth), with relatively broader frontals, much smaller interparietals (best seen in transverse diameter), and smaller bullae. *L. i. texensis* and *L. i. pretiosus* are similar in size, but *texensis* has paler upper parts, slightly broader frontals, smaller interparietals and much less massive rostrum, in which the dorsal arms of the premaxillae are narrower and the nasals are much less expanded anteriorly.

REMARKS.—Specimens from southern Tamaulipas indicate that *texensis*, *pretiosus*, and *alleni* intergrade in that area. A specimen from Acuña has a slightly heavier rostrum and a narrower interorbital space than have specimens from localities to the north; otherwise it agrees closely with them. Examples from Antiguo Morelos are like specimens of *texensis* from northern Tamaulipas in size, color, and dimensions of interparietals and brain case; but in characters of the rostrum

they approach, though by no means match, specimens of *pretiosus* from coastal Veracruz. The examples from Jaumave mostly resemble *alleni* from Zimapan in size and color, and their cranial characters are an assortment of features of the three races. In five of twelve skulls, the rostrum and nasals are almost as broad as in specimens of *pretiosus* from Veracruz; the other seven specimens have the narrower rostrum and nasals similar to those in *alleni* and *texensis*. In nasal length, interparietal length and breadth, interorbital breadth, and bullae size, some specimens match *pretiosus*, some agree with *alleni*, and some are intermediate. All characters and specimens considered, the series fits best with *alleni*.

At the eastern escarpment of the Sierra Madre Oriental, altitudinal and morphological gradients are comparatively steep. This is well seen in the specimens from Antiguo Morelos, Jaumave, and Tula. Antiguo Morelos, elevation about 1000 feet, lies in the lowlands at the base of the Sierra Madre. Jaumave, is situated at an elevation of approximately 2800 feet in the foothills, about sixty miles northwest of Antiguo Morelos; and Tula lies farther upslope, at an elevation of approximately 3900 feet. The examples from Antiguo Morelos are small (greatest length of skull less than 33.0 mm.), and they have a narrow brain case, small interparietals, small bullae, and broad short nasals. The specimens from Jaumave are larger (range in greatest length of skull of adults, 32.7–34.4 mm.), the brain case is relatively broader, and the interparietals are larger. The rostrum and nasals, although of various dimensions, in the majority of the specimens resemble those from Antiguo Morelos. The specimen from Tula has the largest cranium and relatively the largest interparietals, broadest frontals, and narrowest rostrum and nasals of the three series. It resembles specimens of *alleni* from Río Verde and Zimapan. at higher elevations farther south on the plateau. Similar correspondence of morphological and environmental clines obtains in southern Mexico.

SPECIMENS EXAMINED.—A total of twenty-four, from localities as follows: Nuevo Leon, 20 km. northwest of General

Terán, 900 feet, five. Tamaulipas, Antiguo Morelos, 1000 feet, nine; Sierra de San Carlos, 700–2000 feet, nine; Sierra de Tamaulipas, Acuña, 2600 feet, one.

Liomys irroratus canus Merriam

Liomys canus Merriam (1902: 44–45). Chihuahua, near Parral, 6000 feet.

Liomys irroratus canus Merriam, Goldman (1911: 60).

RANGE.—Eastern flank of the Sierra Madre Occidental and adjoining plateau. Known range from the vicinity of Parral and Santa Rosalia, Chihuahua, south to Valparaiso and Hacienda San Juan Capistrano, Zacatecas (*vide* Goldman, 1911: 60). Altitudinal range, approximately 5500–7000 feet.

COMPARISONS.—To judge from the type specimen and three topotypes—the only examples of the race that we have examined—and from Goldman's accounts (1911: 60), *canus* is merely a large and perhaps slightly paler *alleni*. The large size, broad frontals, large interparietals, and other features that are characteristic of the highland populations of northern Mexico attain maximum development in the mountains of western Chihuahua. To populations in that area the name *canus* applies. Specimens from localities to the south and east are smaller and exhibit features variously characteristic of other races.

SPECIMENS EXAMINED.—The type and three topotypes, from near Parral, 6000 feet, Chihuahua, Mexico (U.S.).

CHARACTER GRADIENTS

SIZE.—In *Liomys irroratus* size apparently is correlated with altitude, small size being characteristic of low elevations and large size a feature of high altitudes. We have judged size by the linear dimensions of the body, the hind foot, and the skull, but we have relied principally on skull length, because our values for that dimension are consistently reliable, whereas those for the body and hind foot, taken by various collectors, are less trustworthy. Although we relate size directly to altitude, we infer that the correlation is with tempera-

ture, moisture, barometric pressure, and/or some other factors which vary with altitude, rather than with altitude itself.

The close correlation of size with altitude is apparent at several latitudes and probably obtains throughout the range of the species. This is the general situation in northern Mexico: Smallest size is observed on the Gulf coastal plain and low mountains east of the Sierra Madre Oriental. Specimens from the coast near Nautla, Veracruz, and Brownsville, Texas, and from other low-lying, inland areas below approximately 2000 feet—such as in the Sierra de San Carlos and near Antiguo Morelos and General Terán—have a hind-foot length of about 28–30 mm. and a skull length averaging about 32 mm. From the plain up the face of the Sierra Madre to the interior plateau, size and altitude increase. This is well seen in the samples from Jaumave, 2800 feet, and Tula, 3900 feet, Tamaulipas; Río Verde, 4500 feet, San Luis Potosí; and Zimapan, 6200 feet, Hidalgo. The hind-foot length and skull length, respectively, of the specimens from the interior highlands, as for example from Río Verde and Zimapan, are about 30–32 mm. (foot) and 32–34 mm. (skull). Largest size in the species is seen in the Sierra Madre of western Chihuahua. Some examples from the vicinity of Parral, elevation about 6000 feet, have a hind-foot length of 34 mm. and a skull length of 37 mm.

The clinal relationship is well shown in the central and southern parts of the range of the species whence our samples are more numerous and adequate. Figure 1 shows the close correspondence of size and altitude in central and southern Mexico. The transect shown extends from the lower, western part of the Mexican Plateau eastward to higher elevations in the mountains of Michoacán and Mexico to the vicinity of Mexico City, thence southeastward and downslope to low arid valleys in northern Oaxaca, up again on the plains and mountains around Oaxaca City, thence, finally, northwestward at lower elevations in the Sierra Madre del Sur. The transect, thus, is roughly a profile of parts of two high plateaus and intervening lowlands. Not shown in Figure 1 are data from

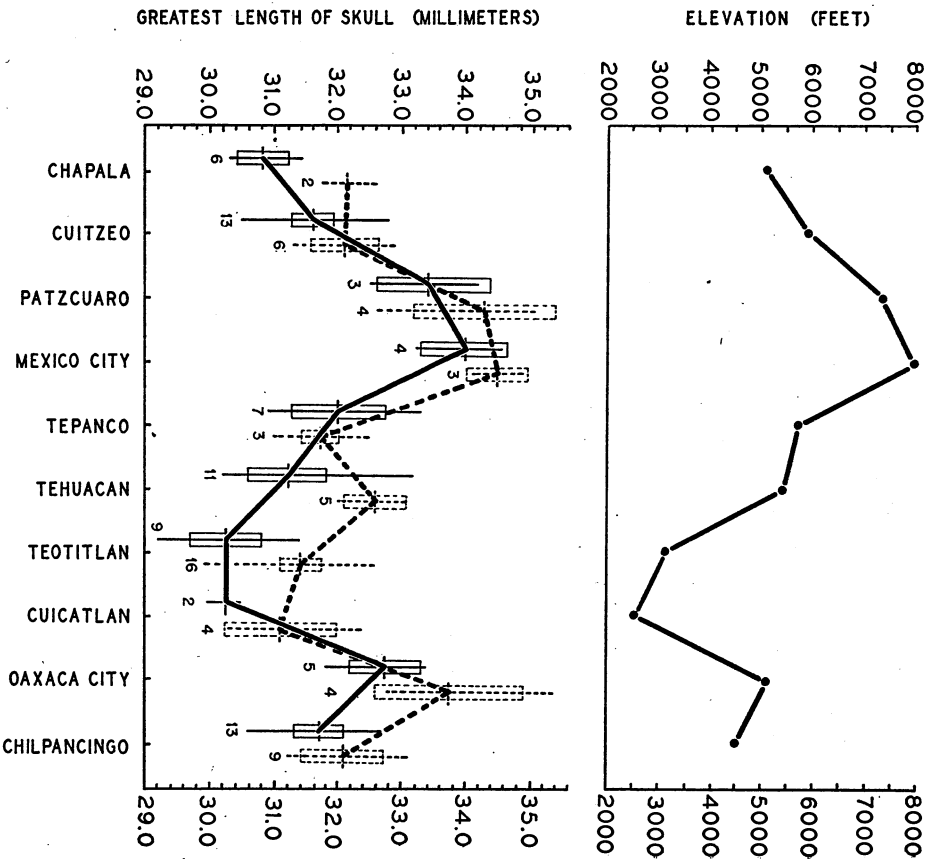


FIG. 1.—Graphs correlating skull length with terrain elevation and its associated environmental factors. Plotted in the upper figure are elevations above sea level of each locality represented by specimens in the lower graph. The cranial length of samples of *Liomys irroratus* from ten localities in central and southern Mexico is given in the lower figure. Symbols refer to items as follows: females (solid lines); males (broken lines); range in skull length (vertical line); mean (cross bar on vertical line); two standard errors of the mean, above and below the mean (rectangular box); see Introduction for further explanations. Diagonal lines connect means of one sex. Figures below the vertical lines indicate the number of specimens represented.

other localities on the transect, which also conform to the trend as here outlined. Maximum size obtains at the highest elevations, 7500–8500 feet, in the cool climate at Mexico City and Patzcuaro. To the south and downslope, size decreases progressively to a minimum—for the entire species—in the hot dry lowlands around Teotitlán and Cuicatlan (2000–3500 feet). The species is not known from lower altitudes in southern Mexico. At consecutively higher elevations south of Cuicatlan the pocket mice show consistently larger size. The sample from the vicinity of Oaxaca City, at 5000 feet, illustrates one size and altitude level. Maximum size of the species in Oaxaca may be present higher in the mountains. A specimen from approximately 8000 feet elevation in the Sierra Juarez is one of the largest specimens at hand from Oaxaca. Its size equals that of specimens from similar altitudes on the mountains and plains of central Mexico. Finally, to the northwest of Oaxaca City, at lower elevations near Chilpancingo, Guerrero, smaller size again obtains.

There is incomplete evidence that size in the species varies with latitude as well as with altitude. For conclusive evidence here, data is needed from a series of north-south transects, each at a single altitudinal level. We have insufficient series for such transects, although specimens at hand do indicate a trend of small to large size from south to north. The specimens from elevations below 3000 feet in the lowlands of southern Mexico—in Oaxaca, Puebla, and Morelos—are smaller than those from the coastal plain of northern Mexico—in Veracruz and Tamaulipas. The amount of difference in skull length amounts, on the average, to 1 or 2 mm. This amount may be more significant than it first appears, because most of the northern localities are several thousand feet lower than those to the south. A similar north-south trend in size is indicated for the highlands. The few specimens from the northwestern segment of the range of the species are the largest known. Those are from an elevation of approximately 6000 feet in the Sierra Madre of western Chihuahua. Specimens of comparable age and from similar elevations in central and southern Mexico,

for example in Oaxaca and Michoacán, have skulls 3 or 4 mm. shorter. The factor, or set of factors, that operates altitudinally in regulating size also may vary with latitude, and effect a similar clinal response in the species.

SKULL CHARACTERS.—Gradients in other cranial dimensions and parts are apparent. Along with body length and length of hind foot, skull length in *Liomys irroratus* is an expression of size of the animal. To a certain extent, so also are the other dimensions of the skull; and a geographic increase or decrease in cranial length is accompanied by a corresponding change in size of parts of the skull. It should be understood, then, that all skull parts and dimensions are related, in the same way that hind-foot length and cranial length are, to size-regulating factors of the environment. The parts that vary disproportionately with respect to cranial length are of especial interest.

The zygomatic breadth, relative to skull length, is approximately constant throughout the range of the species. It is another measure of general size of the animal. The shape of the zygomatic arches, however, varies slightly geographically in south-central Mexico. In the examples from the Valley of Mexico (*pullus*) and from areas in the Balsas basin (*minor*), the arches are broader anteriorly than posteriorly. Elsewhere the zygomata are approximately parallel.

Dimensions of the brain case apparently also are comparatively constant in the several geographic races of the species, increasing and decreasing proportionately with skull length. The cranial breadth averages disproportionately greater in the specimens of *acutus* and, to a less extent, in *jaliscensis*, *pretiosus*, and *minor*; but with our small series of those forms it is not clear that the differences are real in the populations. In depth of cranium all races are similar except *acutus* and, possibly, *minor*, which in our samples have the brain case relatively deeper than it is in the examples of the other subspecies.

Geographic variation in the breadth of the frontal bones is slight. The interorbital diameter is relatively least in the

mice of the mountains of Michoacán (*acutus*) and Oaxaca (*irroratus*) and the lowlands of Veracruz (*pretiosus*), and greatest in those from the coastal plain of Tamaulipas (*texensis*).

In size of the rostrum there is comparatively great disparity among the geographic races. The greatest breadth is seen in the race *pretiosus* of the lowlands of Veracruz. In specimens from that area the nasals and the ascending branches of the maxillae are relatively much broader than they are in examples from any other area in Mexico. The nasals are exceptionally expanded anteriorly, contributing further to the massive appearance of the rostrum. The opposite extreme in rostral development is in the races *torridus* and *irroratus* of Oaxaca. Specimens of these subspecies typically have a long, narrow rostrum, in which the nasals are long and comparatively narrow throughout their length, not short and greatly expanded distally as in *pretiosus*. Various stages of intermediacy obtain in other races of the species, but none closely approaches *pretiosus* in rostral dimensions except in areas of intergradation with that form. It is interesting to note that in the same part of Mexico inhabited by *pretiosus* other species of mammals also have a similar rostral enlargement. *Liomys pictus obscurus* Merriam, which also inhabits the coastal plain of Veracruz, is characterized by broad and anteriorly expanded nasals. A massive rostrum and broad nasals are likewise characteristic of *Peromyscus furvus* Allen and Chapman, *Oryzomys alfaroi dilutior* Merriam, and *Neotoma distincta* Bangs. These forms inhabit mountainous slopes in eastern Puebla and western Veracruz that certainly adjoin, and probably are part of, the range of *Liomys i. pretiosus*. Such apparently parallel development of rostral parts in several species in the same region may well be in response to the same set of environmental factors. It must be emphasized, however, that in that same region there are many other species of rodents that show no corresponding rostral enlargement.

There is disproportionate development of the interparietals in the various subspecies of *Liomys irroratus*. By and large,

the smaller-sized forms have the relatively larger interparietals. Thus, a comparatively larger transverse and longitudinal diameter of the interparietals is observed in *torridus*, *minor*, *jaliscensis*, *pretiosus*, and *texensis*, and smaller dimensions are seen in *pullus*, *acutus*, and *canus*. Our examples of the large form, *alleni*, however, have gross interparietals. There are small differences in proportions of the bones among the various races. The relatively smallest transverse diameter is in *acutus* of the mountains of Michoacán, and the relatively largest breadth in *torridus* of the Oaxacan lowlands. Smallest relative length is observed in the large form, *canus*, of the Sierra Madre of Chihuahua, and the larger lengths are in the smaller-sized forms to the south, in *torridus* for example.

Variation in size of the auditory and mastoidal bullae in *L. irroratus* is largely a function of size of the skull, so far as we can determine. There appear to be average relative differences among some populations. In the examples of *jaliscensis*, *pullus*, and *pretiosus*, the bullae appear by inspection to be relatively smaller than they are in other races. However, without means for accurate measurement of bullae size we cannot express this apparent difference objectively.

The shape of the posterior part of the nasals, used by Goldman (1911) and by Hall and Villa (1948) to distinguish subspecies of *Liomys irroratus*, varies greatly within samples. In some individuals the nasals are posteriorly acuminate (the naso-frontal suture appearing as a V, with the apex directed forward). In others they are truncate, in which the posterior border forms roughly a straight line perpendicular to the long axis of the skull. Various intermediate stages also occur within a series from one locality. The frequency of occurrence of those acuminate and truncate forms of the nasals, however, apparently varies from place to place. Some of the differences in frequencies are outside the range of probable sampling errors; they apparently distinguish populations and geographic races. As judged by our series, a V-shaped posterior border of the nasals characterizes the subspecies *acutus* and *irroratus*. In thirty-four adult

examples of *acutus*, the nasals of twenty-seven are V-shaped and nine are truncate, a ratio of three to one. Each of the examples of *irroratus* from central Oaxaca also has attenuate nasals. Truncate nasals are common in the samples of the other races. In them the frequency of the acuminate and truncate shape varies from approximately one to one (fifteen specimens V-shaped, thirteen specimens truncate) in the series from Chilpancingo, Guerrero, and in several samples from Veracruz and Tamaulipas (*pretiosus* and *texensis*); to one to four (fourteen V-shaped and fifty-five truncate) in pooled series from Distrito Federal (*pullus*) and Puebla and Oaxaca (*torridus*); and to none to eight in a series from Antiguo Morelos, Tamaulipas (*texensis*). Our data indicate that the posterior border of the nasals is usually acuminate in the mice of the mountains of Michoacán and Oaxaca and truncate in those from other areas. The data are incomplete for many parts of the range of the species.

TAIL LENGTH.—Measurements of the tail, when recorded by many different collectors, usually will not stand close comparison. In a few of our series the measurements are believed to be comparable. They were made by the same collector or by others known to use essentially identical techniques in measuring the tail. In those series the recorded differences are evident in the specimens. A long tail apparently is a characteristic of the pocket mice of central and northeastern Oaxaca, where the tail length of adults is usually over 130 mm. and amounts to approximately 120–30 per cent of the head and body length. Such lengths are recorded in specimens from Oaxaca City, Ejutla, Sola de la Vega, Ixtlan, Cuicatlan, and Teotitlán. In those from Tehuacan and Tepanco, in southern Puebla, the tail averages but slightly shorter.

A short tail appears to be characteristic of the mice of southwestern Mexico (Temescaltepec) and Michoacán (Patzcuaro, near Morelia, and Cuitzeo) and of eastern Jalisco (Chapala). The specimens from those localities have shorter

tails than do those from Oaxaca, although the former may average larger in body, hind foot, and skull. In most examples the tail is approximately as long as the combined length of head and body, amounting to less than 120 mm.; it exceeds 125 mm. in only three of thirty-four adult specimens. Since the Oaxacan localities are drier and warmer than those in Mexico and Michoacán, there may be a correlation with amount of aridity and associated density of plant cover in which the pocket mice live.

PELAGE COLORATION.—Geographical gradients in color of the pelage are apparent in the specimens. The darkest pelages are found in the cool highlands of the states of Mexico and Michoacán, where dark, humus-filled soils and blackish igneous flows are common. Specimens from that region are deeply pigmented dorsally and tinted ventrally. The upper parts are blackish or deep brown, the deep tones concentrated on the mid-back to form a broad longitudinal stripe, which contrasts with the paler gray sides. Comparatively few orange or cinnamon bands of the hairs are visible dorsally, the few present being obscured by the abundant black tips. The underparts are lightly tinted pinkish or buffy. The upper surface of the legs and tail are dark brown or dark gray, and the ears are black, rimmed with white.

The palest pelages are from arid interior valleys in northern Oaxaca and southeastern Puebla. Compared with the dark pelages mentioned above, the colors in these are dilute on all pigmented parts. The upper parts are pale creamy gray, sparsely streaked with black. Apart from the few black bands of the hairs, the creamy or buffy hue of the upper parts apparently is largely attributable not to color pigments but rather to the lack of them, particularly in the spines. There appear to be few, if any pigments in the main body of these spines. A dorsal stripe is absent, or at best indistinct. The underparts are usually white, without pigment. The upper surface of the legs and tail is pale gray or white, and the ears are tan or fuscous, rimmed with white.

Between these extremes are various stages, each of which has a limited geographic range. Pallor, a comparatively distinct lateral line, and, at best, an indistinct dorsal stripe are characteristic of almost all of the specimens from the region south of the Río Balsas. Two blackish specimens from the mountains of Oaxaca are exceptions (see account of *L. i. irroratus*). The examples from the western part of that region—from Chilpancingo, Guerrero, and from various localities in central and western Oaxaca—are variously darker than those from the lower, and more arid, eastern valleys. Deep tones, a distinct dorsal stripe, and an indistinct lateral line characterize the specimens from the volcanic areas of Michoacán and Mexico. Moderate tones and a pronounced dorsal stripe and lateral lines are typical of the material from areas to the north. To judge from the comparatively few specimens at hand, the coloration becomes progressively paler toward the north, attaining an extreme in dilution in the lowlands of northern Tamaulipas. Specimens from Jalisco, Hidalgo, San Luis Potosí, Chihuahua, and Tamaulipas are variously paler than those from Michoacán and Mexico. Those from northern Tamaulipas are the most pallid of northern Mexico.

We have insufficient ecological information to correlate with finality the pelage coloration to factors in the animals' environment. It is clear, however, that the darkest pelages occur in volcanic highlands, where dark substrata are common and where dark humus-filled soils were once widespread. Similarly, the palest pelages are in hot, dry lowlands, where the soils are typically bleached alluviums. It is probable that pelage coloration is related to soil color in *Liomys*, just as it is in many other mammals.

SUMMARY

Character gradients in a polytypic species of mammal may run in identical or different geographic directions. Clines in size, in dimensions or shape of the skull, or in some feature

of the pelage may correspond geographically; or they may have dissimilar geographical limits. Some morphological traits, of course, may remain essentially unchanged throughout the range of the species. These features have been observed in many mammal kinds. Although rarely focused for proper attention, they can be inferred from most systematic accounts of geographical variation.

The species *Liomys irroratus*, as judged principally from data from the central and southern parts of its range, offers nothing unusual as regards correspondence of clines. The preceding accounts of variation in the species should have made that point clear. Size varies geographically, and appears to be correlated with altitude and latitude, and factors associated therewith. Small size is characteristic of low elevations and low latitudes; largeness is correlated with high altitudes and latitudes. Pelage coloration is not closely related to size in its distribution. There are large and small, pale and dark populations. Color of pelage may be associated with humidity or, more probably, with color of the substrate. Color and size clines sometimes parallel each other geographically in the species, as is observed in the transect from the arid Oaxacan lowlands upslope to the volcanic and conifer-studded highlands of Mexico and Michoacán. But the correspondence of those clines well may be coincidental, and not attributable to the same set of regulatory factors in the environment. The clines in tail length correspond grossly to those of color, in the central and southern parts of the range of the species. Whether they do in northern Mexico we cannot determine in our small samples from that region. The long tails and pallid coloration of specimens from Oaxaca grade into the short tails and deep body tones in the material from Michoacán and Mexico.

Most of the cranial parts studied vary directly with skull length, increasing or decreasing as it changes. Some, however, seem to vary independently of skull length, other cranial characters, color, and tail length. The auditory bullae are of comparatively the same size over much of the

range of the species, but appear to be relatively smaller on the southern part of the Mexican Plateau and in the lowlands of Veracruz. In the latter area also are observed maximum size of the rostrum and dilation of the nasals. Minimum values of rostral breadth and nasal breadth and length obtain in the examples from various elevations in Oaxaca. Intermediate stages between those two extremes are seen at various other parts of the range of the species. The geographic limits of none of them apparently correspond exactly to that of a color or size level. Interparietal size and brain case depth also exhibit gradients, neither necessarily associated with the other or with clines in other characters.

With the possible exception of *alleni* and *minor*, each subspecies of *Liomys irroratus*, here considered valid, is characterized by an extreme in one or two features of the skin and skull. Those few characters constitute the main basis for recognition of the race. The other traits of the subspecies are subsidiary, unique only as regards their combination, and are developed to a minimum or maximum amount elsewhere.

REFERENCES

- ALLEN, JOEL A.
1906 Mammals from the States of Sinaloa and Jalisco, Mexico, Collected by J. H. Batty During 1904 and 1905. Bull. Amer. Mus. Nat. Hist., 22: 191-262, 14 pls., 3 figs.
- COUES, ELLIOT
1881 *Heteromys alleni*, Coues, Ms. Pp. 187-88. In Joel A. Allen, List of Mammals Collected by Dr. Edward Palmer in Northeastern Mexico, with Field-Notes by the Collector. Bull. Mus. Comp. Zool., 8: 183-89.
- DAVIS, WILLIAM B.
1944 Notes on Mexican Mammals. Journ. Mammalogy, 25: 370-403, 1 fig.
- GOLDMAN, EDWARD A.
1911 Revision of the Spiny Pocket Mice (Genera *Heteromys* and *Liomys*). N. Amer. Fauna, 34: 1-70, 3 pls., 6 figs.
- GRAY, JOHN E.
1868 Synopsis of the Species of *Sacomysinae*, or Pouched Mice, in the Collection of the British Museum. Proc. Zool. Soc. London, pp. 199-206.

HALL, E. RAYMOND, and B. VILLA

- 1948 A New Pocket Gopher (*Thomomys*) and a New Spiny Pocket Mouse (*Liomys*) from Michoacán, Mexico. Univ. Kans. Publ., Mus. Nat. Hist., 1: 249-56, 6 figs.

HOOPER, EMMET T.

- 1947 Notes on Mexican Mammals. Journ. Mammalogy, 28: 40-57.

MERRIAM, CLINTON H.

- 1902 Twenty new Pocket Mice (*Heteromys* and *Liomys*) from Mexico. Proc. Biol. Soc. Wash., 15: 41-50.

MILLER, GERRIT S., JR.

1912. List of North American Land Mammals in the United States National Museum, 1911. Bull. U. S. Nat. Mus., 79: xiv + 455.

RIDGWAY, ROBERT

- 1912 Color Standards and Color Nomenclature. Washington, D. C.: Published by the author. Pp. iv + 44, 53 pls.

RUTHVEN, ALEXANDER G.

- 1908 Variations and Genetic Relationships of the Garter-Snakes. Bull. U. S. Nat. Mus., 61: xii + 201, 1 pl., 82 figs.

